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Committee on Animal Nutrition, Ad Hoc Committee on Nonhuman Primate Nutrition, National Research Council

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THE NATIONAL ACADEMIES
Advisers to the Nation on Science, Engineering, and Medicine

Nutrient Requirements of Nonhuman Primates

Second Revised Edition, 2003

Committee on Animal Nutrition
Ad Hoc Committee on Nonhuman Primate Nutrition
Board on Agriculture and Natural Resources
Division on Earth and Life Studies

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Preface

This report is one of a series issued under the direction of the National Research Council's Committee on Animal Nutrition (CAN) of The National Academies Board on Agriculture and Natural Resources. It was prepared by the CAN Ad Hoc Committee on Nonhuman Primate Nutrition and is a revision of the 1978 edition of *Nutrient Requirements of Nonhuman Primates*. Throughout the study process, input from others has been sought by posing specific questions in widely distributed letters, by hosting workshops and information-gathering sessions, and by inviting sponsors and the general public to attend meetings of the Committee. Information published before 1978 has been reevaluated, that in newer publications has been examined, and both have been used to update this report. Greater emphasis than before has been placed on descriptions of natural dietary habits, gastrointestinal anatomy and physiology, and the special nutrient and dietary husbandry needs of species that traditionally have been difficult to maintain in captivity.

The order Primates is diverse and includes prosimians, New World monkeys, Old World monkeys, apes, and humans. More than 250 species and more than 600 subspecies are recognized, and new species are described nearly every year. Recently, Colin Groves has proposed a revised taxonomic system that includes over 300 primate species (Groves, C. 2001. *Primate Taxonomy*. Washington, DC: Smithsonian Institution Press). The challenge of describing the nutritional needs of primates, which range in size from tiny mouse lemurs and pygmy marmosets to the markedly larger gorillas and orangutans, is daunting, particularly because studies of feeding ecology, gastrointestinal anatomy, and nutrient requirements have been completed for only a few of them. Consequently, data have been sought on one or more model species in eight categories (the suborder Strepsirrhini; the families Hominidae and Pongidae, Hylobatidae, Cercopithecidae, Cebidae, Callitrichidae, and Tarsiidae; and the subfamily Colobinae) in the hope that such data would be representative of the Order. Little information was found on Tarsiidae and Hylobatidae.

Over 500,000 primates live in biomedical research laboratories and conservation institutions throughout the world. Records of the regional primate research centers provided by Leo Whitehair of the National Institutes of Health National Center for Research Resources indicate that 16,820 nonhuman primates of 28 species were present in seven U.S. centers at the end of 1998. In 1999, an eighth U.S. center housing 3,638 animals, including about 3,200 baboons, was added. Records of the International Species Information System (at the Minnesota Zoological Garden, Apple Valley, MN; www.worldzoo.org) indicate that over 9,500 nonhuman primates of 145 species were in U.S. and Canadian zoos at the end of 2000. Additional nonhuman primates can be found in U.S. and Canadian government, university, and commercial laboratories.

Many primate species serve as surrogates in studies of human physiology and disease, and their nutritional status is known to influence susceptibility and tissue responses to infective agents. The validity of such research is open to question if the experimental subjects have not been appropriately nourished. Likewise, the health and reproduction of primates in zoos can be compromised to an extent that renders the maintenance or multiplication of endangered species impossible.

In preparing this report, the Committee was limited in the amount of reliable and specific information available on nutrient requirements, deficiencies, and toxicities in primates. The authors of this publication had as their primary objective the development of guidelines that would ensure that nutrient deficiencies or toxicities and inappropriate dietary husbandry would not limit success in primate research colonies or zoos. We hope that this objective has been fulfilled, in light of the limits of the information available to us, and that researchers will continue to fill the obvious information gaps so that future editions will be more complete.

DUANE E. ULLREY, *Chair*
Ad Hoc Committee on Nonhuman Primate Nutrition

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The Committee wishes to thank the numerous people who provided input by letter or at public forums. In addition, we thank those who took time to meet with the Committee throughout the study process. The financial support provided by the National Center for Research Resources of the National Institutes of Health, the American Zoo and Aquarium Association, The Geraldine R. Dodge Foundation, the Association of Primate Veterinarians, Harlan Teklad, Purina Mills, Inc., and ZuPreem, is gratefully acknowledged.

This report has been reviewed in draft form by individuals chosen for their diverse perspectives and technical expertise, in accordance with procedures approved by the NRC's Report Review Committee. The purpose of this independent review is to provide candid and critical comments that will assist the institution in making its published report as sound as possible and to ensure that the report meets institutional standards for objectivity, evidence, and responsiveness to the study charge. The review comments and draft manuscript remain confidential to protect the integrity of the deliberative process. We wish to thank the following individuals for their review of this report: David J. Baer, US Department of Agriculture Agricultural Research Service, Beltsville, Maryland; Ellen Dierenfeld, The Wildlife Conservation Society, Bronx, New York; Joseph W. Kemnitz, Wisconsin National Primate Research Center, Madison, Wisconsin; Joe Knapka, National Institutes of Health (retired); Terry L. Maple, Zoo Atlanta, Atlanta, Georgia; and Wilson G. Pond, Cornell University, Ithaca, New York. Although the reviewers listed above have provided many constructive comments and suggestions, they were not asked to endorse the conclusions or recommendations nor did they see the final draft of the report before its release. The review of this report was overseen by R. Lee Baldwin, University of California, Davis. Appointed by the National Research Council, he was responsible for making certain that an independent examination of this report was carried out in accordance with institutional procedures and that all review comments were carefully considered. Responsibility for the final content of this report rests entirely with the authoring committee and the institution. Finally, the Committee wishes to thank Charlotte Kirk Baer, program director, Committee on Animal Nutrition, for her encouragement and cheerful guidance of this project to completion. Her exceptional organizational skills contributed in a major way to the success of the Committee. Appreciation also is extended to Stephanie Padgham, project assistant, for her regular communications and helpful provision of supplementary materials.

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Contents

OVERVIEW 1

1 FEEDING ECOLOGY, DIGESTIVE STRATEGIES, AND IMPLICATIONS FOR FEEDING PROGRAMS IN CAPTIVITY, 5
- Feeding Ecology, 5
  - Feeding-Ecology, Methods Involving Visual Observations of Behavior, 5
    - Observation Options, 5
    - Sampling Methods, 5
  - Alternative Feeding-Ecology Methods, 13
    - Analysis of Stomach Contents, 13
    - Fecal Analysis, 16
    - Food Remnants, 16
  - Reporting Feeding Behavior, 18
    - Feeding Time, 18
    - Mass of a Food as Percentage of Total Diet Mass, 18
  - Feeding-Ecology Tables, 18
    - Plant-Feeding Strategies, 19
    - Insect Foraging and Feeding, 19
    - Additional Considerations, 19
    - How to Use This Information, 20
- Digestive Strategies, 20
  - Faunivores, 21
  - Frugivores, 21
  - Folivores, 24
- Implications for Feeding Programs in Captivity, 26
- References, 27

2 ENERGY 41
- Units of Measurement, 41
- Classification, 41
  - Gross Energy, 41
  - Digestible Energy, 41
  - Metabolizable Energy, 42
  - Physiologic Fuel Values, 42
- Requirements, 42
  - Basal Energy Expenditures or Basal Metabolic Rate, 43

72384$CTOC 01-20-03 18:25:05

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Estimating Basal Metabolic Rate, 43
Effects of Age and Body Composition on Basal Metabolic Rate, 43
Energy Requirements for Maintenance, 43
Energy Requirements for Growth, 48
Energy Requirements for Pregnancy and Lactation, 53
References, 54

3 CARBOHYDRATES AND FIBER 58
Carbohydrate Classification, Characteristics, Digestion, and Metabolism, 58
Monosaccharides, 58
Disaccharides, 59
Oligosaccharides, 59
Polysaccharides, 59
Starch and Starch-Like Polysaccharides, 59
Non-Starch Polysaccharides, 59
Analytical Procedures for Carbohydrate and Fiber, 61
Crude Fiber, 61
Total Dietary Fiber, 61
Neutral-Detergent Fiber and Related Fractions, 62
Carbohydrates in Wild Food Plants, 64
Significance of Fiber, 66
Proposed Fiber Intakes by Nonhuman Primates, 68
Fiber Recommendations for Other Species, 68
Fiber in Wild Food Plants as Guides for Captive-Diet Fiber Concentrations, 68
Fiber Digestion by Nonhuman Primates as a Guide for Captive-Diet Fiber Concentrations, 70
Proposed NDF and ADF Concentrations in Captive Nonhuman Primate Diets, 70
References, 70

4 PROTEIN 75
Protein Sources, 75
Assessment of Protein Requirements, 75
Methods, 75
Digestibility, 76
Requirements, 77
Protein Quality, 77
Proteins Limiting in Sulfur Amino Acids, 77
Proteins Limiting in Lysine, 78
Amino Acid Requirements, 78
Lysine and Methionine, 78
Phenylalanine, 79
Tryptophan, 79
Taurine, 79
Efficiency of Protein Use, 79
Protein Deficiency, 80
Protein for Pregnancy and Lactation, 80
Protein-Calorie Malnutrition in Young Primates, 80
Protein Excess, 83
Non-Amino-Acid Effects of Protein Sources, 83
References, 84

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5 FATS AND FATTY ACIDS 87
Fat Absorption, 88
Milk Fats, 89
Essential n-3 Fatty Acids, 89
Essential n-6 Fatty Acids, 90
Detrimental Fatty Acids, 91
Cholesterol, 91
Primates as Cardiovascular Disease Models, 92
References, 92

6 MINERALS 94
Macrominerals, 95
Calcium and Phosphorus, 95
Magnesium, 97
Potassium, 98
Sodium, 98
Chloride, 98
Sulfur, 98
Trace Minerals, 98
Iron, 98
Copper, 100
Manganese, 101
Zinc, 102
Iodine, 104
Selenium, 104
Cobalt, 106
Chromium, 106
Fluorine, 107
References, 107

7 VITAMINS 113
Fat-Soluble Vitamins, 113
Vitamin A and Carotenoids, 113
Measures of Biologic Activity, 113
Absorption and Circulation of Carotenoids, 114
Vitamin A and Carotenoids in Feedstuffs, 114
Absorption, Circulation, and Storage of Vitamin A, 114
Vitamin A Deficiency, 115
Vitamin A Requirements, 115
Hypervitaminosis A, 115
Vitamin D, 116
Photobiology, Metabolism, and Function of Vitamin D, 116
Measures of Vitamin D Activity, 117
Vitamin D Deficiency, 117
Discrimination Between Vitamin D_2 and Vitamin D_3, 118
Metabolic Resistance to Vitamin D_3 in Callitrichids, 118
Animals Not Exposed to Natural Sunlight or Unable to Make Vitamin D in Their Skin, 120
Vitamin D Requirements, 120
Hypervitaminosis D, 121
Vitamin E, 122
Chemistry and Measures of Activity, 122
Absorption, Metabolism, and Excretion, 123

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Biologic Functions, 124
Vitamin E Deficiency, 124
Vitamin E Requirements, 125
Vitamin K, 126
Water-Soluble Vitamins, 128
Thiamin, 128
Riboflavin, 129
Pantothenic Acid, 130
Niacin, 131
Vitamin B_6, 132
Biotin, 133
Folacin, 134
Vitamin B_{12}, 135
Vitamin C, 137
Choline, 140
Carnitine, 141
Inositol, 141
References, 142

8 WATER 150
Water Content of the Body, 150
Effects of Activity Restriction, 152
Effects of Cold, 152
Effects of Heat and Water Deprivation, 152
Water Sources, 153
Liquid Water Intake, 153
Preformed-Water Intake, 154
Metabolic Water, 154
Water Loss, 154
Water Quality, 155
Water Requirements, 156
References, 157

9 PATHOPHYSIOLOGIC AND LIFE-STAGE CONSIDERATIONS 159
Body Weight, 159
Nutrition from Birth to Weaning, 159
Growth, 159
Mother-Reared Infants, 161
Artificially Reared Infants, 161
Milk Volume and Composition, 161
Volume, 161
Composition of Mother's Milk, 164
Nutrient Intakes for Milk Replacers, 164
Formulas Used for Artificially Rearing Infant Nonhuman Primates, 165
Long-Term Consequences of Different Modes of Infant Feeding, 166
Weaning Foods and Strategies, 167
Nutrition and Aging, 167
Dietary Restriction, 167
Bone, 170
Immunology, 170
Wound Healing, 170
Atherosclerosis, 171
Body Composition, 171

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Obesity, 172
Regulation of Glucose Metabolism, 174
Diabetes, 174
References, 176

10 DIET FORMULATION, EFFECTS OF PROCESSING, FACTORS AFFECTING INTAKE, AND DIETARY HUSBANDRY 182
Diet Formulation, 182
Natural Dietary Habits, 182
Digestive System Structure and Physiology, 182
Nutrient Requirements, 182
Feedstuffs, 182
Diet Formulation, 182
Effects of Processing, 183
Factors Affecting Intake, 184
Influence of Visual, Olfactory, Taste, and Tactile Clues on Food Acceptance, 185
Regulation of Food Intake, 185
Dietary Husbandry, 186
Primary Food Source, 186
Supplements, 186
Browse, 187
References, 188

11 NUTRIENT REQUIREMENTS 191
References, 194

12 COMPOSITION OF FOODS AND FEED INGREDIENTS 195
References, 195

13 FOOD AS A COMPONENT OF ENVIRONMENTAL ENHANCEMENT 259
Goal of Environmental Enhancement, 259
Role of Food and Foraging, 259
Wild Environment versus Captivity, 260
Species Differences, 261
Manipulation of Foraging Opportunities, 261
Live Prey, 262
Exudates and Gums, 262
Water, 262
Higher-Fiber Foods, 263
Epilogue, 263
References, 263

APPENDIX 266

ABOUT THE AUTHORS 269

INDEX 273

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Tables and Figures

TABLES

1-1 Prosimian feeding ecology, 6

1-2 Callithrix feeding ecology, 9

1-3 Cebid feeding ecology, 10

1-4 Colobine feeding ecology, 12

1-5 Non-colobine cercopithecine feeding ecology, 14

1-6 Ape feeding ecology, 17

1-7 Form of foregut in genera of subfamily Colobinae, 24

1-8 Examples of food consumed by primates in zoos and in the wild, 27

2-1 Estimated daily metabolizable energy (ME) requirements (as multiples of BMR) for adult captive animals, 45

2-2 Biologic and metabolic parameters of species fed dry diets, 49

2-3 Biologic and metabolic parameters for the young of various species fed liquid or dry diets, 51

3-1 Common dietary carbohydrates and their digestion, 61

3-2 Fiber concentrations in wild-primate diets (% of dry matter) in studies in which over 70% of items were analyzed, 65

3-3 Fiber concentrations in wild-primate diets (% of dry matter) in studies in which under 70% of items were analyzed, 67

3-4 Fiber levels (% of dietary dry matter) fed to primates in captivity, 69

3-5 Proposed fiber concentrations in total dietary dry matter of extruded diets for primate species grouped by relative ability to utilize plant cell wall, 70

4-1 Estimated protein requirements for primates using high-quality reference proteins, 76

4-2 Potency of common proteins measured by bioassay in primates, 78

5-1 Common names, scientific names, and short-form designations of fatty acids, 88

7-1 Survey of data used to estimate vitamin E requirements, 127

72384$CTOC 01-20-03 18:25:05

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7-2 Estimates of thiamin requirement, 130

7-3 Estimates of riboflavin requirement, 131

7-4 Estimates of vitamin B_6 requirement, 133

7-5 Estimates of folacin requirement, 136

7-6 Estimates of ascorbic acid requirement, 139

9-1 Body weight of captive adult primates, 160

9-2 Body weight of captive primates at various stages of development, 162

9-3 Primate species identified as potentially at increased risk of obesity in captive environments, 164

9-4 Proximate composition of milk from several primate species, 165

9-5 Composition of nonhuman-primate milk, human milk, and human-infant formula, 166

9-6 Physical characteristics of control (ad libitum-fed) and diet-restricted (30 percent restriction) *Macaca mulatta* after 4.5 years, 171

9-7 Body fat (%) determined with three methods in Western lowland gorillas, 172

10-1 Plant species used in feeding captive primates, 187

11-1 Estimated nutrient requirements of primate model species fed purified or semipurified diets, 192

11-2 Estimated adequate nutrient concentrations in diets containing conventional feed ingredients intended for post-weaning nonhuman primates, accounting for potential differences in nutrient bioavailabilities and adverse nutrient interactions, but not accounting for potential losses in feed processing and storage, 193

12-1 Composition of important feeds: Energy values, proximate analyses, plant cell wall constituents, data expressed as-fed and dry (100% dry matter), 197

12-2 Composition of important feeds: Minerals, data expressed as-fed and dry (100% dry matter), 213

12-3 Composition of important feeds: Vitamins, data expressed as-fed and dry (100% dry matter), 228

12-4 Composition of important feeds: Amino acids, data expressed as-fed and dry (100% dry matter), 242

12-5 Mineral concentrations in macromineral sources, 256

12-6 Characteristics and energy values of various sources of fats and oils (data on as-fed basis), 258

A-1 Taxonomic relationships, genera, and partial list of species in Order Primates, based on Napier and Napier (1985), Oates et al. (1989), and Nowak (1999), 266

A-2 Weight equivalents, 268

A-3 Weight-unit conversion factors, 268

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FIGURES

1-1 Gastrointestinal Tract of Tarsier, 22

1-2 Gastrointestinal Tract of Squirrel Monkey, 22

1-3 Gastrointestinal Tract of Night Monkey, 22

1-4 Gastrointestinal Tract of Woolly Monkey, 22

1-5 Gastrointestinal Tract of Vervet Monkey, 23

1-6 Gastrointestinal Tract of Macaque, 23

1-7 Gastrointestinal Tract of Baboon, 23

1-8 Gastrointestinal Tract of Bush Baby, 23

1-9 Gastrointestinal Tract of Northern Douc Langur, 25

1-10 Gastrointestinal Tract of Colobus Monkey, 25

1-11 Gastrointestinal Tract of Chimpanzee, 25

1-12 Gastrointestinal Tract of Orangutan, 25

1-13 Gastrointestinal Tract of Howler Monkey, 26

1-14 Gastrointestinal Tract of Adult Human, 26

3-1 Plant Cell Components in the Analytical Fractions of the Sequential Detergent System of Robertson and Van Soest, 63

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Second Revised Edition, 2003

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Overview

Nutrient requirements of monkeys were first considered by the National Research Council's Committee on Animal Nutrition in a section of *Nutrient Requirements of Laboratory Animals* (National Research Council, 1972). The information was updated and expanded in *Nutrient Requirements of Nonhuman Primates* (National Research Council, 1978). The present publication is a second revised edition of the 1978 report that constitutes a further updating and expansion of the topic.

This report is distinctive among most other publications in the Committee on Animal Nutrition series of reports on animal nutrient requirements. Many of the reports in this series deal with a particular species of domestic animal for which there is a significant amount of peer-reviewed research and an abundance of studies that examine specific nutrient requirements for various life stages. This revision is unlike those other reports for several reasons. First, it attempts to address the needs of over 250 species. Second, there are few data on which to draw conclusions and make recommendations for most species. Third, the animals addressed here are not domestic animals raised and bred for maximum efficiency in growth and production, but rather they encompass research animals, educational animals, and rare, endangered, and threatened animals that are maintained in various institutions for conservation purposes. Given the nature and importance of the animals that are the topic of this report and recognizing that the users of this report will span a wide range of professional expertise and practical knowledge of nutrition, the Committee used extreme care in evaluating and summarizing the available information. We chose not to go beyond what the data allow and we have grounded our recommendations firmly in scientific fact. To deviate from this approach, to venture beyond the scientific evidence, or to attempt to provide equations and estimates that cannot be validated—as they are validated in domestic food-producing animals—could potentially do more harm than good to the approximately half million primates currently maintained in biomedical and conservation institutions throughout the world.

Definition of the nutrient requirements of a single primate species at all life stages is difficult because little research specifically aimed at determination of nutrient requirements has been conducted. Definition of the nutrient requirements of each of some 250 primate species is virtually impossible with our current knowledge. Energy requirements of fewer than 20 species have been studied, and protein, mineral, and vitamin requirements of fewer than 10. Although there may be much dissimilarity among primate species in behavior and in the presence of fermentation compartments within the gastrointestinal system, similarities in the other aspects of physiology that influence nutrient requirements tend to be greater than the differences. Some extrapolation from one species to another is possible; this allows the formulation of diets that will usually meet requirements for adult maintenance, reproduction, and growth, even though specific quantitative needs have not been experimentally established. Although much more information is needed in those instances where specialized features of the gastrointestinal tract dictate a comparably specialized diet, research findings are beginning to fill the knowledge gap.

With few exceptions, captive species can be sustained in good health for periods equal to or greater than their life spans in the wild. That does not mean that all institutions housing primates are equally successful, but such an outcome is probable if rational and research-based dietary practices are consistently followed. This document is meant to help those who are struggling with this challenge.

When defining nutrient requirements, it is common to search for minimal dietary concentrations that will support maximal responses in important endpoints, such as growth rate of the young. It would be ideal if the same nutrient concentration produced a maximal response in all important endpoints, but that is seldom the case. For example, vitamin E has little effect on growth rate but is exceedingly important in protecting cellular membranes against the peroxidative damage associated with the stress of capture and handling. Furthermore, the degree of protection appears to be positively related to the dose until tissues

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are fully saturated; to complicate the matter, tissues of some organs become fully saturated with vitamin E before tissues of others. Thus, as satisfying as it would be to have a single minimal dietary concentration that met the requirements of the whole animal, minimal required concentrations vary with the sensitivity of the endpoint selected. Because nutrient-requirement research in primates is so sparse, we have seldom had the option of identifying a need for more than one endpoint. When such information was available, we tried to relate the minimal requirement to it.

Chapter 1 is a new feature of this revision that was not provided in the previous edition. This chapter is provided to give the reader an understanding of variations in feeding ecology and digestive strategies among primates, which is critical knowledge needed to make informed decisions on feeding primates. The discussion is concerned with foraging strategies in natural ecosystems, species differences in gastrointestinal morphology and physiology, and the significance of these factors in development of appropriate systems of dietary husbandry for captive primates. Because the usefulness of data gathered in field studies of feeding ecology varies with the method used, we discuss the strengths and weaknesses of the methods. Relevant field-study data are tabulated by species, and we illustrate the various gastrointestinal types found among nonhuman primates.

Chapter 2 is a detailed review of energy terms, methods used to determine energy requirements, and energy requirements of nonhuman primates for adult maintenance, growth of young, and pregnancy and lactation. Tables include data on body weight, measured energy expenditures, and estimates of daily metabolizable-energy requirements as multiples of basal metabolic rate.

Chapter 3 discusses first the classification of carbohydrates, their characteristics, digestion, metabolism, and analysis and then discusses analytic systems for fiber, the role of dietary fiber in primate gastrointestinal health, and potentially beneficial dietary fiber concentrations.

Chapter 4 covers proteins, protein sources, and methods of assessing protein quality and requirements. Information on protein-calorie malnutrition and on protein deficiencies and excesses is included. Although quantitative requirements of nonhuman primates for specific amino acids could not be defined, evidence of the essentiality of methionine, lysine, phenylalanine, tryptophan, and taurine is presented. Protein requirements, based on high-quality reference proteins and various criteria, are given in tabular form.

Chapter 5 addresses fats and fatty acids, including classification, nomenclature, digestion, absorption, and metabolism. It describes essential fatty acids and presents estimated requirements for n-3 and n-6 fatty acids. Fatty acid composition of primate milks, potentially harmful fatty acids, cholesterol metabolism, and use of nonhuman primates as models for study of cardiovascular disease are discussed.

Perhaps the most greatly expanded chapter in this revision is Chapter 6, which is a review of mineral nutrition and metabolism, including functions and signs of mineral deficiencies and excesses. In the first edition of this report, which was published in 1978, there was no discussion of sulfur, copper, cobalt, or molybdenum needs of nonhuman primates. In Chapter 6 of this second edition, we are able to provide the first recommendations on mineral requirements for copper and selenium based on a comprehensive review of the scientific literature. Similarly, Chapter 6 provides the first review and discussion of sulfur and cobalt in primate nutrition by the National Research Council Committee on Animal Nutrition. Mineral requirements of several primate species at various ages are given.

Chapter 7 is a discussion of fat- and water-soluble vitamins, including form, function, metabolism, and signs of deficiency and toxicity. Estimates of quantitative requirements of nonhuman primates are provided.

Chapter 8 deals with water as a component of the primate body and with the influence of activity and various environmental factors on the proportion of body water. Water sources, water quality, water turnover, water requirements, and important considerations in providing water for nonhuman primates are discussed.

Chapter 9 presents information on a number of pathophysiologic and life-stage considerations that are relevant to nonhuman-primate nutrition. It includes values of body mass (weight) and body composition, studies of the nutritional needs of neonates, effects of aging on nutritional needs, and relationships of nutrition to aging, obesity, and diabetes. Special considerations for hand-rearing of orphaned or abandoned young animals are covered and recommendations for simulating the composition of milk produced by the mother in normal lactation and the mother's normal nursing schedule are provided as well as introducing solid food into the diet as the young progress toward weaning.

Chapter 10 discusses primate-diet formulation, effects of feed processing on nutrient loss, factors that influence food intake, and some general suggestions for dietary husbandry. Plants that have been safely used as browse offerings in captivity are listed.

Providing much more detailed and focused recommendations than the general recommendations provided in the previous edition, Chapter 11 tabulates estimated nutrient requirements of model nonhuman primates in six categories (suborder Strepsirrhini; families Hominidae and Pongidae, Cercopithecidae, Cebidae, and Callitrichidae; and subfamily Colobinae). These requirements were estimated on the basis of a thorough review of the world's scientific literature, input from numerous scientific sources, and the Committee's best judgment. The requirements apply most satisfactorily to purified diets with high nutrient bioavailability and without substantial adverse interactions among nutrients. The estimates represent minimal requirements without safety allowances.

Also provided in this chapter is a table (Table 11-2) of dietary nutrient concentrations proposed as a guide for formulation of diets containing natural ingredients and intended for post-weaning primates. These have been

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expressed per unit of dietary dry matter, assuming an energy density of 4 kcal $ME \cdot DM_g^{-1}$. It should be noted that these nutrient concentrations are intended only as guides, have not been directly tested as a group with any primate, and may not be appropriate for all species or all post-weaning physiologic stages.

Chapter 12 provides tables of the compositions of feeds commonly used in nonhuman-primate diets.

Chapter 13 is a new area of discussion that was not included in the previous edition. This chapter discusses food as a component of environmental enhancement, an application arising from concern for the psychologic well-being of nonhuman primates in captivity. Various food choices and means of presentation are suggested.

The Appendix contains a scheme of taxonomic relationships within the Primate Order, including scientific and common names, plus tables of weight equivalents and weight-unit conversion factors.

The Committee has concluded that appropriately formulated nutritionally complete diets best serve the health and welfare needs of most captive primates. These diets are available in various forms including dry extruded, canned, and gelled. Potential impacts on oral health are among the many factors that must be considered when selecting the form of a diet to be fed.

If fed as size-appropriate, ground, mixed, dry extrusions, oral health will not be compromised. It initially might be necessary to entice some animals to accept dry extrusions by softening them with water, mashed fruit, fruit juices, or nectars. Other foods can be used for behavioral enrichment, but care must be exercised to ensure that their composition and amounts consumed do not distort nutrient concentrations and ratios in total dietary dry matter beyond required minimums and maximums. In general, alternative foods that are high in moisture are least likely to have such effects.

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1 Feeding Ecology, Digestive Strategies, and Implications for Feeding Programs in Captivity

The welfare of nonhuman primates in captivity depends heavily on meeting their nutrient needs in a manner that considers normal foraging and feeding behavior, structure and functions of the digestive system, and the options and constraints of captive dietary husbandry.

FEEDING ECOLOGY

In developing a system for the nourishment of captive nonhuman primates, it is helpful to examine the literature on the feeding ecology of primates in the wild. Several observational methods have been used to record foraging and feeding behavior in natural ecologic systems (Altmann, 1974; Lehner, 1996), and data derived with these methods are summarized in Tables 1-1 through 1-6. To interpret the findings properly, the reader should have a background in the methods used, and a brief discussion of them follows.

Feeding-Ecology Methods Involving Visual Observations of Behavior

Data collected during visual observations of behavior typically include length of feeding bout, plant species eaten, plant parts eaten (for example, fruit and leaf), percentage of part eaten, feeding rate (for example, number of fruits consumed per minute), diameter and height of food plant, and food-plant location.

OBSERVATION OPTIONS

Choosing a data-collection method requires, as a first step, selection of one of two animal-observation options.

Focal-Animal Observation One individual is observed during a given session of data collection (it can also be a pair or a small subgroup). Sessions can vary from 5 min to a whole day. This method is used to identify multiple behaviors in selected individuals. When sessions are only 5-10 min long, it is common to switch observations to another animal in the group for the next session.

All-Animal Observation Primates that are naturally grouped are observed simultaneously. This method is feasible only when observing a few easy-to-see behaviors. It is not recommended for detailed feeding behaviors.

SAMPLING METHODS

After selection of an animal-observation option, the second step is to select a method of sampling foraging and feeding behavior.

Ad Libitum (or Periodic) Sampling This is the classic, pre-1970s field method, used before modern statistical techniques and advanced technologies were commonly applied. Today, it is recommended only for preliminary reconnaissance or the study of rare behaviors. This method is biased toward spectacular behaviors, like hunting, thus overestimating faunivory compared with herbivory.

Continuous-Recording Sampling Method These sampling methods result in the most complete and accurate data. They are recommended for studying feeding ecology but are difficult to use with arboreal animals, such as primates.

- *All-Occurrences Sampling.* All occurrences of one or a few behaviors are recorded over an extended period,

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TABLE 1-1 Prosimian Feeding Ecology

Scientific Name	Common Name	Diet[a]	Behavior	Body Weight[b]	References
100% insectivorous					
Tarsius					
T. bancanus *T. dianae* *T. pumilus* *T. spectrum* *T. syrichta*	Western tarsier Dian's tarsier Pygmy tarsier Spectral tarsier Philippine tarsier	Animal prey 100%; *T. bancanus* example: beetles 35%, ants 21%, locusts 16%, cicadas 10%, cockroaches 8%, vertebrates 11% of feeding time (not seen eaten by all *Tarsius*); also eaten: crickets, mantids, moths	Nocturnal, arboreal, solitary or pairs or multimale/ multifemale, group size 2-6 individuals	77.6-117 g females, 27.5-134 g males	Crompton & Andah, 1986; Fogden, 1974; Gursky, 1996; Kappeler, 1991; MacKinnon & Mackinnon, 1980a; Niemitz, 1984; Nietsch & Niemitz, 1991; Tremble et al., 1993
Mostly insectivorous					
Allocebus					
A. trichotis	Hairy-eared dwarf lemur	In wild, unknown; in captivity, insects 70%, sweetened rice broth, fruit	Nocturnal, arboreal, forage solitary or male/female pair, sleep 2-6	78-90 g females, 75-98 g males	Albignac et al., 1991; Kappeler, 1991; Meier & Albignac, 1991; Mittermeier et al., 1994
Arctocebus					
A. aureus *A. calabarensis*	Golden angwantibo Angwantibo	Animal prey 79% (73-85%), fruit 13% (12-18%), other vegetation 8%; prey: caterpillars 77% (65-90%) crickets, beetles, ants	Nocturnal, arboreal, forage solitary, sleep 1-2	*A. aureus* 150-270 g; *A. calabarensis* 200-465 g	Bearder, 1987; Charles-Dominique, 1974; Charles-Dominique & Bearder, 1979; Gonzalez-Kirchner, 1995; Silva & Downing, 1995; Wolfheim, 1983
Galagoides					
G. demidoff *G. thomasi*[c] *G. zanzibaricus*	Demidoff's bush baby Thomas's bush baby Zanzibar bush baby	Animal prey 75% (70-81%), fruit 17% (4-30%), gums/ resins 5% (0-18%), leaves, buds; prey:moths, beetles, grasshoppers, ants, some birds	Nocturnal, arboreal (mostly), forage solitary, sleep (females) 1-10	*G.demidoff* 46-69 g females, 78-85 g males; *G. thomasi* 55-149 g; *G. zanzibaricus* 118-155 g females, 130-183 g males	Charles-Dominique, 1974; Gonzalez-Kirchner, 1995; Harcourt & Bearder, 1989; Harcourt & Nash, 1986; Hladik, 1979; Kappeler, 1991; Nash et al., 1989; Nash & Harcourt, 1986; Silva & Downing, 1995
Loris					
L. tardigradus	Slender loris	Almost exclusively insects, small amount of young leaves, shoots, hard-rind fruits, flowers, eggs, small vertebrates; often insects strong smelling	Nocturnal, arboreal, forage solitary, sleep 2-4	102-322 g	Butynski, 1982; Petter & Hladik, 1970; Silva & Downing, 1995; Wolfheim, 1983
Omnivorous, gums dominate					
Euoticus					
E. elegantulus (*Galago elegantulus*) *E. pallidus*[c]	Southern needle-clawed bush baby Northern needle-clawed bush baby	Gums 55% (35-75%), animal prey 32% (20-44%), fruit 12% (5-20%), birds	Nocturnal, arboreal, forage solitary, sleep 1-7	271 g female, 270-360 g males	Butynski, 1982; Charles-Dominique, 1974, 1977; Charles-Dominique & Bearder, 1979; Gonzalez-Kirchner, 1995; Hladik, 1979; Kappeler 1991
Galago					
G. senegalensis *G. moholi*	Northern lesser bush baby Southern lesser bush baby	Gums (Acacia) 48%, animal prey 52% (butterflies, moths, beetles), gums from 2 tree species, no vertebrate prey	Nocturnal, arboreal, forage solitary, sleep 1-3	*G. senegalensis* 126-193 g females, 125-212 g males; *G. moholi* 140-229 g females, 160-255 g males	Bearder, 1987; Bearder & Doyle, 1974; Bearder & Martin, 1979; Doyle, 1979; Doyle & Bearder, 1977; Harcourt & Bearder, 1989; Nash & Whitten, 1989; Silva & Downing, 1995
Otolemur					
O. crassicaudatus (*Galago crassicaudatus*)	Thick-tailed greater bush baby	Gums 44% (18-62%), fruit 27% (21-33%), animal prey 14% (1-27%) (invertbrates and vertebrates), nectar 4% (0-8%), seeds 3% (0-7%), misc. vegetable matter 8% (0-16%)	Nocturnal, arboreal, male solitary, female and offspring forage together, sleep 1-6	1122-1497 g females, 1126-1750 g males	Bearder & Doyle, 1974; Butynski, 1982; Doyle & Bearder, 1977; Kappeler, 1991; Masters et al., 1988
Phaner					
P. furcifer	Fork-marked lemur	Tree gum (resins) bulk of diet, some fruit, sap, animal matter 10%, flowers, buds, nectar, secretions of Homoptera insects	Nocturnal, arboreal, solitary or male/ female pairs, sleep 1-4	350-600 g	Charles-Dominique & Petter, 1980; Hladik, 1979; Hladik et al., 1980; Kappeler, 1991; Pariente, 1979; Petter et al., 1971, 1975

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TABLE 1-1 *(continued)*

Omnivorous, plants (especially fruits) dominate					
Cheirogaleus					
C. major *C. medius*	Greater dwarf lemur Fat-tailed dwarf lemur	Fruit, young leaves, flowers, nectar, leaf buds, gums, animal prey (mostly insects, some chameleons); *C. major* lethargic in cool, dry season; *C. medius* increase in body weight 120-250 g during rainy season (6 months), hibernate 7-9 months	Nocturnal, arboreal, forage solitary, sleep 1-5	*C. major* 235-470 g; *C. medius* when feeding (rainy season) 142-217 g, especially tail, hibernate loses 100 g	Hladik, 1979; Hladik et al., 1980; Mittermeier et al., 1994; Petter et al., 1977; Wright & Martin, 1995
Eulemur (Petterus)					
E. coronatus *E. fulvus* *E. macaco* *E. mongoz* *E. rubriventer*	Crowned lemur Brown lemur Black lemur Mongoose lemur Red-bellied lemur	Fruit 45% (7-79%), leaves 45% (20-89%), flowers 10% (1-52%), few insects; dry season diet of *E.mongoz, E. rubriventer, E. fulvus* in some habitats nectar 82% (81-84%), fruit 17%, leaf 1%; *E. fulvus* tolerates high levels of toxic plant compounds	Cathemeral, mostly arboreal, multimale/ multifemale groups, group size 5-18 or just family groups	1.4-2.4 kg	Andriatsarafara, 1988; Colquhoum, 1993; Dague & Petter, 1988; Hladik, 1979; Kappeler, 1991; Overdorff, 1993; Richard & Dewar, 1991; Silva & Downing, 1995; Sussman, 1974, 1977; Sussman & Tattersall, 1976; Tattersall, 1977, 1979; Wilson et al., 1989; Yamashita 1996
Galago					
G. alleni *G. gallarum* *G. matschiei*	Allen's bush baby Somali bush baby Matschie's bush baby (was *Euoticus inustus*)	Fruit 74% (73-76%), animal prey 24% (23-25%) (invertebrates and frogs), 2% other vegetation (fallen fruit, seeds, gums)	Nocturnal, arboreal, forage solitary 86%, sleep (females) 1-4	*G. alleni* 200-445 g; *G. gallarum* 196-225 g	Butynski, 1982; Charles-Dominique, 1977; Gonzalez-Kirchner, 1995; Nash et al., 1989
Lemur					
L. catta	Ring-tailed lemur	Fruit 54% (34-70%), leaves 33% (24-50%), flowers 3% (0-8%), herbs 8% (6-15%), bark, sap, cactus, misc 2% (0-7%); *Tamarindus indicus* is 25% of diet: 12% leaf, 12% pods	Diurnal, arboreal, terrestrial, multimale/ multifemale, with 1 alpha female, group size 5-30	1.96-2.705 kg	Jolly, 1966; Kappeler, 1991; Rasamimanana & Rafidinarivo, 1993; Sauther & Sussman, 1993; Silva & Downing, 1995; Sussman, 1974; Yamashita, 1996
Microcebus					
M. (Mirza) coquereli *M. murinus* *M. myoxinus*[c] *M. rufus*	Coquerel's dwarf lemur Gray mouse lemur Pygmy mouse lemur Brown mouse lemur	Fruit, animal matter (insects, frogs, bird eggs, chameleons), young leaves, flowers, gums, sap/resins, nectar, buds, seeds; spends up to 50% of time in dry season licking larval secretions of Homoptera off branches	Nocturnal, arboreal mostly, forage solitary, some pairs, sleep 1-4; *M. murinus* store fat in tail and less active in dry season, do not hibernate, sleep 1-15	*M. coquereli, M. myoxinus* 302 g female, 308 g male; *M. rufus* 41-63 g females, 35-70 g males; *M. murinus* 40-109 g varies 50-60 g when "hibernates"	Corbin & Schmid, 1995; Hladik, 1979; Kappeler, 1991; Pages, 1980; Petter et al., 1971, 1977; Wright & Martin, 1995
Nycticebus					
N. coucang *N. pygmaeus*[c]	Slow loris Pygmy loris	Fruit 50%, animal prey 30%, gums 15% (10-19%), shoots, bird eggs, insects that have repugnant taste and smell	Nocturnal, arboreal, forage solitary	*N. coucang* 375-900 g female, 850-1207 g male: *N. pygmaeus* 372 g female, 462 g male	Bearder, 1987; Duckworth, 1994; Kappeler, 1991; Silva & Downing, 1995; Tan, 1994; Van Horn & Eaton, 1979
Otolemur					
O. garnettii	Garnett's greater bush baby	Fruit 27% (4-50%), animal prey 61% (44-78%) (beetles, ants, termites, snails, birds), seeds 3% (0-7%), other vegetation 9% (0-18%) (resins, bark, pollen)	Nocturnal, arboreal, male solitary, related females overlap	740-1460 g female, 822-1640 g male	Bearder, 1987; Harcourt & Nash, 1986; Masters et al., 1988; Nash & Harcourt, 1986; Nash et al., 1989; Silva & Downing, 1995
Perodicticus					
P. potto	Potto	Fruit 74% (65-82%), gums 40% (21-60%), animal prey 20% (10-30%) (ants make up 65% of insect prey), some leaf and fungus; when fruit is scarce (dry season)	Nocturnal, arboreal,forage solitary 96%, pairs 4%, sleep 1-2	850-1600 g	Charles-Dominique, 1974; Gonzalez-Kirchner, 1995; Hladik, 1979; Oates, 1984
Varecia					
V. variegata	Ruffed lemur	Ripe fruit 74%, 21% leaves (2% shoots, 1% young leaves, 18% mature leaf), flowers 5% (1-40%), seeds, nectar; 74% nectarivorous in 1 month of year	Diurnal, arboreal mostly, family or larger groups, 5-32 individuals	3.512 kg female, 3.471 kg male	Dew & Wright, 1994; Kappeler & Ganzhorn, 1993; Morland, 1993; Richard & Dewar, 1991; Rigamonti, 1993; White, 1989

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TABLE 1-1 *(continued)*

Leaves dominate other plant parts					
Avahi					
A. laniger	Woolly lemur	Seasonally exclusively folivorous: 91% leaves (40% mature leaves, 51% mixed mature and young), 9% flowers, rarely fruit and bark	Nocturnal, arboreal, monogamous pairs, groups 2-5 individuals	1.3 kg female, 1.0 kg male	Albignac, 1981; Ganzhorn, 1988; Ganzhorn et al., 1985; Harcourt, 1991; Kappeler, 1991; Richard & Dewar, 1991
Indri					
I. indri	Indri (babakoto)	Young leaves, buds, and petioles 45% (1-75%), fruit 38% (5-75%), unripe seeds 12% (10-15%), flowers and buds 3% (1-6%), mature leaves 2% (0-3%), occasionally soil	Diurnal, arboreal, monogamous family groups 2-6 individuals	7.1 kg female, 5.8 kg male	Hladik, 1979; Mittermeier et al., 1994; Pollock, 1975, 1977
Lepilemur					
L. dorsalis	Gray-backed sportive lemur	Leaves primarily, some fruit, bark, seeds, flowers; *L. mustelinus* can tolerate high alkaloid levels; *L. ruficaudatus* may practice caecotrophy and have high tolerance for toxins; *L. leucopus* 100% leaves	Nocturnal, arboreal, solitary or male/ female pairs, sleep 1-3; do not hibernate	544-915 g, *L. edwardsi* 1000g	Albignac, 1981; Charles-Dominique & Hladik, 1971; Ganzhorn, 1988; Hladik, 1979; Hladik & Charles-Dominique, 1974; Hladik et al., 1980; Kappeler, 1990, 1991; Kappeler & Ganzhorn, 1993; Nash, 1994; Silva & Downing, 1995
L. edwardsi	Milne-Edwards' sportive lemur				
L. leucopus	White-footed sportive lemur				
L. microdon[c]	Small-toothed sportive lemur				
L. mustelinus	Weasel sportive lemur				
L. ruficaudatus	Red-tailed sportive lemur				
L. septentrionalis	Northern sportive lemur				
Propithecus					
P. diadema	Diademed sifaka	*P. diadema* and *P. tattersalli*: young leaves 25% (5-44%), mature leaves 25% (0-46%), fruit, ripe or unripe 43% (0-72%), flowers 7% (0-23%); *P. verreauxi*: mature leaves 38% (2-70%), young leaves 40% (0-70%), fruit 7% (5-8%), flowers 10% (0-40%), bark 5% (4-9%)	Diurnal, mostly arboreal, pairs to multimale/ multifemale groups, 2-12 individuals	*P. diadema*: 5.6-7.2 kg, *P. tattersalli*: 2.1-3.8 kg, *P. verreauxi*: 3.5-3.6 kg	Hemingway, 1998; Hladik, 1979; Jolly, 1966; Kappeler, 1991; Meyers & Wright, 1993; Richard, 1974, 1977, 1978; Yamashita, 1996
P. tattersalli	Golden-crowned sifaka				
P. verreauxi	Verreaux's sifaka				
Mostly bamboo					
Hapalemur					
H. aureus	Golden bamboo lemur	Bamboo 95% (85-98%) (shoots 89%, mature leaves 6%, young leaves 1%, petioles 1%), flowers 1%, fruit 2%, fungus 2%; *H. griseus* also eats phragmites leaves and shoots, Papyrus pith; *H. aureus* eats a bamboo containing 12 × lethal dose (for humans) of cyanide	Diurnal or cathemeral, arboreal, family 2-6 individuals; *H. simus* 1 male + multifemale or multimale/ multifemale groups 4-30 individuals	*H. aureus* 1.5 kg female, 1.7 kg male; *H. griseus* 800-939 g; *H. simus* 1.3-2.4 kg	Glander et al., 1989; Kappeler, 1990; Meier & Rumpler, 1987; Overdorff et al., 1997; Petter & Peyrieras, 1970a; Petter et al., 1975, 1977; Silva & Downing, 1995; Wright, 1986; Wright & Randrimanantena, 1989; Wright et al., 1987
H. griseus	Lesser bamboo lemur				
H. simus	Greater bamboo lemur				
Was thought of as insectivorous but is omnivorous-frugivorous					
Daubentonia					
D. madagascariensis	Aye-aye	Seeds/nuts 47% (12-84%), nectar 8% (1-20%), larvae 20% (2-45%), canker 20% (5-42%), other (soft fruit, fungus, galls, bamboo) 5% (0-12%); larvae extracted with long thin finger; eat coconuts (0-58% where available) same way.	Nocturnal, arboreal, forage solitary, sleep 1-2	2.6 kg female, 2.8 kg male	Ancrenaz et al., 1994; Andriamasimanana, 1994; Erickson, 1995; Iwano & Iwakawa, 1985; Kappeler, 1991; Petter & Peyrieras, 1970b; Pollock et al.,1985; Sterling, 1994; Sterling et al., 1993

[a] Diet format: mean (range).
[b] Body weights in ranges whenever possible; single numbers are not averages but indicate that only one individual of the species has been weighed in the wild.
[c] No data available from the wild but assumed to be similar to congenerics.

often 1 day. Usually combined with focal-animal sampling, this is an excellent but difficult method for recording foraging and feeding behavior. Start-and-stop rules, independent of the behavior being studied, are required.

- *Sequence Sampling*. A sampling period starts with the beginning of a sequence of a chain of behaviors, such as foraging for insects and feeding. The sampling period ends when the observed sequence ends. This method is of lim-

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TABLE 1-2 Callitrhix Feeding Ecology

Scientific Name		Diet[a]	Behavior	Body Weight[b]	References
Fruit and insect foraging dominate diet, gums seasonally important					
Callithrix					
C. argentata	Bare-ear marmoset	27% (24-30%) of total daily activity foraging for insects; therefore, total feeding time spent on insect foraging 56% (50-63%), fruit 33% (28-37%), exudates (gums) 11% (5-16%); when fruit scarce, exudate intake increased	Diurnal, arboreal mostly, multimale/ multifemale group size 3-20 individuals	190-320 g females, 357-450 g males; *C. nigriceps* 370 g male, 390 g female	Ferrari, 1993; Ferrari & Ferrari, 1989; Ferrari & Rylands,1994; Ford & Davis, 1992; Harrison & Tardif, 1994; Koenig, 1995; Muskin, 1984; Rylands, 1993; Rylands & de Faria, 1993; Stevenson & Rylands, 1988
C. aurita	Buffy tufted-eared marmoset				
C. geoffroyi	Geoffroy's tufted-eared marmoset				
C. humeralifer	Tassel-eared marmoset				
C. kuhlii	Wied's tufted-eared marmoset				
C. mauesi[c]	Maues marmoset				
C. nigriceps	Black-headed marmoset				
Fruit dominates, insects important, gums or nectar seasonal					
Leontopithecus					
L. caissara[c]	Black-faced lion tamarin	Ripe fruit 53% (32-78%), insect foraging 25% (14-50%) of feeding time, unripe fruit 6-7%, exudates (gums) 9% (1-20%), nectar 7% (0-43%)	Diurnal, arboreal mostly, pairs or multimale/ multifemale 2-3 adults/group, 2-16 total	361-794 g females, 437-710 g males	Albernaz, 1997; Butynski, 1982; Dietz et al., 1997; Ferrari, 1993; Ferrari & Ferrari, 1989; Ford & Davis, 1992; Rylands, 1993; Tardif et al., 1993
L. chrysomelas	Golden-headed lion tamarin				
L. chrysopygus	Black lion tamarin				
L. rosalia	Golden lion tamarin				
Gums dominate, insects important, fruit can depend on location					
Callithrix					
C. jacchus	Common marmoset	Exudates (gums) 45% (24-70%), fruit 16% (14-30%), insect foraging 39% (30-70%), nectar in dry season; *C.pygmaea* exudates (gums) 60% (30-77%), fruit 8% (0-10%), insects 30% (20-33%)	Diurnal, arboreal mostly, multimale/ multifemale, groups 1-15; *C. pygmaea* monogamous families, up to 4 litters living together	182-354 g females, 225-406 g males; *C. pygmaea* 112-140 g females, 99-160 g males	Coimbra-Filho & Mittermeir, 1978; Ferrari & Ferrari, 1989; Ferrari & Rylands, 1994; Ford & Davis, 1992; Ramirez, 1985a; Rylands & de Faria, 1993; Silva & Downing, 1995; Soini, 1982, 1988, 1993
C. flaviceps	Buffy-headed marmoset				
C. penicillata	Black tufted-eared marmoset				
C. pygmaea (was genus *Cebuella*)	Pygmy marmoset				
Insects and fruit dominate, gums and nectar seasonally important					
Callimico					
C. goeldii	Goeldi's monkey	Preferred food insects; also soft, sweet fruit in wet season, sticky coating of gum on pods in dry season; rarely buds or young leaves; diet similar to *Saguinus* spp, sometimes live with mixed *Saguinus* troops	Diurnal, arboreal mostly, monogamous pairs, some within group, 2-8 individuals	400-535 g	Ford & Davis, 1992; Heltne et al., 1981; Mittermeier & Coimbra-Filho, 1977; Pook & Pook, 1981, 1982
Saguinus					
S. bicolor	Bare-faced tamarin	Insects 45% (30-77%), fruit 35% (13-74%), exudate 10% (0-37%), nectar 7% (0-35%), young leaves 3%, seeds; 34.8% of total activities foraging for insects, 17% plant foods; insect capture rate might be only 5.4% of prey-foraging time	Diurnal, arboreal, multimale/ multifemale groups, 2-16 individuals; *S. imperator, S. labiatus*, and *S. midas* multimale/ multifemale, but only 1 reproducing female	272-600 g females, 242-633 g males	Crandlemire-Sacco, 1988; Egler, 1992; Ferrari & Ferrari, 1989; Ford & Davis, 1992; Garber, 1984, 1988, 1993a,b; Harrison & Tardif, 1994; Lopes & Ferrari, 1994; Pack et al., 1999; Peres, 1993a; Ramirez, 1985a,b; Skinner, 1985; Silva & Downing, 1995; Soini, 1987; Terborgh, 1983
S. fuscicollis	Saddleback tamarin				
S. geoffroyi	Red-crested tamarin				
S. imperator	Emperor tamarin				
S. inustus[c]	Mottled-faced tamarin				
S. labiatus	Red-bellied tamarin				
S. leucopus	Silvery-brown bare-faced tamarin				
S. midas	Golden-handed tamarin				
S. mystax	Mustached tamarin				
S. nigricollis	Spix's black-mantled tamarin				
S. cedipus	Cotton-top tamarin				
S. tripartitus[c]	Golden-mantled saddleback tamarin				

[a] Diet format: mean (range).
[b] Body weights in ranges whenever possible; single numbers are not averages but indicate that only one individual of the species has been weighed in the wild.
[c] No data available from the wild but assumed to be similar to congenerics.

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TABLE 1-3 Cebid Feeding Ecology

Scientific Name	Common Name	Diet[a]	Behavior	Body Weight[b]	References
More insectivorous than frugivorous					
Saimiri					
S. boliviensis	Bolivian squirrel monkey	Animal prey, particularly insects 60% (47-100%), vertebrates 1%, fruit 25% (15-39%), flowers 5% (2-13%), leaves 13% (11-18%), seeds/nuts, successful in 61% of insect foraging; during dry season, rely on figs	*S. boliviensis, S. oerstedii*: diurnal, arboreal, multimale/multifemale, groups, up to 23 individuals; *S. sciureus, S. vanzolinii*: groups, 22-50 individuals	0.54-1.25 kg females, 0.48-1.2 kg males	Costello et al., 1993; Ford & Davis, 1992; Janson & Boinski, 1992; Mittermeier & vanRoosmalen, 1981; Rosenberger, 1992; Silva & Downing, 1995; Souza et al., 1997; Terborgh, 1983
S. oerstedii	Red-backed squirrel monkey				
S. sciureus	Common squirrel monkey				
S. ustus[c]	Golden-backed squirrel monkey				
S. vanzolinii[c]	Black squirrel monkey				
Primarily frugivorous					
Ateles					
A. belzebuth	White-bellied spider monkey	Total fruit 78% (18-100%), including unripe fruit 6%; seed 5% (0-19%); total leaves 16% (0-38%), including mature leaves 3%; flowers 3% (1-10%); epiphytes 2%; dead wood, buds, insects 1%	Diurnal, arboreal (salt licks on ground), fission-fusion, groups 3-35 individuals	5.0-11.0 kg females, 5.8-9.8 kg males	Chapman, 1987, 1988; Ford & Davis, 1992; Hladik, 1975; Klein & Klein, 1975, 1977; MendesPontes, 1997; Milton, 1981; Mittermeier & vanRoosmalen, 1981; Nunes, 1998; Robbins et al., 1991; Silva & Downing, 1995; Simmen & Sabatier, 1996; Symington, 1988; VanRoosmalen, 1985; VanRoosmalen & Klein, 1988; White, 1986
A. chamek	Black-faced black spider monkey				
A. fusciceps[c]	Brown-headed spider monkey				
A. geoffroyi	Black-handed spider monkey				
A. marginatus[c]	White-whiskered spider monkey				
A paniscus	Black spider monkey				
Primarily frugivorous, seasonally seeds or leaves important					
Aotus					
A. nigriceps	Southern red-necked night monkey				
A. trivirgatus	Northern gray-necked owl monkey	Fruit (soft) 44% (16-75%), leaves 32% (5-46%), insects 13% (5-15%), other (especially flowers) 11%; *Aotus* diet similar to *Callicebus* but ate less vegetation, more insects in abundant season	Nocturnal, arboreal, monogamous family groups, 2-5 individuals; feed in groups 25-55 at low elevations	0.78-1.1 kg females, 0.825-1.05 kg males	Durham, 1975; Engqvist & Richard, 1991; Kinzey, 1992; Wright, 1981,1989, 1994
Callicebus					
C. brunneus	Brown titi monkey	Fruit 61% (30-87%) (of which seeds may be as much as 28%), leaves (mostly young) 21% (2-66%), insects 12% (0-28%), flowers 2% (0-18%); when food scarce, ate 25% bamboo and vine leaves	Diurnal, arboreal, monogamous family 2-6 individuals	0.7-1.5 kg	Crandlemire-Sacco, 1988; Easley, 1984; Ford & Davis, 1992; Heiduck, 1997; Kinzey, 1977, 1981, 1992; Kinzey & Gentry, 1979; Muller, 1996; Palacios, 1997; Robinson et al., 1987; Silva & Downing, 1995; Terborgh, 1983, Wright, 1994
C. caligatus[c]	Chestnut-bellied titi monkey				
C. cinerascens[c]	Ashy gray titi monkey				
C. cupreus[c]	Red titi monkey				
C. donacophilus[c]	Bolivian gray titi monkey				
C. dubius[c]	Hershkovitz's titi monkey				
C. hoffmannsi[c]	Hoffmann's titi monkey				
C. modestus[c]	Bolivian titi monkey				
C. moloch	Dusky titi monkey				
C. oenanthe[c]	Andean titi monkey				
C. olallae[c]	Beni titi monkey				
C. personatus	Masked titi monkey				
C. torguatus	Collared titi or widow monkey				
Cebus					
C. albifrons	White-fronted capuchin	Fruit 55% (10-95%), of which seeds are 8% (0-39%); leaves (mostly young) 8% (0-39%); insects 33% (2-100%); flowers 2% (0-14%); *C. apella* in Argentina ate bromeliad leaves 72%, fruit 3%, insects 25%	Diurnal, arboreal mostly, multimale/multifemale groups of 2-40 individuals; *C. apella, C. olivaceus*: with alpha male	1.4-3.8 kg females, 1.3-4.8 kg males	Brown & Zunino, 1990; Chapman, 1987; Chapman & Fedigan, 1990; Ford & Davis, 1992; Hladik et al., 1971; Janson, 1985; Janson & Boinski, 1992; Mittermeier & vanRoosmalen, 1981; Peres, 1994a; Robinson, 1984; Simmen & Sabatier, 1996; Teaford & Robinson, 1989; Terborgh, 1983
C. apella	Tufted or brown capuchin				
C. capucinus	White-throated capuchin				
C. olivaceus	Weeper or wedge-capped capuchin				

(continues)

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TABLE 1-3 *(continued)*

Both fruit and seeds rank high, sometimes seeds dominate					
Lagothrix					
L. flavicauda	Yellow-tailed woolly monkey	Fruit 67% (6-95%), seeds 10% (0-35%); insects 7% (0-34%), leaves (mostly young) 12% (2-48%); flowers 2% (0-9%), pod exudates eaten at some sites	Diurnal, arboreal, multimale/ multifemale groups of 5-70 individuals; highlands groups 6-7; lowlands groups 10-20 individuals	3.5-6.5 kg females, 3.6-10.2 kg males	Butynski, 1982; Defler & Defler, 1996; Durham, 1975; Ford & Davis, 1992; Kinzey, 1997; Luna, 1987; Peres, 1994b; Ramirez, 1988; Robinson & Janson, 1987; Soini, 1987; Stevenson et al., 1994
L. lagothricha	Woolly monkey				
Cacajao					
C. calvus	Bald uacari	Seeds (mostly unripe) 59% (20-97%), fruit pulp 22% (1-60%), nectar 6% (0-58%), insects 5%, leaves and so on 3%; seeds of unripe fruit important as for all pithecines	Diurnal, arboreal mostly, multimale/ multifemale groups 5-30 up to 100 individuals	2.4-4.0 kg	Ayres, 1989; Barnett & Brandon-Jones, 1997; Fontaine, 1981; Ford, 1994; Kinzey, 1992; Mittermeier & Coimbra-Filho, 1977
C. melanocephalus	Black-headed uacari				
Chiropotes					
C. albinasus	White-nosed saki	Seeds (mostly unripe) 53% (12-96%), fruit 37% (6-84.5%); leaves 2% (0-4%), flowers 5% (1-11%), insects 3% (0-24%); seed predators on 52 species and seed dispersers of 7 species; *C. satanas* ingest unripe fruit with hard pericarp	Diurnal, arboreal, multimale/ multifemale groups 10-30 individuals	1.9-3.3 kg females, 2.2-4.0 kg males	Ayres, 1989; Ford & Davis, 1992; Kinzey, 1992; Kinzey & Norconk, 1993; Mittermeier & vanRoosmalen, 1981; Mittermeier et al., 1983; Norconk et al., 1998; Robinson et al., 1987; van Roosmalen et al., 1981, 1988
C. satanas	Bearded saki				
Pithecia					
P. aequatorialis[c]	Equatorial saki	Seeds 38% (17-88%), other fruit 43% (3-51%), leaves (mostly young) 12% (0-32%), insects 1.0% (0-6%), flowers 6% (0-15%); *P. monachus* may eat more leaves or insects, *P. pithecia* more young seed (>60%)	Diurnal, arboreal, monogomous family groups, groups 2-8; *P. aequatorialis*, *P. monachus*: cryptic	0.779-2.5 kg females, 0.964-3.1 kg males	Buchanan et al., 1981; Ford & Davis, 1992; Happel, 1982; Kinzey, 1992; Kinzey & Norconk, 1993; Mittermeier & vanRoosmalen, 1981; Norconk, 1996; Norconk & Kinzey, 1990; Norconk et al., 1998; Peres, 1993b
P. albicans	Buffy saki				
P. irrorata[c]	Bald-faced saki				
P. monachus	Monk saki				
P. pithecia	White-faced saki				
Primarily folivorous, some fruit, no animal prey					
Alouatta					
A. belzabul[c]	Red-handed howler	*A. palliata, A. seniculus, A. pigra*: total leaves 54% (20-100%), including 38% young, 16% mature leaf; total fruit, especially figs, 39% (0-80%), including 34% ripe, 5% unripe; flowers 9% (0-90%); *A. fusca, A. caraya*: 72% leaves (45-89%); fruit 20% (2-55%); flowers 8% (0-24%)	Diurnal, arboreal (drink on ground, *A. palliata* can swim), 1,2 or multimales/ multifemales, groups 4-21 individuals; One-male groups common	2.4-7.6 kg females, 4.2-11.4 kg males	Bicca & Calegaro, 1994; Chapman, 1987; Crockett & Eisenberg, 1987; de Thoisy & Richard-Hansen, 1997; Estrada, 1984; Estrada & Coates-Estrada, 1986; Ford & Davis, 1992; Galetti et al., 1987; Garcia, 1994; Gaulin & Gaulin, 1982; Glander, 1978; Hladik el al., 1971; Julliot & Sabatier, 1993; Milton, 1980; 1981; Mittermeier & van Roosmalen, 1981; Neville et al., 1988; Oftedal, 1991; Prates et al., 1987; Simmen & Sabatier, 1996; Smith, 1977; Stoner, 1996; Strier, 1992.
A. caraya	Black-and-gold howler				
A. colibensis[c]	Colba Island howler				
A. fusca	Brown howler				
A. palliata	Mantled howler				
A. pigra	Black howler				
A. sara[c]	Bolivian red howler				
A. seniculus	Red howler				
Brachyteles					
B. arachnoides	Woolly spider monkey or muriqui	Leaves 58% (range 41-93%); fruit 28% (7-59%), within which unripe seeds were 8% (0-32%); flowers 14% (0-38%)	Diurnal, arboreal, multimale/ multifemale and fission-fusion, groups 5-45 individuals	9.4 kg female, 12.1 kg male	Ford, 1994; Lemos, 1988; Milton, 1984; Neville et al., 1988; Nishimura et al., 1988; Strier, 1991, 1992

[a] Diet format: mean (range).
[b] Body weights in ranges whenever possible; single numbers are not averages but indicate that only one individual of the species has been weighed in the wild.
[c] No data available from the wild but assumed to be similar to congenerics.

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TABLE 1-4 Colobine Feeding Ecology

Scientific Name	Common Name	Diet[a]	Behavior	Body Weight[b]	References
Strongly folivorous					
Colobus					
C. guereza	Abyssinian, guereza, or eastern black-and-white colobus	*C. guereza*: young leaves and buds 64% (52-90%), mature leaves 13% (2-22%), whole fruit 15% (0-34%), flower and bud 6% (0-17.1%); seeds 1%, stems 0.5%; other 0.5%	Diurnal, arboreal mostly; *C. guereza*: 1 male or multimale/ multifemale group 2-50; others: multimale/ multifemale	6.8-8.92 kg females, 9.7-13.5 kg males	Clutton-Brock, 1975; McKey, 1978; Napier, 1985; Oates, 1977, 1978, 1994, Oates et al., 1994; Struhsaker, 1978a; Struhsaker & Oates, 1975
C. vellerosus[c]	Geoffroy's or white-thighed black-and-white colobus				
Folivorous but >30% seed-eating					
Colobus					
C. angolensis	Angolan black-and-white colobus	Young leaves 31% (2-85%), mature leaves 18% (4-75%), fruit 8% (0-55%), seeds 35% (0-89%), flowers and buds 5% (0-31%), stems 1% (0-15%), other 1.5%	Diurnal, arboreal mostly; *C. angolensis* 1 male or multimale/ multifemale groups 2-50; others multimale/ multifemale	4.32-9.67 kg females, 9.7-13.5 kg males	Dasilva, 1992, 1994; Groves, 1973; Harrison & Hladik, 1986; Maisels et al., 1994; McKey, 1978; McKey & Waterman, 1982; McKey et al., 1981; Silva & Downing, 1995; Tutin et al., 1997
C. polykomos	King or western black-and-white colobus				
C. satanas	Black colobus				
Strongly folivorous, some seed					
Procolobus (Piliocolobus or Colobus)					
P. badius	Western red colobus	Young leaves and buds 52% (7-85%) mature leaves and petiole 16% (1-60%), fruit (especially unripe) 9% (0-41%), seeds 12% (0-31%), flowers and buds 9% (0-36%), stems and miscellaneous 1% (0-17%)	Diurnal, arboreal, multimale/ multifemale groups 5-80; *P. rufomitratus*, 1 male or multimale/ multifemale *P. verus*: 1 or 2 males + multifemale	4.2-8.2 kg females, 4.7-11.0 kg males	Brandon-Jones, 1985; Clutton-Brock, 1975; Decker, 1994; Gatinot, 1977; Maisels et al., 1994; Marsh, 1981, 1983; McKey, 1978; Mowry et al., 1996; Oates, 1988; Oates & Whitesides, 1990; Oates et al., 1994; Silva & Downing, 1995; Struhsaker, 1975, 1978a; Struhsaker & Oates, 1975; Wachter et al., 1997
P. pennantii	Pennant's red colobus				
P. preussi[c]	Preuss's red colobus				
P. rufomitratus	Tana river red colobus				
P. verus	Olive colobus				
Folivorous/frugivorous (>50% leaf, <50% fruit)					
Nasalis					
N. larvatus	Proboscis monkey	Young leaf 45% (38-48%), mature leaves 4%, fruit 40% (17-50%), of which seeds are 15-20%, flowers and buds 3%; stems 3%; other 2.5%; insects <1%; fruit eaten usually unripe; frugivorous January-May, folivorous June-December	Diurnal, arboreal, swimmers, 1 male + multifemale and bachelor troops, groups 2-20; *N. (Simias)* concolor also in pairs or multimale/ multifemale	7.1-11.8 kg females, 8.8-23.6 kg males	Bennett & Davies, 1994; Bennett & Sebastian, 1988; Ross, 1992; Watanabe, 1981; Yeager, 1989
N. (Simias) concolor	Pig-tailed langur				
Presbytis					
P. comata	Grizzled leaf monkey	Young leaves 41% (15-71%); mature leaves 4% (0-11%); fruit 42% (3-80%), of which about 7% is seeds (1-30%) and unripe fruit and seeds up to 30%; flowers and buds 10% (1-30%); other 3%; very little insect eaten <1%. *P. rubicunda*: seed predators	Diurnal, arboreal, male + multifemale, monogamous pairs, groups 2-21; *P. melalophos*: 1 male or multimale/ multifemale	3.0-6.7 kg females, 5.6-8.2 kg males	Adiputra, 1994; Aldrich-Blake, 1980; Bennett & Davies, 1994; Brandon-Jones, 1985; Chivers, 1994; Curtin, 1980; Davies, 1991; Davies et al., 1988; Goodman, 1989; Gurmaya, 1986; Leutenegger & Cheverud, 1982; MacKinnon & MacKinnon, 1980b; Rodman, 1978; Ruhiyat, 1983; Silva & Downing, 1995; Ungar, 1995; Watanabe, 1981
P. femoralis	Banded leaf monkey				
P. frontata[c]	White-fronted leaf monkey				
P. hosei	Hose's leaf monkey				
P. melalophos	Mitered leaf monkey				
P. potenziani	Mentawai Island leaf monkey				
P. rubicunda	Maroon leaf monkey				
P. thomasi	Thomas's leaf monkey				
Pygathrix					
P. nemaeus	Red-shanked douc langur	Young leaves and buds 37% (7-93%), mature leaves 37% (31-88%), fruit 15% (5-47%), seeds 3% (0-15%), flowers 7% (0-28%), lichen 5% (0-50%); figs important, almost no insects	Diurnal, arboreal (some also terrestrial), multimale/ multifemale or 1 male + multifemale, groups 3-200 individuals	6.5-10 kg females, 10.9-20.3 kg males	Bennett & Davies, 1994; Bleisch & Xie, 1994; Bleisch et al., 1998; Ji & Bleisch, 1994; Kirkpatrick, 1994; Lippold, 1995; Long, 1994; Nhat, 1993, 1994; Silva & Downing, 1995
P. nigripes[c]	Black-shanked douc langur				
P. (Rhinopithecus) avunculus	Tonkin snub-nosed monkey				
P. (Rhinopithecus) bieti	Black or Yunnan snub-nosed monkey				
P. (Rhinopithecus) brelichi	Guizhou snub-nosed monkey				
P. (Rhinopithecus) roxellana	Sichuan golden snub-nosed monkey				

(continues)

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TABLE 1-4 *(continued)*

Semnopithecus (Presbytis)					
S. entellus	Hanuman langur	In remote, wild areas: young leaves 26% (0-69%), mature leaves 26% (0-79%) fruit 34% (0-72%), of which about 3% is seeds (0-45%), flowers and buds 9% (0-43%), stem 1.6%; other 3%; more insects than other colobines; near farms: 90% of diet is cultivated crops; Himalayan subspp eat pinecones, bark, twigs during snowy winter months	Troops near temples eat offerings, raid crops; diurnal, terrestrial, and arboreal, 1 male or multimale/ multifemale, groups 11-262 individuals	6.7-15.6 kg females, 10.6-20.9 kg males	Bennett & Davies, 1994; Hladik, 1975, 1988; KarGupta & Kumar, 1994; Newton, 1992; Oppenheimer, 1977; Silva & Downing, 1995; Srivastava, 1991; Starin, 1978
Trachypithecus (Presbytis)					
T. auratus	Ebony langur	Young leaves and shoots 32% (9-52%), mature leaves and petioles 26% (1-61%), fruit 32% (1-55%), of which 7% is seeds (0-40%); flowers and buds 10% (0-43%), insects <1%, other 0.5%; more mature leaves than *Presbytis* and much of fruit eaten unripe; raids crop; *T. pileatus* - animal prey 1.6%, gum and termite soil	Diurnal, arboreal (some also terrestrial), 1 (some 2) male and multifemale, groups 2-40 individuals	3.0-10.9 kg females, 6.0-13.6 kg males	Aldrich-Blake, 1980; Bennett & Davies, 1994; Brandon-Jones, 1985; Brotoisworo & Dirgayusa, 1991; Chivers, 1994; Curtin, 1980; Curtin & Chivers, 1978; Fleagle, 1978; Hladik, 1975, 1977, 1988; Hladik & Hladik 1972; Islam & Husain, 1982; Kool, 1992, 1993; Kumar-Gupta & Kumar, 1994; Li, 1993; MacKinnon & MacKinnon, 1980b; Mukhergee, 1978; Oates et al., 1980; Silva & Downing, 1995; Stanford, 1988; 1991a, 1991b; Whitten, 1987, Wrangham et al., 1993
T. cristatus	Silvered langur				
T. delacouri[c]	Delacour's langur				
T. francoisi[c]	Francois's langur				
T. geei	Golden langur				
T. (Kasi) johnii	Nilgiri langur				
T. obscurus	Dusky or spectacled leaf monkey				
T. phayrei	Phayre's leaf monkey				
T. pileatus	Capped leaf monkey				
T. (Kasi) vetulus	Purple-faced leaf monkey				

[a] Diet format: mean (range).
[b] Body weights in ranges whenever possible; single numbers are not averages but indicate that only one individual of the species has been weighed in the wild.
[c] No data available from the wild but assumed to be similar to congenerics.

ited use for quantifying a diet, because the time required for food acquisition varies.

Time Sampling Methods Less complete but more manageable methods for recording feeding behavior, these are probably the most commonly used today. These methods also require independent start-and-stop rules, and dawn and dusk are often used.

- *One-Zero Sampling*. A behavior is scored only once per observation period, regardless of the number of times it occurs. This method is adequate for preliminary reconnaissance. It is not recommended for detailed feeding-ecology studies, because it generally yields poor "time-spent" estimates.
- *Instantaneous Sampling*. The observer records a focal-animal's behavior at predetermined times. This method works well with ongoing behavior that can be timed with a stopwatch, such as feeding behavior. For example, during a feeding bout, what the animal is eating every 30 or 60 seconds is recorded. Another approach is to observe the focal animal every 15 min and record all behaviors for 5 min. A limitation of this approach is that rare events often are not recorded. However, when continuous observations prove impossible, this generally is considered the next-best method.
- *Scan Sampling*. Instantaneous observations are made of several animals simultaneously. This is useful for studying less-detailed behavior.

Alternative Feeding-Ecology Methods

In some circumstances, particularly if terrestrial primates are being studied in dense rainforest, visual observations of feeding behavior are impractical. It can be impossible to see the animals well enough to determine what they are eating or how much time they spend eating it, and alternative methods might be needed. Some researchers studying nocturnal animals use both visual observations and alternative methods (Nash 1983). Alternative methods for studying feeding ecology are outlined below.

ANALYSIS OF STOMACH CONTENTS

Measurement of stomach contents, now rare, can be used to estimate the mass of different food categories consumed (for example, fruit, leaves, or insects); with care and skill, one can identify the species eaten (Booth, 1956; Fooden, 1964; Charles-Dominique, 1974; Gautier-Hion et al., 1980). However, because the animal must be killed, only a single measure per animal is obtained. An additional

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TABLE 1-5 Non-colobine Cercopithecine Feeding Ecology

Scientific Name	Common Name	Diet[a]	Behavior	Body Weight[b]	References
Omnivorous but predominantly frugivorous (depending on habitat)					
Macaca					
M. arctoides *M. assamensis*[c] *M. cyclopis* *M. maura*[c] *M. ochreata*[c] *M. radiata* *M. silenus* *M. tonkeana*[c]	Stump-tailed macaque Assamese macaque Formosan rock macaque Celebes moor macaque Booted macaque Bonnet macaque Lion-tailed macaque Tonkean macaque	Fruit and seeds, young leaves, flowers and buds, other plant parts, gums, grass, clover, sprouts, roots, bark, resin, animal prey (insects and vertebrates), fungus, raid crops/dumps; most species, little field work; *M. radiata* eat temple offerings	Diurnal, arboreal and terrestrial, multimale/ multifemale, some 1 male + multifemale, group size 5-50; *M. silenus*: rarely on ground, but swim, as do many macaques	3.69-8.5 kg females, 4.86-12 kg males	Bynum, 1994; Krishnamani, 1994; Kurup & Kumar, 1993; Kuruville, 1980; Leutenegger & Cheverud, 1982; Richard et al., 1989; Silva & Downing, 1995; Wolfheim, 1983
M. fascicularis *M. nemestrina* *M. nigra* *M. sinica*	Long-tailed or crab-eating macaque, or cynomolgus monkey Pig-tailed macaque Celebes or crested black macaque Toque macaque	Fruit 67% (2-100%); flowers and buds 3% (0-68%); leaves 12% (1-62%); bark, roots, pith and other 6% (0-73%); grass 1%; fungi, resins and other 2%; prey items 11% (0-46%); *M. fascicularis'* diet at one site was 51% temple offerings	Diurnal, arboreal and terrestrial, multimale/ multifemale, group size 10-90 individuals	*M. fascicularis, M. sinica*: 1.5-5.7 kg females, 3.9-8.39 kg males; *M. nemestrina, M. nigra*: 3.5-10.9 kg females, 6.2-14.5 kg males	Aldrich-Blake, 1980; Butynski, 1982; Caldecott, 1986a,b; Davies et al., 1983; Dittus, 1977; Hladik, 1975; Lucas & Corlett, 1991; MacKinnon & MacKinnon, 1980b; O'Brien & Kinnaird, 1997; Richard et al., 1989; Rodman, 1978; Silva & Downing, 1995; Sussman & Tattersall, 1981; Temerin et al., 1984; Ungar, 1995; Wheatley, 1982; 1987; Whitten & Whitten, 1982; Wolfheim, 1983; Yeager, 1996
M. fuscata	Japanese macaque	Fruit 47% (0-100%); flowers 5% (0-40%); leaves 22% (0-94%); herb/grass 6% (0-65%); roots, bark, twigs, and other 13% (0-95%); fungi, resins, and other 1% (0-18%); prey 9% (0-50%); winter diets high in seeds in cedar forest, high in winter buds in other habitats	Diurnal, arboreal and terrestrial, multimale/ multifemale group size 40-194 individuals	8.3-18.0 kg females, 11.0-18.0 kg males	Agetsuma, 1995a,b; Agetsuma & Nakagawa, 1998; Agetsuma & Noma, 1995; Hill, 1997; Iwamoto, 1982; Maruhashi, 1980; Nakagawa, 1997, 1989a; Suzuki, 1965
M. mulatta *M. sylvanus*	Rhesus macaque Barbary macaque	Fruit 24% (0-70%); flowers 5% (0-40%); leaves 47% (2-99%); bark, pith, roots, and other 11% (0-34%); herbs or grass 9%, (0-56%); fungi or sap 1%; prey 6% (0-66%); in some sites, *M. sylvanus* feed heavily on acorns and cedar leaves, cones, and cambium; *M. mulatta* eat temple offerings	Diurnal, multimale/ multifemale; *M. sylvanus*: group size 12-59 individuals; *M. mulatta*: group size 10-200 individuals	*M. sylvanus*: 10.2-11.2 kg females, 15.3-17.0 kg males; *M. mulatta*: 3.0-10.9 kg females, 5.08-10.9 kg males	Deag, 1983; Goldstein & Richard, 1989; Lindburg, 1977; Malik, 1986; Mehlman, 1988, 1989; Menard & Vallet, 1986; Richard, et al., 1989; Seth & Seth, 1986
M. thibetana	Tibetan macaque	Reproductive plant parts 35% (10-59%), ground-layer foods 22% (11-33%), leaves and other vegetative parts 43% (30-56%), prey not quantified; fed by humans near temples	Diurnal, mostly terrestrial, multimale/ multifemale	7.81-14.2 kg females, 10.7-13.0 kg males	Richard et al., 1989; Silva & Downing, 1995; Zhao & Deng, 1988; Zhao et al., 1991
Allenopithecus					
A. nigroviridis	Allen's swamp monkey	Fruit 81%; pith 2%; roots, flowers, nectar, animal prey (vertebrates and invertebrates) 17%; little studied	Diurnal, arboreal and terrestrial (swim), multimale/ multifemale, group size up to 40 individuals	3.7 kg female, 5.95 kg male	Gautier-Hion, 1988a,b; Zeeve, 1991
Cercocebus					
C. agilis[c] *C. galeritus* *C. torquatus* *C. torquatus atys*	Agile mangabey Tana river mangabey White-collared mangabey Sooty mangabey	Fruit 76% (14-100%); leaves 12% (0-83%); flowers and buds 1% (0-5%); other plant parts 4% (0-50%); prey 8% (0-22%)	Diurnal, arboreal and terrestrial, multimale/ multifemale, group size 14-95 individuals	4.7-5.47 kg females, 9.2 - 10.8 kg males	Davies et al., 1983; Fleagle, 1988; Gautier-Hion, 1978, 1983; Gautier-Hion et al., 1980; Homewood, 1978; Mitani, 1989, 1991; Napier, 1981; Quris, 1975; Ross, 1991; Silva & Downing, 1995; Waser, 1984; Wolfheim, 1983

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TABLE 1-5 *(continued)*

Cercopithecus					
C. campbelli	Campbell's guenon	Fruit (and seeds) 54.6-90%, animal prey 5.0-25%, leaves 6.0 -18.9%, flowers 3-6%, gums 1.9-2.8%, shoots, mushrooms, nectar; eat more leaves when fruit is scarce; raid crops; many species little studied	Diurnal, arboreal (*C. campbelli* most terrestrial of all the guenons); 1 male, multifemale; group size: *C. campbelli, C. hamlyni, C. preussi., C. solatus* 2-15; *C. erythrogaster, C. erythrotis, C. mona, C. petaurista, C. sclateri* 4-35; *C. sclateri* multimale/ multifemale	1.8-4.5 kg females, 2.4-7.0 kg males	Bourliere et al., 1970; Caldecott, 1986a; Colyn, 1994; Napier, 1981; Oates, 1985; Silva & Downing, 1995; Wolfheim, 1983
C. dryas[c]	Dryas guenon				
C. erythrogaster	White-throated guenon				
C. erythrotis	Red-eared guenon				
C. hamlyni	Owl-faced monkey				
C. mona	Mona monkey				
C. petaurista	Lesser spot-nosed guenon				
C. preussi[c]	Preuss's monkey				
C. sclateri	Sclater's guenon				
C. solatus[c]	Sun-tailed guenon				
C. ascanius	Red-tailed guenon	Fruit 67% (5-100%) (seed only 8%); leaves 15% (0-96%); flowers 4% (0-51%); bark, pith, and other 2% (0-30%), fungi 2% (0-39%), invertebrates 14% (0-45%); *C. mitis* eat bamboo; *C. pogonias* eat more prey when food is scarce; *C. mitis* in southern Africa: fruit 21%; leaves 27%; cambium, pith, twigs 46%; fungi 6%; invertebrates less than 1%	Diurnal; arboreal; 1 male-multifemale groups. (*C. neglectus*; some monogamous pairs); group size: *C. ascanius, C. cephus, C. neglectus*: 5-35; *C. mitis, C. nictitans*: 7-70; *C. pogonias, C. wolfi*: 1-19 individuals	*C. ascanius, C. cephus, C. pogonias, C. wolfi*: 2.4-3.4 kg females, 3.2-4.8 kg males; *C. mitis, C. neglectus, C. nictitans*: 2.7-8 kg females, 4-9.99 kg males	Beeson, 1989; Butynski, 1982, 1990; Colyn, 1994; Conklin et al., 1998; Cords, 1986, 1987; Gautier-Hion, 1978, 1980, 1983, 1988a; Gautier-Hion & Gautier, 1974, 1978, 1979; Gautier-Hion et al., 1980; Kaplin & Moermond, 1998; Kaplin et al., 1998; Lawes, 1991; Lawes et al., 1990, Moreno-Black & Maples, 1977; Napier, 1981; Rudran, 1978; Schlichte, 1978; Silva & Downing, 1995; Struhsaker, 1978b, 1980; Tutin et al. 1997; Wahome et al., 1993; Wolfheim, 1983; Wrangham et al., 1993
C. cephus	Mustached guenon				
C. mitis	Blue monkey				
C. neglectus	DeBrazza's monkey				
C. nicitans	Putty-nosed or greater spot-nosed guenon				
C. pogonias	Crowned guenon				
C. wolfi	Wolf's guenon				
C. diana	Diana monkey	Fruit 39%; leaves 10%; flowers and buds 12%; bark, pith, and so on 1%; fungi 10%; invertebrates 31%; some reports claim more fruit or leaf	Diurnal, arboreal, 1 male-multifemale, group size 5-50 individuals	4.3-7.1 kg	Oates & Whitesides, 1990; Ross, 1991; Silva & Downing, 1995; Wachter et al., 1997; Wolfheim, 1983
C. lhoesti	L'Hoest's monkey	Fruit 42% (22-80%), leaves 19%, herbs 35% (because are terrestrial), flowers 4%, prey 9%	Diurnal, terrestrial, somewhat arboreal, 1 male-multifemale, group size 5-17 individuals	3-4 kg females, 6-7 kg males	Colyn, 1994; Kaplin & Moermond, 1998; Silva & Downing, 1995; Wolfheim, 1983
Chlorocebus					
C. (Cercopithecus) aethiops	Vervet, grivet, green, or tantalus monkey	Fruit 46%; leaves 23% (more mature leaves than young); flowers and buds 10%; bark, twig, or pith 6%; fungi or gums 3%; grass 1%; prey 13%, raid crops; take handouts	Diurnal, terrestrial and arboreal; multimale/ multifemale, group size 5-76 individuals	1.5-5.23 kg females, 3.1-8 kg males	Butynski, 1982; Davies et al., 1983; Dunbar & Dunbar, 1974; Galat & Galat-Luong, 1977, 1978; Harrison, 1983, 1984; Kavanagh, 1978; Moreno-Black & Maple, 1977; Napier, 1981; Silva & Downing, 1995; Whitten, 1983, 1988; Wolfheim, 1983; Wrangham & Waterman, 1981
Erythrocebus					
E. patas	Patas monkey	Fruit 20% (5-34%); leaves 17% (6-27%); flowers and buds 36% (7-65%); stems, shoots and pith 3%; sap and gum 10%; prey 16% (except Kenya: fruit and seeds 6%, leaves 3%, flowers 7%, gum 39%, prey 43%).	Diurnal, mostly terrestrial, 1 male-multifemale, group size 5-34 individuals	4.08-7.1 kg females, 7.48-12.6 kg males	Isbell, 1998; Koster, 1985; Nakagawa, 1989b; Napier, 1981; Olson & Chism, 1984; Silva & Downing, 1995
Lophocebus					
L. (Cercocebus) albigena	Grey-cheeked mangabey	Fruit 69% (21-91%), up to 32% of which was figs; leaves 7% (0-65%); flowers and buds 4% (0-35%); bark, pith, or stems 3% (0-22%); other plant parts 1% (0-33%); prey 17% (2-44%); raid crops	Diurnal, arboreal, occasionally come to ground to drink, multimale/ multifemale, group size 6-28 individuals	*L. albigena*: 5.4-6.4 kg females, 6.8-8.98 kg males; *L. aterrimus*: 13.0-18.0 kg females, 21.0 kg male	Conklin-Brittain et al., 1998; Davies et al., 1983; Freeland, 1979; Gautier-Hion, 1977, 1978, 1983; Gautier-Hion et al., 1980; Horn, 1987; Mitani, 1991; Napier, 1981; Olupot et al., 1997; Olupot, 1998; Silva & Downing, 1995; Struhsaker, 1978b; Tutin et al., 1997; Waser, 1975, 1977, 1984
L. aterrimus	Black mangabey				

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TABLE 1-5 *(continued)*

Mandrillus					
M. leucophaeus *M. sphinx*	Drill Mandrill	Fruit 71% (42-99%); leaves 9%; flowers 4% (0-47%); stems, pith, or bark 5%; sap or gum 3%(0-26%); fungi 3% (0-52%); grass or crops 3% (0-23%); prey 6% (0-27%); roots; mandrills are seed predators and raid crops	Diurnal, arboreal and largely terrestrial; *M. leucophaeus* 1 male, multifemale (up to 20), group size 14-179; *M. sphinx* multimale/ multifemale	*M. leucophaeus*: 6.9-10.0 kg females, 17.0 kg male; *M. sphinx*: 11.5 kg female, 26.9 kg male	Fleagle, 1988; Gautier-Hion, 1978; Gautier-Hion et al., 1980; Harvey et al., 1987; Hoshino, 1985; Jouventin, 1975; Lahm, 1986; Norris, 1988; Rogers et al., 1996; Tutin et al., 1997; Wolfheim, 1983
Miopithecus					
M. talapoin	Dwarf guenon or southern talapoin monkey	Fruit 52% (0-90%); leaves and shoots 5% (0-22%); flowers 2%; stems, pith or bark 4% (0-10%); grass or crops 8% (0-80%); prey 35% (0-50%); fungus; raid crops	Diurnal, arboreal, swim, multimale/ multifemale, group size 60 to 112 individuals	0.745-1.12 kg females, 1.0-1.38 kg males	Butynski, 1982; Gautier-Hion, 1971, 1973, 1988a; Gautier-Hion et al., 1980; Gonzalez-Kirchner, 1994; Napier, 1981; Wrangham et al., 1993
Papio hamadryas					
P. h. anubis *P. h. cynocephalus* *P. h. papio* *P. h. ursinus*	Olive baboon Yellow baboon Guinea baboon Chacma baboon	Fruit and seeds 46% (0-86%); grass, sedge, herb 16% (0-97%); corms or roots 10% (0-85%); tree leaves 10% (0-61%); flowers 8% (0-27%); exudates or sap 4% (0-15%); other plant parts 6% (0-19%); prey 7% (0-72%); raid farms; beg from tourists; *P. h. ursinus* near sea eat crab	Diurnal, mostly terrestrial, part arboreal; multimale/ multifemale group size 7-200; *P. h. papio*: rudimentary fission-fusion	7.9-18.6 kg females, 14.1-43.6 kg males	Butynski, 1982; Byrne et al., 1993; Dunbar & Dunbar, 1974; Hamilton et al., 1978; Harding, 1976; Harvey et al., 1987; Moreno-Black & Maples, 1977; Napier, 1981; Norton et al., 1987; Post, 1982; Rhine et al., 1989; Ross, 1991; Rowell, 1966; Silva & Downing, 1995; Stacey, 1986; Whiten et al., 1990; Wolfheim, 1983
Exceptional Diets					
Papio hamadryas hamadryas	Hamadryas baboon (5 subspecies)	Only one study found quantifying diet: fruit or pods with seeds 44%, fig fruit 13%, grass seeds 6%, grass plants 17%, leaves 10%, flowers 6%, roots 5%; prey consumption not quantified	Diurnal, terrestrial, fission-fusion, 1 male + multifemales, group size foraging 25-38, troops up to 750	12.0 kg female, 21.3 kg male	Boug et al., 1994; Fleagle, 1988; Wolfheim, 1983
Theropithecus gelada	Gelada baboon	Grass leaves 62% (0-93%), grass root or stem 13% (0-67%), grass seed 13% (0-70%), fruit 3% (0-7%), tree leaves 6% (0-62%), herbs and flowers 2% (0-8%), other roots or bulbs 1% (0-3%), prey 0.1%; raid crops	Diurnal, terrestrial, multimale/ multifemale; group size: 3-20 reproductive unit, band 30-300	11.7-13.6 kg females, 20.0 kg male	Dunbar & Dunbar, 1974; Dunbar, 1976, 1977; Fleagle, 1988; Iwamoto, 1979; Napier, 1981; Silva & Downing, 1995; Stammbach, 1987

[a] Diet format: mean (range).
[b] Body weights in ranges whenever possible; single numbers are not averages but indicate that only one individual of the species has been weighed in the wild.
[c] No data available from the wild but assumed to be similar to congenerics.

limitation is the bias introduced by persistence of fibrous items compared with more easily digested foods.

FECAL ANALYSIS

Recognizing cell structures of different plants in feces and identifying them, even to the genus level, requires considerable microscope training. Most researchers send fecal samples to specialized laboratories for plant identification (Moreno-Black 1978). Fecal analysis has been used effectively in studying the feeding ecology of the nocturnal galagos (Nash, 1983; Harcourt 1984) and some cercopithecines (Moreno-Black and Maples, 1977). Tutin et al. (1991), and Tutin and Fernandez (1993), studying lowland gorillas, used a macroscopic method to evaluate feces, looking for seeds and fibrous material. However, fecal analysis has the same limitation as does analysis of stomach contents: that is, the items that persist tend to be fibrous, whereas the more easily digested foods leave no trace.

FOOD REMNANTS

This method often is used in combination with fecal analysis or visual observation. It is useful when the animal

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TABLE 1-6 Ape Feeding Ecology

Scientific Name	Common Name	Diet[a]	Behavior	Body Weight[b]	References
The Small Apes					
Hylobates					
H. (Bunopithecus) hoolock	Hoolock or white-browed gibbon	All fruit 72% (38-100%) (30% is fig), flowers 6% (0-24%); leaves (and shoots, petiole, and other 15% (0-62%) (mostly young leaves), prey 7% (0-25%); honey; leaf galls	Diurnal, arboreal, monogamous with offspring, group size 2-12	4.4-8.6 kg females, 4.5-10 kg males	Ahsan, 1994; Aldrich-Blake, 1980; Alfred, 1992; Choudhury, 1990; Ellefson, 1974; Gittins, 1982; Islam & Feeroz, 1992; Leutenegger & Cheverud, 1982; MacKinnon & MacKinnon, 1980a, 1980b; Mitani, 1990; Mukhergee, 1986; Palombit, 1997; Raemaekers, 1978, 1979, 1984; Roonwal & Mohnot, 1977; Silva & Downing, 1995; Ungar, 1995; Whitten, 1982, 1984; Wolfheim, 1983
H. agilis	Dark-handed or agile gibbon				
H. klossii	Kloss's gibbon				
H. lar	White-handed gibbon				
H. pileatus	Pileated or capped gibbon				
H. (Nomascus) gabriellae[c]	Golden-cheeked gibbon				
H. (Nomascus) leucogenys[c]	Chinese white-cheeked gibbon				
H. moloch	Silvery Javan gibbon	Fruit 60% (range 56-62%), flowers 2% (0-4%), leaves 37% (32-44%), prey 1% (0-2%)	Same	5-8 kg	Kappeler, 1984; Leighton, 1987; Robbins et al., 1991; Rodman, 1978; Silva & Downing, 1995
H. muelleri	Mueller's Bornean gibbon				
H. (Nomascus) concolor	Black gibbon	Fruits 21%, flowers 7%, leaves 11%, leaf buds and shoots 61%, bamboo	Same	4.5-9 kg	Lan, 1993; Liu et al., 1989; Sheeran, 1993; Sheeran & Mootnick, 1995; Yang & Zuu, 1990
H.(Symphalangus) syndactylus	Siamang	Fruit 40% (6-59%) (figs are 28%), flowers 6% (0-32%), leaves 49% (24-70%) (42% young leaves), prey 5%	Same	9-11.14 kg females, 10.4-14.77 kg males	Aldrich-Blake, 1980; Chivers, 1974, 1977; Chivers et al., 1975; Curtin & Chivers, 1978; MacKinnon & MacKinnon, 1978, 1980b; Palombit, 1997; Raemaekers, 1978, 1979, 1984; Silva & Downing, 1995
The Great Apes					
Pongo					
P. abelii	Sumatran orangutan	Fruit 74% (22-98%) (seeds were 26% in the fruit category), leaves and shoots 15% (7-42%), bark and wood 4% (0-16%), insects 5% (0-40%, includes search time), other (including flowers) 2%, eat succulent fruits and large fruits with hard husk	Diurnal, arboreal mostly, males solitary, females travel with offspring, group size 1-3 individuals	33-45 kg females, 75-91 kg males	MacKinnon, 1974; Rijksen, 1978 ; Ungar, 1995; Wolfheim, 1983
P. pygmaeus	Borneo orangutan	Fruit 62% (0-100%), flowers 4% (0-60%), leaves and shoots 19% (0-77%), pith 1% (0-22%), bark and wood 11% (0-73%), insects 2% (0-27%), other 3% (0-41%)	Same	33-45 kg females, 75-91 kg males	Hamilton & Galdikas, 1994, Galdikas & Teleki, 1981; Knott, 1999, 1998, 1996; Leighton, 1993; MacKinnon, 1974; Rodman, 1977, 1978, 1988; Silva & Downing, 1995; Suzuki, 1994; Wheatley, 1982
Gorilla gorilla					
G. g. beringei	Mountain gorilla	Pith, shoots, leaves and stems of herbs and shrubs 91% (range 85-96%); wood or bark 2% (0-7%) roots 1% (0-4%); flowers 2% (0-3%); fruit 1% (0-2%); dung 0.5% (0-2%); prey 1% (0-1%); fungus and miscellaneous 2% (0-5%)	1 male (occasionally 2), multifemale group size about 9 individuals	83-98 kg females, 159-278 kg males	Fossey, 1974; Fossey & Harcourt, 1977; Goodall, 1977; Silva & Downing, 1995; Vedder, 1984; Watts, 1984, 1996; Wolfheim, 1983
G. g. gorilla	Western lowland gorilla	Pith, shoots, and stems of herbs and shrubs 17% (7-43%); leaves 21% (6-34%); bark 5% (0-32%); roots 1% (0-4%); flowers 1% (0-6%); seeds 4% (1-13%); fruit 48% (17-68%); prey 1% (0-4%); miscellaneous 2% (0-11%)	Diurnal, terrestrial, some arboreal; 1 male, multifemale; group size 3-21	72 kg female, 139-170 kg males	Kuroda, 1992; Kuroda et al., 1996, Nishihara, 1992, 1995; Remis, 1995, 1997; Rodgers et al., 1990; Sabater Pi, 1966, 1977; Tutin 1996; Tutin et al., 1984, 1991, 1997; Tutin & Fernandez, 1993; Williamson et al., 1990

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TABLE 1-6 *(continued)*

G. g. graueri	Eastern lowland gorilla	Pith, shoots, and stems of herbs and shrubs 19% (11-33%), leaves 41% (17-51%), bark 13% (0-29%), root 2% (0-5%), flowers 2% (0-3%), fruit 23% (9-47%), miscellaneous 1% (0-29%)	Diurnal, arboreal and terrestrial, 1 male, multifemale group	71-75 kg females, 140-168 kg males	Casimir, 1975; Goodall, 1977; Silva & Downing, 1995; Yamagiwa et al., 1992, 1994, 1996
Pan					
P. paniscus	Bonobo or pygmy chimpanzee	Fruit 52% (1-100%), flower 2% (0-7%), seed 3% (0-6%), leaves 14% (0-28%), terrestrial herbaceous vegetation 24% (0-55%), bark or root 2% (0-11%), prey 2% (0-3%), fungus, honey; do not hunt or eat monkeys	Diurnal, arboreal and terrestrial, multimale/ multifemale group size 6-15 foraging parties, communities 50-120 individuals	31-34 kg females, 39 kg male	Badrian et al., 1981; Badrian & Malenky, 1984; Hashimoto et al., 1998; Kano, 1983; Kano & Mulavwa, 1984; Malenky & Stiles, 1991; Nishida a & Hiraiwa-Hasegawa, 1987; Silva & Downing, 1995; Uehara, 1990; Wolfheim, 1983
P. troglodytes	Chimpanzee	Fruit 64% (19-99%), seeds 3% (0-30%); flowers 2% (0-18%), leaves 16% (0-56%) (mostly young), pith, stem, and stalk 7% (0-27%), bark/ cambium 2% (0-26%), gum, gall, root, wood, fungus, miscellaneous 2% (0-41%), and all prey items 4% (0-28%); will eat monkeys	Diurnal; arboreal and terrestrial; multimale/ multifemale group size 7-25 females, 5-16 males, fission-fusion	32-68 kg females, 40-80 kg males	Conklin-Brittain et al., 1998; Galdikas & Teleki, 1981; Ghiglieri, 1984; Goodall, 1996; Hladik, 1973, 1977; Isabirye-Basuta, 1989; Kuroda, 1992; Kuroda, et al., 1996; Matsumoto-Oda & Hayashi, 1999; McGrew et al., 1981; Newton-Fisher, 1999; Peters & O'Brien, 1981; Sabater-Pi, 1979; Sugiyama & Koman, 1987; Suzuki, 1969; Tutin & Fernandez, 1993; Tutin et al., 1984, 1991, 1997; van Lanwick-Goodall, 1968; Wrangham, 1977; Wrangham et al., 1998; Yamagiwa et al., 1992

[a] Diet format: mean (range).
[b] Body weights in ranges whenever possible; single numbers are not averages but indicate that only one individual of the species has been weighed in the wild.
[c] No data available from the wild but assumed to be similar to congenerics.

is not directly visible but the researcher is close enough to identify the species on which it is feeding. When the animal has moved on, the feeding location can be investigated and food remnants characterized (Tutin et al., 1991, Tutin and Fernandez, 1993; Rogers et al., 1996).

Reporting Feeding Behavior

Once collected, feeding-behavior data may be reported in various ways. The following are some examples.

FEEDING TIME

Feeding time may be reported as a percentage of all daily activities or as a percentage of feeding time. For example, 35% of the day might be spent in foraging for insects, 19% feeding on plants, 25% in traveling, and the remainder in other activities. Within the time spent on plants, 60% of it may have been on fruit, 40% on leaves.

MASS OF FOOD AS PERCENTAGE OF TOTAL DIET MASS

The contribution that each food category makes to the total diet in mass terms may be expressed as a percentage of dry weight or of wet weight. The estimated grams consumed of each type of food may also be reported.

Feeding-Ecology Tables

The feeding ecology of all extant primates that have been studied is summarized in Tables 1-1 through 1-6. The data in these tables were derived from studies that used nearly all the above methods. Although the methods varied, grand averages (with ranges in parentheses) were calculated because no correction factors have been developed to make data gathered with different methods comparable. We assumed that the predominant food items (such as fruits, leaves, and insects) would remain predominant regardless of the method used and that the variability in diets due to habitat and seasonal differences would overwhelm most differences due to methods. Studies of some

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primate species did not report percentages of different foods in the diet but provided only a food list and general food preferences. A few studies lasted 3-6 months, but most lasted a year or more.

The feeding-ecology data provide only general guidelines for captive-diet formulation, and the proportions of foods in wild diets, as measured, should not be taken literally. Some seasonal extremes in food choices represent selections based on necessity, not on preference. Most primates can survive for a few weeks or months on an extreme diet; otherwise, they could not survive seasonal changes in food supply. However, primates are more likely to flourish on diets that are matched to their gastrointestinal systems and thus are typical for their species.

PLANT-FEEDING STRATEGIES

Classification of primates on the basis of feeding strategies, such as folivory or frugivory, seems straightforward and rational. However, it is clear from the tabular data that young leaves, mature leaves, petioles, shoots, and other plant parts are eaten with various degrees of preference. Fruit-eaters sometimes consume only the pulp and spit out the seed, or they might consume the whole fruit and digest the pulp and seeds or pass the seeds intact in the feces. Some fruit is consumed only for the seeds, and the pulp and pod or husk are discarded. Gummivores (gum-eaters and sap-eaters) tend to feed heavily on one or a few species of trees. Reproduction of gummivore diets is facilitated by information on the chemistry of the preferred exudates.

INSECT FORAGING AND FEEDING

Some primates specialize on immature insect forms (grubs, caterpillars, and larvae) rather than adult insects. Many primates, however, do not specialize. The nutritional value of insects and the issue of foraging time versus capture rate are elements of feeding ecology in need of much more study. There is little information on the chemical composition of insects, although larval forms are commonly assumed to be high in fat and adults high in protein. Many adult insects have a chitinous exoskeleton, and chitin contains nitrogen, but the effect on estimates of concentration of usable protein is often ignored (Oyarzun et al., 1996). In addition, most chemical-composition data have been generated in studies of temperate, rather than tropical, insects (Redford and Dorea, 1984; Studier and Sevick, 1992).

In the contribution of invertebrates to the total diet of a primate, foraging time versus capture rate is critical. Janson and Boinski (1992) reported that insect capture by *Saimiri* spp. was successful in 61% of total insect-foraging time; *Cebus* spp. had a capture rate of 38-42% of total insect-foraging time. Wright (1985, 1989) concluded that the insect-capture rate for *Callicebus brunneus* must be low inasmuch as the animals spent 15% of their foraging time searching for insects, but only 15% of their feces contained insect parts. Indigestible insect parts in the feces tend to overrepresent insects as a dietary item, so it appeared that the proportion of insect foraging time resulting in successful capture was limited.

Egler (1992) found that 59.1% of total food-foraging and feeding time of tamarins (*Saguinus bicolor*) was spent foraging for insects (14.3% of total daily activities), but only 5.4% of insect-foraging time resulted in successful capture and consumption of prey; thus, the fraction of total food-foraging and feeding time spent in eating insects was 3.2% (5.4% of 59.1%). Foraging for and feeding on plants are basically identical, considering how most plant-foraging and feeding data are collected. Assuming that the time spent in foraging for plants was identical with the time spent in feeding on plants (reported by Egler as 9.9% of total daily activities), then 24.2% (14.3% + 9.9%) would be the fraction of total daily activities devoted to foraging and feeding. However, if only 3.2% of total food-foraging and feeding time was spent in eating insects, then only 0.8% (3.2 % of 24.2%) of the total day was devoted to this activity. Adding the percentages of the day devoted to eating plants (9.9%) and to eating insects (0.8%) and dividing the latter by the total (10.7%) yields a fraction of 7.5% of total feeding time spent in eating insects (instead of 59.1%), leaving 92.5% of feeding time spent in eating plants (instead of 40.9%). However, the insects that the tamarins hunted were very large, perhaps a whole meal by themselves. This situation creates an interesting question: How does the size of the insect meal relate to the mass of plant material consumed? It is clear that the mass of each food item consumed would provide a more accurate measure of the composition of the natural diet than would timed records of foraging and feeding activity. The data in Tables 1-1 through 1-6 have not been adjusted for insect-capture rate, because for the vast majority of primates these rates are not known.

ADDITIONAL CONSIDERATIONS

As previously stated, the percentage of time spent in feeding is probably the most common factor used in describing a primate diet, but if foraging time is included as eating time, it can be inflated (Kurland and Gaulin, 1987). In addition, a measure based on grams consumed would be sometimes more accurate than time spent in feeding. To estimate grams consumed, one needs to determine, for example, how many fruits are eaten in an hour (or a feeding bout), what portion of the fruit is consumed, and how much the consumed portion weighs. The weight of seeds may or may not be included, depending on whether they are digested.

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Because foods vary greatly in their water content, dry weights are more useful indicators of nutrient intake than wet weights and allow more accurate comparisons among studies. Daily dry-matter intakes can be calculated by multiplying the grams of dry matter consumed per hour or per feeding bout by the hours or feeding bouts per day. That yields a good estimate of total dry matter consumed. If the time spent in eating is clearly separated from foraging time, the total time spent in feeding on a given food and the total dry matter taken in from eating that food tend to lead to the same answer (Knott, 1999).

Total dry matter consumed, however, is still not the best method for evaluating usable energy and nutrient intake, because losses during digestion are not considered. Ideally, the diet should be analyzed for fiber components, partly or mostly indigestible fractions of dry matter, depending on the consuming species (see Chapter 3, "Carbohydrates and Fiber"). If laboratory support is available, data on gross energy and nutrient concentrations in natural foods are additional useful measures. However, gathering such data is extremely time-consuming, expensive, and in some field situations almost impossible. For many small, fast-moving, and unhabituated arboreal primates, it is extremely difficult to collect all the needed bits of information. The percentage of time spent in feeding on particluar items is often as good a measure as is realistically possible to determine.

The designation of the different feeding strategies (folivory, frugivory, insectivory, and gummivory) is based on the food category with the highest percentage of use (Chapman, 1987). Seasonal differences can make a normally frugivorous species appear folivorous and vice versa (Chapman and Chapman, 1990). Many primates exploit a small number of plant species heavily but sample small amounts of many species (Hladik et al., 1971; Glander, 1975; Smith, 1977; Chapman, 1988). Insectivory and gummivory are two feeding strategies predominantly of very small primates. *Tarsius* are small and can survive by eating only insects. *Saimiri* (the second commonest experimental primate but not well studied in the wild) is the smallest cebid and the most insectivorous. Some prosimians and most *Callithrix*, are small and can survive by eating mostly gums. The cercopithecines have been separated into two groups, colobine (Table 1-4) and noncolobine (Table 1-5). All colobines are foregut fermenters and are folivorous or granivorous (seed-eating). The noncolobine cercopithicines are hindgut fermenters and are generally more omnivorous.

HOW TO USE THIS INFORMATION

Considering the different methods and circumstances under which feeding-ecology data are collected, the information gathered will be variable in quality and subject to potential errors. The various data collection systems are described in this chapter, and the reader is urged to identify the system used in gathering the data of interest and to use personal judgement in interpretation of their applicability. Feeding-ecology data can be used to evaluate the appropriateness of a captive diet but do not provide a basis for setting quantitative nutrient requirements. They are used to classify primate species as primarily granivorous, folivorous, omnivorous, gummivorous, or insectivorous and provide guidance to food preferences and to probable qualitative and roughly quantitative nutrient needs. For example, leaves are generally higher in protein (dry basis) than are fruit, although wild fruits are much higher in protein than are fruits cultivated for human use (Conklin-Brittain et al., 1998, 1999, 2002). Consequently, folivores generally consume a diet higher in protein than do frugivores. An even more important consideration might be the presence of physical factors, such as fiber, in the natural foods of folivores and the effects these factors have on digestive function and health. Thus, evidence from feeding ecology studies and controlled research with captive primates has been used to develop the proposed dietary fiber concentrations shown in Chapter 3.

Many primate species consume diversified, omnivorous diets. Most of the primates that are routinely used in research fall into this category, in part because their diverse and omnivorous diet seems to make them more adaptable, and they are easier to keep in captivity than are more specialized species. For species that are rarely kept successfully in captivity, a close examination of their feeding ecology may be helpful in formulating a diet that is most appropriate for them. The folivorous monkeys pose a particular problem, and only recently have research trials begun to identify those combinations of formulated complete diets and cultivated foods that can substitute for their normal wild diet.

DIGESTIVE STRATEGIES

The primary function of the digestive system is to extract energy and essential nutrients from an animal's environment in support of metabolic processes. Performing that function requires a series of physical and chemical steps that are related to the anatomy of the digestive system. The primary significance of gut structure is related to its effect on food selection and processing (Clemens and Phillips, 1980). Specialized structures are involved in food acquisition, ingestion, maceration, deglutition, and digestion. Secretions from the salivary glands, stomach, pancreas, liver, and intestinal tract provide lubrication and enzymes in a watery medium with a pH that is optimal for digestion. Symbiotic microorganisms in the foregut or hindgut of some animals provide energy and nutrients by degrading structural carbohydrates that are unaffected by endogenous enzymes and by synthesizing amino acids and

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vitamins that are essential to their host. It is common for different orders of mammals to have different gastrointestinal tract specializations, but primates are unique among mammals in having diverse digestive tract arrangements within their own order (Chivers and Hladik, 1980).

Faunivores

The digestive systems of primates that consume animal material are typically simpler and shorter than those of plant-eating species. The basic gastrointestinal tract of faunivores includes a simple globular stomach, a tortuous small intestine, a short conical cecum, and a simple smooth-walled colon (Chivers and Hladik, 1980).

Primate faunivores, which tend to be small and nocturnal, feed primarily on invertebrates but can supplement their diet with plant materials. The diet of the angwantibo (*Arctocebus calabarenis*) consists of animal prey (85%) and fruits (15%). Similarly, *Galago senegalensis*, *Microcebus* spp., and *Loris tardigradus* are highly insectivorous, although *Galago* and *Microcebus* supplement their diet with gums and other plant exudates. The tarsiers (*Tarsius* spp.) are principally insectivorous, but they also eat such small vertebrates as geckos and other lizards (Napier and Napier, 1985).

Galago has a balloon-like stomach, a relatively short small intestine, a moderate-size cecum, and a smooth, noncomplex colon (Clemens, 1980). The gastrointestinal tract of *Tarsius* includes a colon that is about one-fifth as long as the small intestine and a spiral cecum that is half as long as the colon (Figure 1-1).

Frugivores

Most primates are frugivorous, but none consume diets entirely of fruit. Fruit intake is augmented with variable proportions of invertebrates, vertebrates, and other plant parts, including leaves, flowers, and exudates. The gastrointestinal tracts of primates in this broad group exhibit little structural specialization, but variations among species have been described (Chivers and Hladik, 1980).

The basic frugivorous stomach is simple and globular (Hill, 1958). The marmoset stomach has a more elongated fundus than that of cebids, which is more specialized, with a globular fundus, conical body, and cylindrical pylorus (Chivers and Hladik, 1980).

Squirrel monkeys (*Saimiri*), douroucoulis (*Aotus*), woolly monkeys (*Lagothrix*), and spider monkeys (*Ateles*) have gastrointestinal tracts comparable with those of other frugivores (Figures 1-2 through 1-4), but in most of these species, the proximal portion of the colon is expanded and haustrated along its entire length (Hill, 1960; Hill and Rewell, 1948; Stevens and Hume, 1995). The cecum itself is not haustrated (Stevens and Hume, 1995).

Marmosets (*Callithrix* spp.) and tamarins (*Saguinus* spp., *Leontopithecus* spp.), as well as *Saimiri* and *Aotus*, have similar diets in the wild; fruits make up the majority of foods consumed, with invertebrate prey about 20%. The larger-bodied *Lagothrix* and *Ateles* consume diets composed mainly of fruit, with various proportions of leaves and seeds. Both *Cebuella* and *Callithrix* have a "short-tusked" tooth pattern in which the lower canines are incisiform and barely longer than the adjacent incisors; such dentition enables these species to create holes in bark to extract plant exudates (sap and gums) (Izawa, 1975).

Cercopithecine primates, except colobines, have cheek pouches that permit short-term storage of harvested ingesta. The stomach of these species (*Cercopithecus*, *Macaca*, and *Papio*) is relatively simple and smooth-walled, followed by a short small intestine (Figures 1-5 through 1-7). The cecum is typically haustrated by three taeniae, and can support some microbial breakdown of plant material. The galago (*Galago crassicaudatus*) (Figure 1-8) and the ruffed lemur (*Varecia variegata*) are prosimians that have a prominent cecum, but the cecum of the ruffed lemur is longer and more complex than that of the galago. The cecum of the vervet monkey (*Cercopithecus pygerythrus*) is sacculated (Clemens, 1980).

The enlargement of the colon or cecum in gibbons (*Hylobates* spp.), rhesus macaques (*Macaca mulatta*), Syke's monkeys (*Cercopithecus mitis*), and vervet monkeys (*Cercopithecus aethiops*) is consistent with bacterial fermentation of leaf material in the diet (Sakaguchi et al., 1991; Bruorton et al., 1991). When they are fed identical diets, the production of volatile fatty acids (VFAs, end products of microbial fermentation) in the hindgut of the more omnivorous (Morris and Goodall, 1977) baboon (*Papio cynocephalus*) (Clemens and Phillips, 1980) is similar to that in the hindgut of the largely herbivorous Syke's monkey (*Cercopithecus mitis*) (Hill, 1966).

The rates of digesta passage among frugivorous primates depend on proportions of fruit, leaf, and animal prey in the diet. Three groups of frugivorous lemurs—*Varecia variegata variegata*, *Varecia v. rubra*, and *Lemur catta*—fed a similar, mixed-ingredient diet exhibited median gut passage times of 1.71, 1.69, and 4.75 hours, respectively (Cabre-Vent and Feistner, 1995). Slightly longer mean transit times (2.7 hours) were reported for *Varecia v. variegata* and *V. v. rubra* fed experimental diets containing 15% and 30% acid detergent fiber (Edwards and Ullrey, 1999a).

Fiber type, not concentration, reduced passage time from 10 to 6 hours in *Callithrix jachus* and *Saguinus fuscicollis* (Krombach et al., 1984). Fiber concentration in diets consumed by macaques had no effect on the mean transit time of either particulate or liquid markers (Sakaguchi et al., 1991).

Baboons (*Papio cynocephalus*) had shorter mean transit times than Syke's monkeys (*Cercopithecus mitis*), when

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Primate Gastrointestinal Tracts

FIGURE 1-1 Tarsier

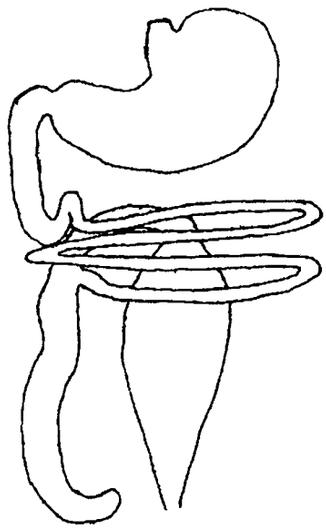

FIGURE 1-2 Squirrel Monkey

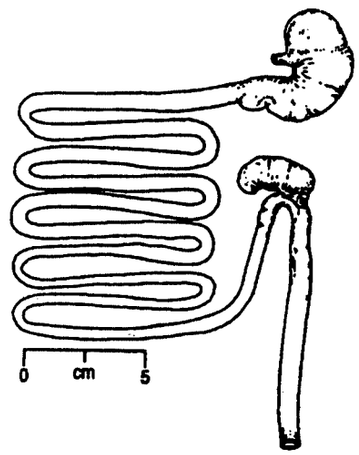

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FIGURE 1-3 Night Monkey

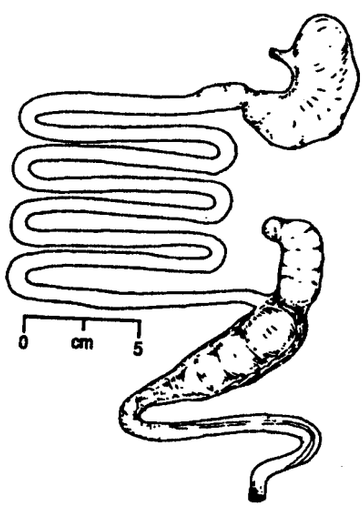

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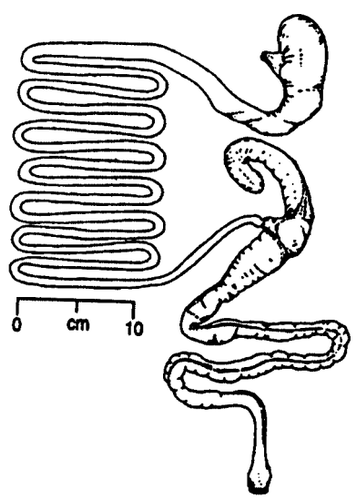
FIGURE 1-4 Woolly Monkey



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Primate Gastrointestinal Tracts

FIGURE 1-5 Vervet Monkey

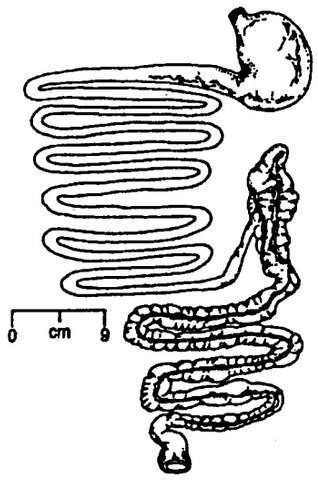

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FIGURE 1-6 Macaque

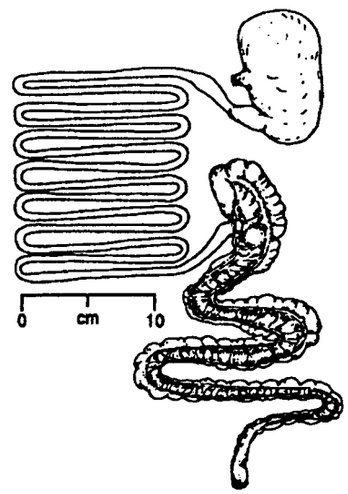

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FIGURE 1-7 Baboon

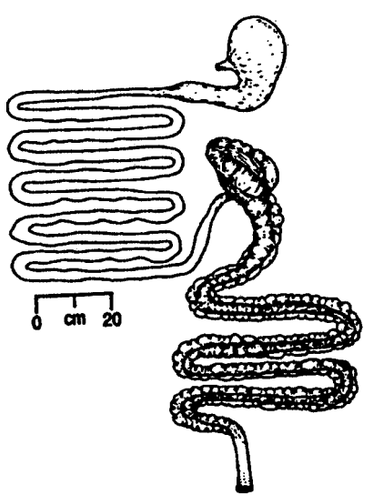

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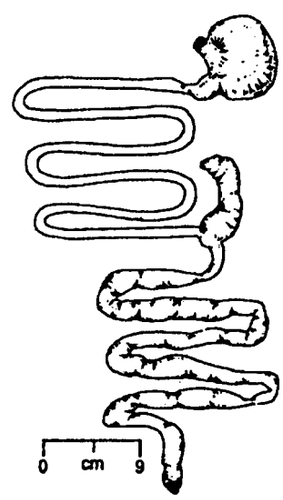
FIGURE 1-8 Bush Baby



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fed the same diet, for both fluid markers (35.0 vs. 39.9 hours) and 10-mm particulate markers (39.6 vs. 48.0 hours) (Clemens and Phillips, 1980). The mean transit times for the same diet fed to vervet monkeys (*Cercopithecus aethiops*) and the more insectivorous bushbaby (*Otolemur crassicaudatus*) were about 30 and 12 hours, respectively (Clemens, 1980).

Folivores

Primate folivores have a variety of physical adaptations that promote, through symbiotic microbial fermentation and mechanical action, the degradation of the structural and chemical defenses of plants. The two principal adaptations involve enlargements of the stomach or the hindgut to accommodate microbial fermentation (Parra, 1978; Langer, 1988). The extent of gastrointestinal tract modification is related to the proportions of plant parts (leaves, seeds, and fruits) consumed.

Members of the subfamily Colobinae have capacious and morphologically complex adaptations of the foregut, providing a primary site of microbial activity (Bauchop and Martucci, 1968; Caton, 1998; Kuhn, 1964). Colobines can be further divided into two large groups on the basis of the presence (quadripartite) or absence (tripartite) of a presaccus that can act as a preliminary storage compartment proximal to the principal region of fermentation (saccus) (Table 1-7). The tubus gastricus and pars pylorica are distal to the saccus. This arrangement allows the separation of ingesta between more neutral or alkaline (proximal) and acidic (distal) environments, supporting microbial fermentation in advance of gastric and enzymatic digestion. Anaerobic cellulolytic bacteria and other microbial symbionts in the saccus produce enzymes that degrade plant cell walls and promote access to the cellular contents. Thus, these species exhibit evolutionary convergence with ruminants in their adaptations of foregut structure for herbivory (Moir, 1968). As previously noted, in contrast with more-omnivorous cercopithecine primates, the colobines lack cheek pouches (Stevens and Hume, 1995).

TABLE 1-7 Form of Foregut in Genera of Subfamily Colobinae

Form of Foregut	Genus	Source
Presaccus absent (tripartite)	*Colobus*	Polack, 1908; Stevens and Hume, 1995
	Semnopithecus	Ayer, 1948
	Trachypithecus	Otto, 1835; Kuhn, 1964
	Presbytis	Caton, 1990
Presaccus present (quadripartite)	*Procolobus*	Hill, 1952; Kuhn, 1964
	Rhinopithecus	Ye et al., 1983
	Pygathrix	Edwards, 1995; Höllihn, 1971; Pilliet and Boulart, 1898
	Nasalis	Höllihn, 1971; Langer, 1988; Martin, 1837

The large sacculated forestomach of Asian colobines (such as *Trachypithecus*, *Presbytis*, and *Pygathrix*) includes a gastric canal in the presaccus, which might be analogous to the reticular groove in ruminants that shunts highly digestible milk, consumed during suckling, past the sites of fermentation to the distal portion of the stomach (Figure 1-9).

The small and large intestines of Asian colobines are about eight and two times body length, respectively. The cecum, serving as a secondary site of microbial fermentation, is one-fourth body length (Stevens and Hume, 1995).

Although the gastrointestinal tract of African colobines such as *Colobus* and *Procolobus* (Figure 1-10) is generally similar to that of Asian colobines, the small and large intestines are shorter, and the cecum is less well developed (Stevens and Hume, 1995). There is no evidence of rumination (regurgitation and chewing of a food bolus) in any colobine primate (Owen, 1835).

Several primate species exhibit hindgut fermentation, again reflecting the contribution of less-digestible plant materials in the natural diet. In these species, the symbiotic microorganisms occupy enlarged areas distal to the gastric and enzymatic sites of digestion. Quantitative recovery of nutrients produced by fermentation is not as high as in foregut fermenters (Edwards and Ullrey, 1999b).

The large intestine is enlarged in prosimians that feed on leaves or gums, both of which require microbial fermentation for digestion, and the cecum is elongated in *Lepilemur*, *Phaner*, *Euoticus*, and *Indri* (Chivers and Hladik, 1980).

The diet of the nocturnal sportive lemur (*Lepilemur mustelinus*) consists of flowers and leaves. This species practices coprophagy (ingestion of fecal material), which increases the recovery of nutrients from the relatively indigestible diet (Napier and Napier, 1985).

All great apes exhibit hindgut modification. The chimpanzee colon is haustrated by three taeniae over its length; the taeniae continue along the cecum and terminate in a vermiform appendix (Figure 1-11) (Stevens and Hume, 1995). The gastrointestinal tract of the gorilla is similar to that of the chimpanzee, although the small intestine is relatively long and the hindgut is more voluminous, indicative of its highly herbivorous diet. The small intestine and colon of the orangutan are longer than those of the chimpanzee, with an expanded proximal segment (Figure 1-12). The gastrointestinal tract of the gibbon is similar to that of other apes, although the colon is shorter. For purposes of comparison, the gastrointestinal tract of the adult human is shown in Figure 1-14.

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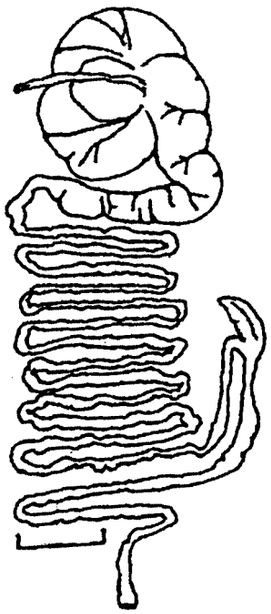
Primate Gastrointestinal Tracts

FIGURE 1-9 Northern Douc Langur



Edwards, 1995

FIGURE 1-10 Colobus Monkey

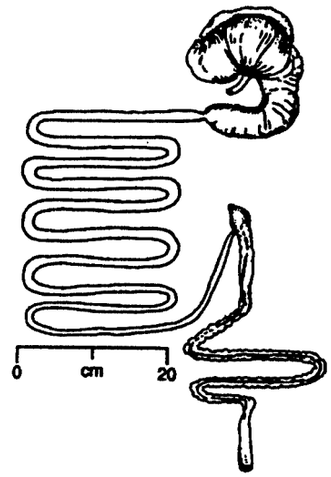


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FIGURE 1-11 Chimpanzee

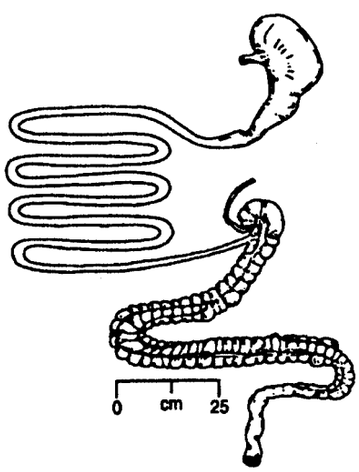

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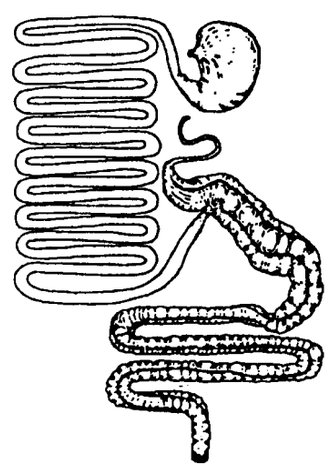
FIGURE 1-12 Orangutan



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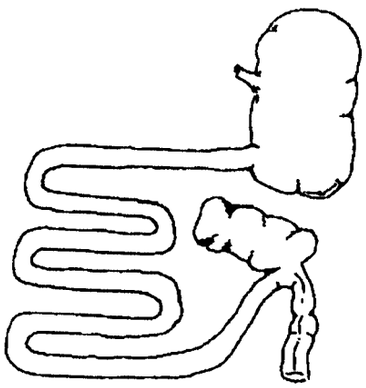
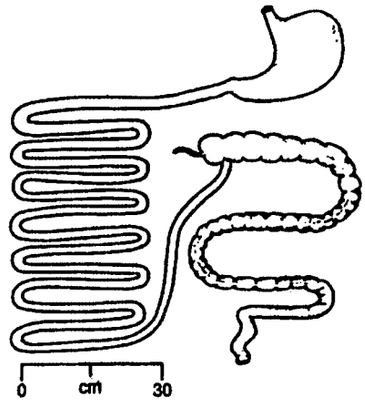
Primate Gastrointestinal Tracts (continued)

FIGURE 1-13 Howler Monkey



Edwards, 1995

FIGURE 1-14 Adult Human



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Adaptations for hindgut fermentation are most pronounced in the highly folivorous howler monkeys (*Alouatta* spp.) and Indrids (*Avahi*, *Indri*, and *Propithecus*). In these species, the complex nature of the hindgut is demonstrated by the presence of sacculations (haustra), longitudinal bands (taeniae), and flexures that presumably trap or slow the movement of digesta (Clemens and Phillips, 1980). Increased retention of food particles in this region facilitates microbial degradation by symbiotic organisms.

Some hindgut fermenters have adaptations in the foregut. For example, the stomach of *Alouatta*, which consumes a diet of at least 40% leaf material by weight (Hladik and Hladik, 1972; Edwards, 1995), is the most complex among the hindgut fermenters (Figure 1-13). It is a capacious globular sac, narrowing toward the bent tubular pylorus, guarded by strong pillars running longitudinally with the body (Chivers and Hladik, 1980).

Median gut passage time for a mixed-ingredient diet, including browse plants, fed to the highly folivorous *Hapalemur griseus alaotrensis* was 18.21 hours (Cabre-Vent and Feistner, 1995). Three species of howler monkeys fed two manufactured diets with different fiber concentrations (15% and 30% acid-detergent fiber [ADF]) exhibited no significant difference between diets in mean transit time of solids (28.0 vs. 21.5 hours) or liquids (14.6 vs 16.1 hours) (Edwards, 1995).

When fed a manufactured diet containing 15% ADF, silvered leaf monkeys (*Semnopithecus cristatus*) exhibited a mean transit time of 13.6 hours for both solid and liquid phases of digesta (Sakaguchi et al., 1991). Francois' leaf monkeys (*Trachypithecus f. francoisi*) fed a comparable (15% ADF) diet had a comparable transit time for liquid digesta (13.5 hours), but the mean transit time for solid digesta was 27 hours (Edwards, 1995). When the same animals were fed a diet with twice the fiber concentration (30% ADF), there was no significant effect of the dietary change on the transit time of either liquids (15.5 hours) or solids (28.5 hours) (Edwards, 1995).

Digestibility studies with the Yunan snub-nosed monkey (*Rhinopithecus bieti*), a foregut fermenter that feeds primarily on lichens, revealed apparent dietary dry matter digestibilities of 71 to 80%. Mean ($\pm$ SD) retention time of plastic digesta markers was 47 $\pm$ 17 hr (Kirkpatrick et al., 2001).

IMPLICATIONS FOR FEEDING PROGRAMS IN CAPTIVITY

Development of scientifically sound feeding programs for captive primates requires a balance of information on the species of concern. Gastrointestinal tract structure, natural feeding behavior, and nutrient composition of foods consumed by free-ranging individual animals are some of the items required to address dietary husbandry requirements. Identifying readily available foods to meet physio-

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TABLE 1-8 Examples of Food Consumed by Primates in Zoos and in the Wild (Oftedal and Allen, 1997)

Food Type	Dry Matter, %	Crude Protein, %	Fiber Fractions[a] NDF, %	ADF, %	AL, %	Ca, %	P, %
Market produce used in primate diets[b]							
Apples	12.8	2.3	17.4	12.6	3.8	0.0	0.0
Green beans	10.7	17.9	28.0	25.1	2.2	0.4	0.4
Cabbage	8.9	14.7	20.6	21.9	1.7	0.6	0.3
Carrots	12.2	7.7	15.2	16.5	1.5	0.2	0.4
Kale	12.3	32.5	19.3	24.7	4.6	0.9	0.4
Foods eaten in the wild by red howler monkeys (*Alouatta seniculus*)[c]							
Flowers	25.1	14.4	50.6	35.8	17.1	0.5	0.3
Fruits	23.7	7.0	53.8	35.2	16.6	0.6	0.2
Mature leaves	36.5	16.6	57.2	40.5	20.4	1.4	0.1
Young leaves	32.2	21.2	54.4	36.4	21.1	0.3	0.3

Note: all values, except dry matter, are expressed on a dry matter basis.
[a] NDF = neutral detergent fiber; ADF = acid detergent fiber; AL = acid lignin.
[b] All data except calcium and phosphorus from Oftedal et al., 1982; calcium and phosphorus values from USDA Standard Release 14.
[c] Unpublished data of M.S. Edwards, S.D. Crissey, O.T. Oftedal, and R. Rudran, as cited in Oftedal, 1991.

logic and behavioral needs of the species in captivity might be a greater challenge.

Diets for strict faunivores in a captive setting—including *Arctocebus*, *Galago*, *Loris*, *Microcebus*, and *Tarsius*—are limited by the availability of suitable vertebrate and invertebrate prey. Although crickets (*Acheta domestica*) and mealworm larvae (*Tenebrio molitor* and *Zophobas morio*) are readily available, they are not adequate to support the estimated nutritional requirements of these nonhuman primates (Oftedal and Allen, 1997). Guidelines on the handling and care of invertebrate prey to improve their nutrient quality as foods, specifically their calcium content, are provided by Allen and Oftedal (1989).

Food consumption by *Tarsius* appears to be influenced by movement of the prey offered as food. Thus, dietary prey must not only be living when presented, but must also be maintained in an environment (for example, with proper temperature, humidity, and photoperiod) that supports their needs and encourages natural movement.

As one reviews the literature on natural feeding habits of primates, it should be noted that biologists identify wild plant foods with botanic terms (such as fruit, flower, and petiole). However, these plant parts and their compositions are substantially different from commercially available produce that has been selectively cultivated for human consumption (Table 1-8). Thus, if commercial produce is to be offered to captive primates, that selection should be based on suitable nutrient composition and not solely on the basis of botanic classification.

Free-ranging primates devote a large percentage of their daily activity to acquisition and processing of food, and foraging not only satisfies a physiologic need, but plays a behavioral and social role in the life of primates. Provisioning captive populations of primates removes the need to forage in order to survive. However, if the diet is presented as a meal or on a predictable schedule, the behavioral needs of the animal might not be satisfied. Caretakers are encouraged to offer the diet in small portions distributed irregularly throughout the species-typical feeding period. The manner of diet preparation and presentation can also influence feeding behavior and the opportunity for equitable acquisition of food by individual animals in groups (Smith et al., 1989).

Leaf-eating primates—including *Propithecus*, *Indri*, *Alouatta*, *Nasalis*, and *Pygathrix*—have long been recognized as specialist feeders that are difficult to adapt to a "captive" diet. The impression that plant fiber is a negative dietary component and that a diet low in fiber is "preferred" by these captive primates has produced many of the health problems commonly seen (Edwards and Ullrey, 1999b). That conclusion is supported by a number of reports of a high incidence of gastrointestinal disorders among leaf-eating primates, many of which might be a result of consuming rapidly fermentable foods such as commercial fruits and vegetables (Hill, 1964; Bauchop and Martucci, 1968; Hick, 1972; Höllihn, 1973; Benton, 1976; Benirschke and Bogart, 1978; Heldstab, 1988; Taff and Dolhinow, 1989; Janssen, 1994). The beneficial role of plant fiber in promoting satiety, normal fecal consistency, and gastrointestinal health is well documented (Cummings, 1978).

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2 Energy

Energy is not a nutrient in the sense of chemically identifiable substances, such as essential amino acids, fatty acids, minerals, or vitamins. Energy is an abstraction that can be measured only during its transformation from one form to another. An animal requires energy for basal metabolic functions, for muscular activity, and for tissue accretion, reproduction, or lactation. Kleiber (1975) draws an analogy between animal life and fire: As wood is a fuel supporting fire, food is a fuel supporting animal metabolism, and energy provided by either fuel can be measured in units of heat.

UNITS OF MEASUREMENT

The traditional unit of food energy in the United States is the calorie (cal), the amount of energy required at 1 atmosphere of pressure to raise the temperature of 1 g of water from 14.5°C to 15.5°C. The joule (J) has been adopted as the preferred unit by the Système International d'Unités (International System of Units, or SI) and is often used. These units can be interconverted: 1 cal = 4.184 J. Derivative units are the kilocalorie (kcal) and kilojoule (kJ), which are 10^3 times as great as the calorie and the joule, respectively, and the megacalorie (Mcal) and megajoule (MJ), which are 10^6 as times great. In much of the human food literature and on food labels, the kilocalorie is known as the large calorie or, commonly, Calorie (C).

CLASSIFICATION

Gross Energy

When organic substances are completely oxidized to carbon dioxide and water, the energy released is known as gross energy (GE) or total energy. In animal research, GE is usually determined with a bomb calorimeter. In determining the GE of food, a weighed sample in a superoxygenated atmosphere in a heavy-walled stainless-steel cylinder called a bomb is immersed in a bucket that contains a weighed amount of water. The food sample is ignited with an electric current and burned, releasing heat that passes through the bomb into the surrounding water. The temperature of the water increases in proportion to the amount of energy released from the food. The GE of the food may be expressed in kilocalories per gram ($kcal \cdot g^{-1}$). Average GE concentrations of carbohydrates, proteins, and fats have been estimated to be 4.1, 5.6, and 9.4 $kcal \cdot g^{-1}$, respectively.

Not all the GE in food is available to the consuming animal, because of losses in digestion and metabolism. And one food can have a higher GE concentration than another but be a poorer source of available energy. A food that contains cellulose has a greater GE concentration than if cellulose is replaced with sucrose (Watt and Merrill, 1963), because combustion releases more energy from cellulose than sucrose. However, cellulose cannot be digested by endogenous mammalian enzymes, and in the absence of substantial microbial fermentation in the gastrointestinal tract, the GE in cellulose will be lost in the feces.

Digestible Energy

The GE of a food minus the GE of feces resulting from eating the food equals the apparent digestible energy (DE) of the food. It is termed apparent DE because some of the fecal energy is of nonfood origin and would be present even if no food were consumed. An estimate of true DE is attained if apparent DE is corrected for fecal metabolic energy losses, gaseous energy losses, and heat of fermentation. However, the nonfood energy losses in the feces must eventually be replaced with energy from food, and apparent DE values are most commonly used in practice.

Unlike the GE of a food, apparent DE is not a constant but is a function of food composition, the amount of food consumed per unit of time, and the ability of the consuming animal to digest it. For example, high-fiber foods usually

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have a higher DE for animals with substantial gastrointestinal microbial fermentation than for animals that must depend exclusively on endogenous digestive enzymes. As a consequence, DE concentrations in foods are most meaningful if determined during consumption of those foods by the target species in typical amounts per day. Such determinations have seldom been made with nonhuman primates, and it is presently necessary to use DE values for foods coming from studies of other species (usually domestic) that have gastrointestinal anatomy and physiology similar to that of the target primate species.

Metabolizable Energy

Apparent metabolizable energy (ME) of a food is equal to food GE minus GE lost in the feces, urine, and combustible gases. Subtraction of the latter quantity is an obviously arbitrary feature of the definition of apparent ME, in that the loss of food GE in combustible gases is a consequence of digestive processes. In most cases, gaseous GE lost is largely in the form of methane from microbial fermentation in the foregut or hindgut. That loss is not accounted for in apparent DE but for some species could account for a high proportion of the food energy that is unavailable for support of metabolic processes. Analogously to the calculation of true DE, true ME is calculated by subtracting metabolic losses of nonfood origin from apparent ME. Apparent ME values are used much more commonly than true ME values.

For some animal species, systems for expressing energy and nutrient requirements are based on ME intake. It is desirable to express requirements based on ME; however, research in primates has not been conducted to allow use of an ME-based system. Given the diversity of primate species and food items fed to these primates, ME values for the majority of food items have not been determined. This lack of data presently hampers development of more refined estimates of nutrient needs.

Research is needed to determine ME values of particular food items for specific primate species. Obviously, not all species can be studied, due to the intensive nature of the research and the limited availability of research animals. A reasonable approach to obtaining critical information on ME would be to conduct experiments with several model primate species, from which estimates could be extrapolated for other similar species. Primate species most important to study might be those 10 model species identified in Chapter 11: (1) macaques, (2) baboons, (3) squirrel monkeys, (4) cebus, (5) howlers, (6) marmosets and tamarins, (7) colobus and langurs, (8) lemurs, (9) chimpanzees, and (10) humans.

Physiologic Fuel Values

Nitrogen-corrected ME, net energy, and other expressions of energy concentrations in foods are presented in *Nutritional Energetics of Domestic Animals* (National Research Council, 1981b). The system that has been most widely applied to foods for primates involves calculation of physiologic fuel values (or physiologically available energy, an approximation of apparent ME); the system has been reviewed by Widdowson (1955) and is based on the German studies of Rubner in 1880-1901 and studies of Atwater (Rubner's student) in 1895-1906 in the United States. Most tables of composition of foods for humans list physiologically available energy values (and conversion factors for carbohydrates, protein, and fat in specific foods) based on digestibility trials conducted by Atwater and others (Merrill and Watt, 1955). The general physiologically available energy conversion factors of 4 $kcal \cdot g^{-1}$ for carbohydrates and protein, and 9 $kcal \cdot g^{-1}$ for fat yield reasonable approximations of apparent ME in the typical US human diet but not in specific foods or in high-fiber diets (National Research Council, 1989). For those, specific conversion factors, such as those in *US Department of Agriculture Handbook No. 8* (Watt and Merrill, 1963) should be used.

Souci et al. (1994) used the general conversion factors of 4 and 9 $kcal \cdot g^{-1}$ for protein and fat, respectively, but applied the carbohydrate conversion factor of 4 $kcal \cdot g^{-1}$ only to available carbohydrate. Available carbohydrate was defined as monosaccharides, disaccharides, oligosaccharides, nonstructural polysaccharides, and the sugar alcohols sorbitol, xylitol, and glycerol. If concentrations of those compounds were unknown, available carbohydrate was defined as 100 − (water + protein + fat + minerals + total dietary fiber + available lactic, citric, and malic acids). The conversion factor used for available organic acids was 3 $kcal \cdot g^{-1}$. Total dietary fiber included primarily cellulose, hemicellulose, and lignin (or water-soluble + water-insoluble fiber) and was assigned an available energy value of 0 $kcal \cdot g^{-1}$. Ethanol was assigned a value of 7 $kcal \cdot g^{-1}$.

The general conversion factors of Souci (1994) assume that there is no energy derived from dietary fiber and ignore interactions among macronutrients that may impact energy availability. A more robust approach to estimate dietary energy has been proposed by Livesey (1999, 2001). This empirical approach accounts for energy derived from all macronutrients and accounts for nutrient-nutrient interactions (Baer et al., 1997).

REQUIREMENTS

To conform with the first and second laws of thermodynamics, energy intake by an animal must equal energy used plus energy lost. Thus, GE in ingested food must equal

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GE used for support of basal metabolic functions, voluntary activity, maintenance of body temperature, and product formation (for example, tissue growth, integument, conceptus, and milk) plus GE lost in feces, urine, and combustible gases and as waste heat.

Basal Energy Expenditures or Basal Metabolic Rate

ESTIMATING BASAL METABOLIC RATE

A first measure of energy expenditure (or energy requirement) is the amount of energy required to support the basic life functions (vital cell activity, respiration, and cardiovascular distribution of blood) of an animal in repose (awake but resting and unstressed), in a postabsorptive state, and in a thermoneutral environment (no shivering or other special activity to maintain body temperature). Rubner proposed that basal energy expenditure was related to body surface area and concluded that fasting homeotherms produce 1,000 kcal of heat per square meter body surface (Kleiber, 1975). Because the surface area of a sphere is related to its volume and can be related to its weight when it has a density of 1 $kg \cdot L^{-1}$, attempts were made to relate basal energy requirements of animals to measurements of body surface area.

However, animals are not spheres and do not have a density of 1, and body-surface area measurements are difficult to reproduce consistently. Thus, a search began for a relationship between basal energy requirements and body weight. Using data published by others, Kleiber (1975) explored the concept of metabolic body size as a power function of body weight (BW^n) and concluded that basal metabolic rates (BMR) of fasting adult animals varying in body weight from mice (0.021 kg) to cattle (600 kg) could be expressed in kilocalories per day as $70BW_{kg}^{0.75}$. Nonhuman-primate data included in his calculations were derived from studies of macaques (Benedict, 1938) weighing 4.2 kg, with a BMR of 207 $kcal \cdot day^{-1}$, and chimpanzees (Bruhn and Benedict, 1936) weighing 38 kg, with a BMR of 1,090 $kcal \cdot day^{-1}$.

It should be noted that it is difficult to measure energy expenditure in the exact circumstances specified for determination of BMR. It is questionable whether ruminants reach a true postabsorptive state; Colobinae might not, and few animals appear to be stress-free during the measurement experience. Therefore, resting energy expenditure (REE) may be used instead. In studies with humans, BMR and REE differ by less than 10%, and the terms are used interchangeably (National Research Council, 1989). Prediction equations have been used for estimating BMR when analytic methods were not available (FAO/WHO/UNU, 1985; National Research Council, 1989).

EFFECTS OF AGE AND BODY COMPOSITION ON BASAL METABOLIC RATE

Energy expenditure (EE) and therefore energy requirement generally decreases with advancing age because of a decrease in BMR, which is characterized by loss of fat-free mass (FFM). Age-related changes probably vary in rate, timing, and extent among individuals in response to differences in physical activity, disease, and other factors. Information on rates of change in BMR and FFM is limited by study design (cross-sectional rather than longitudinal) and possibly by methodology (use of imprecise or biased methods for assessment of changes in body composition) (Murray et al., 1996). The age-related decline in BMR has been partly explained by a reduction in the quantity, as well as metabolic activity, of lean-tissue components as measured by dual-energy x-ray absorptiometry (DEXA). However, even when BMR was adjusted for differences in lean-tissue and fat components, it was significantly lower in older people (50-77 years old) by 644 $kJ \cdot day^{-1}$ (Piers et al., 1998). When the BMR of similarly aged people (average, 71 years) was measured in a respiratory chamber, BMR was significantly ($P < 0.01$) lower after FFM, fat mass, and sex were accounted for (Vaughn et al., 1991).

When REE of 40 healthy men and women (51-82 years old) was measured with indirect calorimetry, REE was highly correlated with FFM ($r = 0.88$; $P < 0.001$) and body weight ($r = 0.85$; $P < 0.001$); this supports the idea that active tissue mass determines daily EE (Fredrix et al., 1990). Total EE and activity level, measured by the doubly labeled water (DLW) method in combination with measurements of BMR, showed that EE was lower in elderly (68-71 years) than in younger (27-30 years old) subjects partly because of a significantly lower BMR (Pannemans and Westerterp, 1995).

When EE (adjusted for body composition and activity) was measured in two age groups (20-30 years, $n = 98$; 50-65 years, $n = 39$), older subjects had a 4.6% lower BMR than younger subjects, independently of sex, body size, body composition, and activity (Klausen et al., 1997). An effect of sex was noted among healthy men and women (over 50 years old to control for effect of menstrual status) when 24-hour EE, BMR, and sleeping metabolic rate were measured in a respiratory chamber. Men had significantly higher 24-hour EE and sleeping metabolic rates than women after adjustment for differences in fat-free mass, fat mass, and age (Ferraro et al., 1992).

Energy Requirements for Maintenance

Age and body composition affected energy requirements of 101 infants, 82 girls, and 27 adults when energy expenditures were scaled for differences in body size to test the effects of age and body fatness in humans (Butte et al.,

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1995). As humans increase in weight and fatness from infancy to adulthood, energy requirements increase as a power function ($BW^{0.63}$) of body weight.

The capabilities of aging people need not diminish if they maintain a healthy, active lifestyle. Energy requirements and EE of healthy, active older people (63-77 years) and younger people (average, 28 years) were reported in a study of men receiving a diet with a defined formula for 47 days under controlled conditions. Energy expenditure while they were at rest: 1.22 × BMR, and while sitting quietly: 1.30 × BMR, were the same for older and younger men (Calloway and Zanni, 1980). Moderate activity, such as walking on the level at about 2.5 mph, cost 4.51 ± 0.34 (mean ± SD) $kcal \cdot min^{-1}$ (about 1.4 × BMR). Cycling at a comfortable load (300-400 kpm) cost only slightly more energy than did walking for both age groups. Metabolizable energy intake required to maintain a constant BW for these men, who were sedentary except for 30 min of cycling per day, was 2,554 ± 222 $kcal \cdot day^{-1}$, or about 1.6 × BMR. The minimal maintenance ME requirement (ambulatory but inactive) of healthy older men was 1.5 × BMR, the same as for younger men, and similar to the averages of 1.55 × BMR for adult macaques and 1.56 × BMR for adult baboons of various ages (Table 2-1). The estimate of total daily EE, determined by multiplying energy costs of a given level of activity by the individual estimate of BMR, was 1.55 × BMR for sedentary men, as reported by Almendingen et al. (1998) in describing methods for predicting individual energy intakes.

The "factorial approach" to estimating ME requirements as multiples of BMR was based on the factorial method used to determine protein requirements (Payne and Waterlow, 1971). It provides a way of partitioning the ME required for maintenance into BMR, activity, and heat increment (Lloyd et al., 1978; National Research Council, 1981b; FAO/WHO/UNU, 1985). The idea has been expanded to encompass estimates of total EE whether determined according to dietary intake, DLW, or other indirect measures of energy requirements or expenditures (Roberts, 1996; Shetty et al., 1996; Scholler, 1998; DeLany, 1998). A measure of error can be introduced into the estimate in that activity (work) is determined by mass and distance traveled in the horizontal or vertical planes and is not a function of age or gender (Mathers, 1997).

When cross-sectional energy-balance measurements were made on groups of rhesus monkeys (*Macaca mulatta*) 6.5-7.0 years old, 8.5-10 years old, and over 24 years old, the 24-hour EE tended to decrease with age when it was expressed in absolute or $BW_{kg}^{0.75}$ terms (Lane et al., 1995). Absolute EE (mean ± SD) declined for the juvenile, adult, and aged ad libitum-fed control groups to 1,008 ± 326, 853 ± 188, and 603 ± 148 $kcal \cdot d^{-1}$, respectively. Energy expenditures expressed in relation to $BW_{kg}^{0.75}$ for the groups declined in a similar manner 194 ± 64, 167 ± 32, and 122 ± 46 $kcal \cdot d^{-1}$, respectively. There was no significant effect of age on either measurement. In another study of young (7-9 years), middle- (13-17 years) and older-aged (> 23 years) rhesus monkeys, energy expenditure (kJ/min) tended to decrease with age but the decrease was not significant. In this study, older animals spent less time in vertical movement and thus had the lowest energy expenditure (Ramsey et al., 2000).

The ME intake required for maintenance must provide the chemical energy to meet basal metabolism, thermoregulation, and activity energy costs (Lloyd et al., 1978; McNab, 1986; Scott, 1986; Robbins, 1993a; Torun et al., 1996). In other words, ME intake must equal heat production. Such biologic factors as sex, growth, age, health, and reproductive status affect energy requirements of nonhuman primates. Evidence suggests that some nocturnal primates have lower relative basal requirements than diurnal primates (Ross, 1992). Although the maintenance energy requirement is often defined as the energy intake that sustains a constant BW, care must be taken in using weight as the sole criterion of energy balance because body composition may change, particularly with age (Robbins, 1993a). Similarly, the expression of food intake data per kilogram BW rather than per unit of metabolic body size can lead to variable conclusions, especially when small and large animals or those with different body compositions are compared (Brody, 1945; Ausman et al., 1985).

In humans and rats, about 60-75% of the ME supplied by the diet is used to meet BMR requirements (Lloyd et al., 1978; Rothwell and Stock, 1981; Curtis, 1983; FAO/WHO/UNU, 1985). About 5-10% is used to support the thermogenic effect (heat of digestion) of food (Mayes, 1996; Forsum et al., 1981). The heat increment (HI) associated with digestive and metabolic processes is energy that cannot be used for productive purposes but can be used to help to maintain body temperature in cold environments. Except for temperature extremes, the influence of environmental temperature on apparent digestibility of the energy in food is relatively small compared to that of differences in food composition (Curtis, 1983). It also is difficult to measure because climatic effects are often confounded with amounts of food consumed and the foods selected, choices that may vary seasonally among free-living mammals (National Research Council, 1981a; McNab, 1986).

The ambient temperature range in which thermoregulation occurs without increasing metabolic heat production is termed the thermoneutral zone and is bounded by the upper and lower critical temperatures (Curtis, 1983; Robbins, 1993a). As ambient temperature rises above the upper critical temperature, metabolic heat production increases because of the energy-demanding processes, such as panting and sweating, required for heat dissipation. Declines in ambient temperature below the lower critical temperature require increased metabolic heat production by such activi-

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TABLE 2-1 Estimated Daily Metabolizable Energy (ME) Requirements (as Multiples of BMR) for Adult Captive Animals. (Based on Studies of Estimated Ad Libitum Energy Intake and Controlled, Long-term Dietary Restriction, or Analyzed Total Energy Expenditures. Activity Levels Typical for Captivity, Environmental Conditions Measured, and Animals Maintaining Bodyweight.)

n	Sex	BW_{kg}	Kcal ME Intake[a] · BMR^{-1}	TEE[b] Kcal · BMR^{-1}	TEE Kcal · BW_{kg}^{-1}	EE[c] Kcal · BMR^{-1}	BMR[d]	MMR[e]	Diet Type[f]	Reference
Apes (Pongidae: orangutan, gorilla)										
7	M/F	76.5	2583/1811 = 1.43 **$100(BW^{0.75})$**				1277	3621	M	King, 1978
Aye-aye										
4	M/F	2.46	260/137 = 1.9 **$133(BW^{0.75})$**				109	275	M	Sterling et al., 1994
Baboon										
11	F	15.6	748/551 = 1.36				409	1099	N	Wene et al., 1982
17	F	18.8	956/631 = 1.55				467	1264	N	Bielert & Busse, 1983
6	F	20.0	1169/662 = 1.77 **X = 1.56, $109(BW^{0.75})$**				489	1324	N	Roberts et al., 1985
Colobines										
Langurs										
7	M	7.54	629/319 = 1.97				243	637	N, ADF15	Edwards & Ullrey, 1999b
7	M	7.46	506/316 = 1.60 **X = 1.78, $125(BW^{0.75})$**				241	632	N, ADF30	Edwards & Ullrey, 1999b
Proboscis										
5	F	9.0	1055/364 = 2.90 **$203(BW^{0.05})$**				276	727	M	Dierenfeld et al., 1992
1	M	15.0	1758/534 = 3.29 **$230(BW^{0.75})$**				398	1067	M	Dierenfeld et al., 1992
Howlers										
7	M	7.52	430/318 = 1.35				243	636	N, ADF15	Edwards & Ullrey, 1999b
7	M	7.61	440/321 = 1.37 **X = 1.36, $95(BW^{0.75})$**				245	641	N, ADF30	Edwards & Ullrey, 1999b
Lemurs										
13	M/F	2.5	194/139 = 1.42				110	278	M	King, 1978
3	F	4.6	303/219 = 1.38				171	440	N, ADF15	Edwards & Ullrey, 1999a
2	F	4.8	286/228 = 1.25 **X = 1.35, $95(BW^{0.75})$**				176	454	N, ADF15	Edwards & Ullrey, 1999a
Macaca rhesus										
3	M	9.0	367/364 = 1.01				276	727	SP	Robbins and Gavin, 1966
14	F	6.6	277/287 = 0.97				221	576	SP	Robbins and Gavin, 1966
6	M	9.0	681/364 = 1.87	1008/364 = 2.77	112.0		276	727	N	Lane et al., 1995
6	M	9.0	754/364 = 2.07	853/364 = 2.34	94.7		276	727	N	Lane et al., 1995
3	M	8.3	369/342 = 1.08	603/342 = 1.76	72.6		260	685	N	Lane et al., 1995
15	M	13.7	706/498 = 1.41			1183/498 = 2.38	373	997	P	Ramsey et al., 1997
8	M	16.5	882/573 = 1.54	884/537 = 1.54	53.5		426	1146	N	DeLany et al., 1998
M. fasicularis										
16	M	5.7	627/255 = 2.46 **X = 1.55, $109(BW^{0.75})$**				196	516	P	Cefalu et al., 1997

(continues)

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TABLE 2-1 *(continued)*

n	Sex	BW_{kg}	Kcal ME Intake[a] · BMR^{-1}	TEE[b] Kcal · BMR^{-1}	TEE Kcal · BW_{kg}^{1}	EE[c] Kcal · BMR^{-1}	BMR[d]	MMR[e]	Diet Type[f]	Reference
Macaca, diet restricted										
rhesus										
6	M	6.0	441/268 = 1.64	903/268 = 3.36	(31%DR)[g]		206	537	N	Lane et al., 1995
6	M	8.5	531/348 = 1.53	790/348 = 2.27	(26%DR)		265	697	N	Lane et al., 1995
7	M	11.0	582/423 = 1.38		(35%DR)		318	846	N	Bodkin et al., 1995
6	M	11.5	507/437 = 1.16	511/437 = 1.17	(40%DR)		329	874	N	DeLany et al., 1998
M. fasicularis										
			432/345 = 1.25							
16	M	5.5	**X = 1.39, 97($BW^{0.75}$)**		(30%DR)		194	328	N	Cefalu et al., 1997
Marmoset										
8	M/F	0.44	86.8/37.8 = 2.30				31.8	76	M	King, 1978
5	M/F	0.133	26.5/15.4 = 1.72				13.5	31	P	Power, 1991
			70.8/32.2 = 2.19							
8	M/F	0.355	**X = 2.07, 145($BW^{0.75}$)**				27.2	64	P	Power, 1991
Squirrel monkey										
11	M/F	0.79	164/59 = 2.77				48.3	117	SP	Ausman et al., 1985
			167/67 = 2.49							
4	M	0.95	**X = 2.63, 184($BW^{0.75}$)**				55	135	N	Weindruch et al., 1995
Squirrel monkey, diet restricted										
			128/59.2 = 2.16							
13	M	0.80	**151($BW^{0.75}$)**		(28%DR)		48.8	118	N	Weindruch et al., 1995
Tamarin										
6	M	0.430	66.4/37.3 = 1.78				30.4	74	P	Escajadillo et al., 1981
>10	M/F	0.300	42.7/28.4 = 1.50				24.2	57	N	Wirth and Buselmaier, 1982
39	M/F	0.534	124/43.7 = 2.80				36.5	87	N	Barnard et al., 1988
7	M/F	0.311	92.6/29.1 = 3.18				24.8	58	P	Power, 1991
10	M/F	0.472	101.3/39.9 = 2.54				33.4	80	P	Power, 1991
9	M/F	0.678	109.8/52.3 = 2.09				43.4	105	P	Power, 1991
4	M/F	0.471	65.1/39.8 = 1.64				33.4	80	N	Kirkwood & Underwood, 1984
			X = 2.22, 155($BW^{0.75}$)							
Chimpanzee										
7	M	12.9					357	953	?	Dale et al., 1967
		(26% adult weight)				893/557 = 1.60				
7	F	15.9					415	1115	?	Dale et al., 1967
		(39% adult weight)				836/477 = 1.75				

[a] Kilocalories of ME intake relative to estimates of basal metabolic rate (BMR, $70BW^{0.75}$) provide factors by which basal energy requirements can be multiplied to accommodate energy costs of physical activity typical of captivity. Averaged factors × $70BW^{0.75}$ provide estimates of daily energy requirements.

[b] Total energy expenditures (TEE) was measured with doubly labeled water method. Ratios of TEE:BMR provide factors by which basal energy requirements can be multiplied to accommodate energy costs of physical activity typical of captivity. When TEE was reported separately for males and females, there were no apparent differences between sexes in magnitude of factors (FAO/WHO/UNU, 1985).

[c] Energy expenditure analyzed with indirect calorimetry used as above to determine multiple of BMR.

[d] BMR in kcal per day as function of body weight (kg) for eutherians: $BMR = 57.2BW_{kg}^{0.716}$ (McNab, 1988).

[e] MMR (maintenance metabolic rate) in kcal of ME per day as function of body weight (kg) to meet daily maintenance energy requirements for placental mammals: $MR = 140BW_{kg}^{0.75}$ (Scott, 1986; Robbins, 1993a).

[f] Diet type: M = mixed, N = natural ingredient, P = purified, SP = semipurified, ADF15 = 15% acid-detergent fiber, ADF30 = 30% acid-detergent fiber.

[g] Level of dietary restriction below ad libitum (DR).

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ties as shivering to maintain body temperature. Measures of heat production and heat dissipation have been made in chimpanzees at an ambient temperature of 23.9°C, presumably within the thermoneutral zone of this species (Dale et al., 1967). When heat loss was partitioned, losses were approximately equal via radiation, convection, and evaporation of moisture. Basal levels of heat production (or energy expenditure) for chimpanzees with estimated ages from 42 to 74 months and BW from 11.3 to 27.2 kg averaged 2.222 kcal·BW_{kg}^{-1}hour^{-1}, equivalent to 53 kcal·BW_{kg}^{-1}·day^{-1}.

BMR can be used as a baseline index of daily EE to which that of activity can be added. This basal EE is usually expressed on a metabolic body-weight basis with the equation noted previously—BMR in kcal·day^{-1} = 70 × $BW_{kg}^{0.75}$ (Clarke et al., 1977; Lloyd et al., 1978; King, 1978; Feldman and McMahon, 1983; McNab, 1983; Kurland and Pearson, 1986; Nagy, 1987; McNab, 1988; Mori, 1995; Tilden and Oftedal, 1995; Leonard and Robertson, 1997). The true value of the exponent has been debated, and other relative BMR scaling relationships have been described for captive and wild mammals, including primates (Stahl, 1967; Stahl and Malinow, 1967; King, 1978; Heusner, 1985; McNab, 1986; Robbins, 1993a; Stevens and Hume, 1995; Leonard and Robertson, 1997), with consideration of animal type, species, and quality of diet (Ross, 1992).

In housed domestic or wild animals, energy in addition to basal requirements for ingestion and metabolism of food is required, but little is needed for thermoregulation or physical activity (Curtis, 1983; Stevens and Hume, 1995). Under these husbandry conditions, ME requirements for daily maintenance are about double the BMR of 293kJ (70 kcal) × $BW_{kg}^{0.75}$ for eutherians (Kleiber, 1961; Robbins, 1993a). Voluntary ME intakes of 120 species of zoo animals, grouped in families (including primates), were related to their predicted BMR requirements (Evans and Miller, 1968). The mean ME intake, 146 kcal × $BW_{kg}^{0.75}$ was about twice the energy required for basal metabolism, or 2.08 × BMR.

The reported addition to BMR to accommodate minimal physical activity (minimal survival requirement) of humans was 1.27 × BMR (89 kcal × $BW_{kg}^{0.75}$), increasing to 1.4 × BMR (98 kcal × $BW_{kg}^{0.75}$) over 24 hours if 1.5 hours·day^{-1} of walking or 2 hours·day^{-1} of standing was included. The 1.4 value serves as a guide for estimating maintenance ME requirements of humans (FAO/WHO/UNU, 1985). A factor of 1.3 × BMR (91 kcal × $BW_{kg}^{0.75}$) has been proposed as a maintenance ME requirement for carnivores and omnivores (Scott, 1986), whereas a maintenance ME requirement of 1.5 × BMR (105 kcal × $BW_{kg}^{0.75}$) has been proposed for a range of animals when relative energy requirements were determined by a factorial approach similar to that used for estimating protein requirements (Payne and Waterlow, 1971). With increasing activity of adult omnivores (including humans) and adjustment of BMR for HI, 2 × BMR (140 kcal × $BW_{kg}^{0.75}$) has been proposed as the maintenance ME requirement for moderate activity and 3 × BMR (210 kcal × $BW_{kg}^{0.75}$) for high activity (Scott, 1986). Net costs for standing require a 20% energy increase above basal for mammals, or 1.2 × BMR (84 × $BW_{kg}^{0.75}$) (Robbins, 1993a). The energy requirement for terrestrial locomotion (TL) is an inverse function of BW, and bipeds and quadrupeds can be represented with the same regression equation, Y_{kcal}·BW_{kg}^{-1}·TL_{km}^{-1} = 2.57 × $BW_{kg}^{-0.316}$ (Taylor et al., 1982). Climbing adds an average of 6 kcal·BW_{kg}^{-1}·per vertical kilometer climbed (Robbins, 1993a). The cost of brachiation (use of the arms to swing between objects) varies with speed, and the net cost (kcal·BW_{kg}^{-1}·km^{-1}) is 1.5 times as high as for normal walking by spider monkeys (Parsons and Taylor, 1977). Hanging motionless was reported to increase resting metabolism of the spider monkey and slow loris by 65 ± 32%, which is 3 times more costly than the 20% increment for standing over resting in mammals. When energy expenditures over 24-hour periods were measured in 177 closely observed human subjects, it was demonstrated that much of the variability in daily energy expenditure, independent of differences in body size, was due to differences in spontaneous physical activity, or fidgeting. This activity accounted for energy expenditures of 100-800 kcal·d^{-1} in these subjects (Ravussin et al., 1986) and might apply to nonhuman primates as well.

Clinical practitioners often use a simplified formula (1 kcal·BW_{kg}^{-1}·hour^{-1}) to approximate average daily basal energy requirements of adult humans (Williams, 1997). Adjustments for various levels of activity may be added to this basal estimate as follows: 20%, 30%, 40%, or 50% for very sedentary, sedentary, moderately active, or very active, respectively. The normal activity of most free-living animals would be considered sedentary to moderate, requiring an energy expenditure addition of 30%-40% to the BMR. Caged animals generally would require additions of only 13%-35% to the maintenance requirement for activity (Lloyd et al., 1978; Scott, 1986).

Daily total EE, the sum of all caloric costs for maintenance and activity of male and female adult wild howlers, *Alouatta palliata,* estimated with the DLW method, averaged 85 kcal·BW_{kg}^{-1} or 135 kcal·$BW_{kg}^{0.75}$ (Nagy and Milton, 1979). By comparison, the mean total EE of adult caged *M. mulatta*, also determined with DLW, was 87 kcal·BW_{kg}^{-1}·day^{-1} (Stein et al., 1996). The total 24-hour EE of ad libitum-fed adult *M. mulatta* ranged between 112 and 73 kcal·BW_{kg}^{-1} when measured with DLW (Lane et al., 1995).

The 24-hour EE of prepubertal male and female chimpanzees, determined with indirect calorimetry, were about 65 and 56 kcal·BW_{kg}^{-1}, respectively (Dale et al., 1967). The mean daily EE of two adult male and two adult female Gelada baboons, measured with indirect calorimetry, was

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94 kcal·$BW_{kg}^{0.75}$ or 1.34 × BMR (Iwamoto, 1979). When EE was estimated from ME intake and BMR was calculated (70 kcal·$BW_{kg}^{0.75}$) as presented in Table 2-1, the daily ME requirement for lean adult squirrel monkeys was 184 kcal·$BW_{kg}^{0.75}$ (2.63 × BMR) compared with 152 kcal·$BW_{kg}^{0.75}$ (2.17 × BMR) for obese squirrel monkeys (Ausman et al., 1985).

A study comparing energy intakes and requirements among adults of three primate families found ME intakes of 137-255 kcal·$BW_{kg}^{0.75}$ by marmosets (Callitrichidae), 87.9-118 kcal·$BW_{kg}^{0.75}$ by apes (Pongidae), and 86.3-122.8 kcal·$BW_{kg}^{0.75}$ by lemurs (Lemuridae)(King, 1978). Those ME intakes were equivalent to an average of 198, 34, and 78 kcal·BW_{kg}^{-1}·day^{-1} for the three groups, respectively (Table 2-2). For marmosets, the average ME intake was 2.07 × BMR, whereas for both lemurs and apes, ME intake was about 1.4 × BMR (for BMRs shown in Table 2-1).

Body weights were sustained in adult male and female rhesus monkeys (*M. mulatta*) when animals were fed an amount of a commercial diet (3.47 kcal ME·g^{-1}) targeted to meet an expected daily maintenance requirement of 93 kcal·$BW_{kg}^{0.75}$ (Robbins and Gavan, 1966). Daily estimated ME intakes of 40.8 kcal·BW_{kg}^{-1} for males and 42.2 kcal·BW_{kg}^{-1} for females were less than those reported for *M. mulatta* in other studies (Table 2-2).

Adult female baboons (*Papio* sp.), weighing an average of 15.6 kg, were fed a commercial diet (about 3.1 kcal ME·g^{-1}) providing an average ME intake of 48 kcal·BW_{kg}^{-1}·d^{-1} (Table 2-2). That energy intake apparently met maintenance requirements on the basis of sustained body weights over a 4-week period (Wene et al., 1982).

Mixed zoo diets containing an average calculated ME concentration of 3.6 kcal·g^{-1} and fed ad libitum to adult female proboscis monkeys (*Nasalis larvatus*) with an estimated mean body weight of 9 kg resulted in an estimated maintenance ME requirement of 3 × BMR, 1.5 times as great as the predicted maintenance requirement (2 × BMR) based upon body weight (Dierenfeld et al., 1992) (Table 2-1).

Intakes of mixed diets by adult wild and captive aye-ayes (*Daubentonia madagascariensis*) were measured, and ME intakes were estimated to be 260-342 and 260 kcal·day^{-1} for wild and captive animals, respectively. A combined daily ME requirement was established at 280 kcal (Sterling et al., 1994). The ME intake by captive aye-ayes in relation to body weight was 106 kcal·BW_{kg}^{-1}·day^{-1} (Table 2-2).

Wild adult female and male orangutans (*Pongo pygmaeus*) have been estimated to weigh an average of 37.8 and 83.6 kg, respectively (Rodman, 1984). For an estimated ME requirement of 40 kcal·kg^{-1}·day^{-1}, the daily ME requirements of the female and male orangutans would be 1,512 and 3,344 kcal, respectively. During the month of greatest fruit consumption, wild adult female and male orangutans of unknown weight consumed an estimated 7,404 and 8,422 kcal ME·day^{-1}, respectively. During the month of lowest fruit consumption, female and male orangutans consumed only an estimated 1,793 and 3,824 kcal ME·day^{-1}, respectively (Knott, 1998). Although energy intakes during the period of low fruit availability appear adequate, on the basis of the above estimates of body weight and ME requirements, urinary ketone concentrations indicated that the wild orangutans were not maintaining energy balance but were losing weight.

Commercial diets for long-term maintenance of marmosets and tamarins, formulated to contain 3.5-4.2 kcal ME·g^{-1}, have helped to prevent "marmoset wasting syndrome" among *Callithrix jaccus, C. jaccus jaccus, C. jaccus penicillata, Saguinus oedipus oedipus,* and *S. fuscicollis illigeri* (Wirth and Buselmaier, 1982; Clapp and Tardif, 1985). Purified diets fed to adult male cotton-top tamarins (*Saguinus oedipus*) and providing 160 kcal GE·BW_{kg}^{-1}·day^{-1} (154 kcal ME·BW_{kg}^{-1}·day^{-1}) (Table 2-2) alleviated signs of the wasting syndrome (Escajadillo et al., 1981). An open-formula, natural-ingredient diet providing 335 kcal GE·BW_{kg}^{-1}·day^{-1} (232 kcal ME·BW_{kg}^{-1}·day^{-1}) (Table 2-2) alleviated signs of the wasting syndrome in mustached tamarins (*Saguinus mystax*) (Barnard et al., 1988). The daily ME intake for maintenance of adult cotton-top tamarins (*Saguinus oedipus oedipus*) was found to decrease with age—208 kcal·BW_{kg}^{-1} for a 2-year-old male and 113 kcal·BW_{kg}^{-1} for an aged male (Kirkwood and Underwood, 1984).

Energy Requirements for Growth

Infant nonhuman primates require more energy per unit of BW for growth than do adults of their species (Stahl and Malinow, 1967; Kerr, 1972; Nicolosi and Hunt, 1979; King, 1978; Ausman, 1995). Energy requirements for growth depend on the rate and composition of gain, which can vary, particularly among wild animals influenced by seasonally variable environments (Robbins, 1993b). The mass-specific BMRs of young, rapidly growing animals are higher than those of adults because body surface area per unit of body mass is greater in the young (Scott, 1986; Robbins, 1993b); the mass-specific BMR can reach 3-4 times that of the adult (Clarke et al., 1977).

Although growth of an animal is commonly described by a sigmoid curve, most of the growth occurs during a relatively linear intermediate phase. Maximal growth rates of the young of different species during this linear phase tend to increase as a power function of adult BW. The relationship between adult BW (X in g) and growth rate (Y in g·day^{-1}) of neonates in 160 species of placental mammals has been calculated to be $Y = 0.0326X^{0.75}$ ($r^2 = 0.94$). The same relationship in 32 species of primates was calculated to be $Y = 0.2165X^{0.35}$ ($r^2 = 0.66$) (Robbins,

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TABLE 2-2 Biologic and Metabolic Parameters of Species Fed Dry Diets

Species	Sex	n	Age (y)	Body Weight (kg)	DM[a] Intake ($g \cdot BW_{kg}^{-1} \cdot d^{-1}$)	ME[b] Intake ($kcal \cdot BW_{kg}^{-1} \cdot d^{-1}$)	DM[c] (% dig.)	GE[d] (% dig.)	Reference
Aye-aye									
Daubentonia madagascariensis	M/F	4	adult	2.46	45.9	106			Sterling et al., 1994
Baboons									
Papio sp.	F	11	adult	15.6	15.4	48			Wene et al., 1982
P. ursinus	F	17	adult	18.8	16.0	51			Bielert and Busse, 1983
P. cynocephalus and *P. anubis*	F	6	adult	20.0	17.1	58			Roberts et al., 1985
Guerezas (values for 3):									
Colobus guereza kikuyuensis, Pygathrix nemaeus nemaeus, Trachypithecus f. francoisi	M	7	adult	7.54	28.3	110_{DE}	81.2	80.9	Edwards and Ullrey, 1999b
Howlers (values for 3):									
Alouatta caraya, A. villosa palliata, A. seniculus sara	M	7	adult	7.52	17.6	57.9_{DE}	69.3	68.5	Edwards and Ullrey, 1999b
Lemuridae (values for 3):									
Lemur fulvus mayottensis,	M/F	13	adult	2.5	22.0	78.0			King, 1978
L. mongoz mongoz, L. catta	F	3	adult	4.58	30.0	66.2_{DE}	53.3	48.8	Edwards and Ullrey, 1999a
	F	2	adult	4.83	27.4	61.7_{DE}	47.7	44.4	Edwards and Ullrey, 1999a
Macaca									
Macaca mulatta	M	3	adult	9.0	11.6	40.8			Robbins & Gavan, 1966
M. mulatta	F	14	adult	6.6	12.0	42.2			Robbins & Gavan 1966
M. mulatta	F	9	7-12	7.8	21.1	71.3			Henderson et. al., 1993
M. mulatta	M	6	6.5-7	9.0	22.2	75.7		84.0	Lane et al., 1995
M. mulatta	M	6	8.5-10	9.0	23.8	83.8		87.0	Lane et al., 1995
M. mulatta	M	3	>24	8.3	15.2	44.5		80.0	Lane et al., 1995
M. mulatta	M	15	11-17	13.8	13.0	51.4			Ramsey et al., 1997
M. mulatta	M	8	>20	16.5	15.0	53.5			DeLany et al., 1998
M. mulatta	M	7	21	16.4	14	54.5			Bodkin et al., 1995
M. fasicularis	M	16	9-10	5.7	30.0	110.0			Cefalu et al., 1997
Marmoset									
Callithrix jacchus jacchus and *C. argentata*	M/F	8	adult	0.44	52	198			King, 1978
Cebuella pygmaea	M/F	5	adult	0.133	55	208_{DE}	84.0	84.0	Power, 1991
Callithrix jacchus	M/F	8	adult	0.355	63	208_{DE}	77.0	75.0	Power, 1991
C. j. jaccus	M/F	>10	adult	0.300	41	142			Wirth and Buselmaier, 1982
Pongidae (values for 3):									
Gorilla gorilla gorilla, Pongo pongo pygmaeus, P. pongo abelii	M/F	6	adult	76.5	8.8	34			King, 1978
Proboscis monkey									
Nasalis larvatus	F	5	adult	9.0	25.7	93	88.5		Dierenfeld et. al., 1992
Squirrel monkey									
Saimiri sp.	M	4	10-15	0.95	44.5	176			Weindruch et. al., 1995
Tamarin									
Saguinus oedipus linneaus	M	4	adult	0.432	40.5	154	73.0		Escajadillo et. al., 1981
S. mystax	M/F	39	adult	0.534	72.0	232	85.7		Barnard et. al., 1988
Leontopithecus rosalia	M/F	9	adult	0.678	44.0	169_{DE}	85.4	86.0	Power, 1991
S. fuscicollis	MF	7	adult	0.311	97.0	310_{DE}	74.3	71.0	Power, 1991
S. oedipus	M/F	10	adult	0.472	61.0	224_{DE}	83.0	82.0	Power, 1991

[a] Dry matter intake.
[b] Metabolizable energy unless designated as digestible energy (DE).
[c] Dry matter digestibility in percent.
[d] Gross energy digestibility in percent.

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1993b). A comparative description of growth in humans and chimpanzees has been published by Smith et al. (1975) and in chimpanzees and gorillas by Leigh and Shea (1996). However, energy requirements for growth were not reported.

Because dietary energy requirements differ so widely among various animal species, generalizations about daily requirements for growth must be viewed cautiously. The composition of tissues deposited during growth and measured as weight gain significantly influences required dietary energy inputs. Each gram of protein deposited represents about 5.4 kcal of net energy; each gram of fat, about 9.1 kcal of net energy (Scott, 1986; Robbins, 1993b). However, this is far from the full story. Energy losses are associated with digestion of the gross energy in food and with metabolism of the absorbed energy as growing tissues are synthesized. In low-birth-weight human infants, it has been calculated that 10.8 kcal of dietary ME is invested for each gram of fat gain and 13.4 kcal for each gram of protein gain; this is similar to calculations for other animal species with simple stomachs (Roberts and Young, 1988). The average amount of dietary ME used for maintenance and activity in low-birth-weight infants fed different diets was 34.7 $kcal \cdot BW_{kg}^{-1} \cdot day^{-1}$. Total EE data collected with DLW from low-birth-weight infants suggests that these infants have a total EE and, therefore, an energy requirement about 20% greater than that of normal-birth-weight infants (Davies, 1998). Reviews of total EE measurements of normal-weight babies indicate that energy intakes during the first year of life are considerably below current international recommendations. Those recommendations—95 and 84 kcal $ME \cdot BW_{kg}^{-1} \cdot day^{-1}$ for infants from birth to 6 months and from 6 to 12 months, respectively—were based on intakes by healthy infants in developed countries (FAO/WHO/UNU, 1985). They are based on energy expenditure plus energy storage as determined with deuterium. The estimates can be used to calculate dietary ME requirements if the ME values of foods consumed are estimated correctly.

Energy stored in new tissue of growing human infants can be estimated by monitoring changes in BW over time, assuming that each gram of BW gained or lost represents 5.6 kcal (FAO/WHO/UNU, 1985; Davies, 1998). If an infant gains 40 g in a week, 224 kcal of energy would be stored as new tissue per week, assuming that that new tissue has a consistent energy density of 5.6 $kcal \cdot g^{-1}$. Dietary energy (as ME) expended each day for growth has been estimated to be 1.9 $kcal \cdot BW_{kg}^{-1}$ at 10-15 years, 0.96 $kcal \cdot BW_{kg}^{-1}$ at 15 years, and 0.48 $kcal \cdot BW_{kg}^{-1}$ at 16-18 years (FAO/WHO/UNU, 1985).

A similar assumption has been made for growth in other animals, in that 5.6 kcal per gram of expected BW gain is intermediate between a theoretical maximum of about 9 $kcal \cdot g^{-1}$ for fat deposition and a low of 1.5-3.5 kcal per gram of BW gain reported for white-tailed deer, field mice, and voles, animals that accumulate relatively little fat during neonatal growth (Robbins, 1993b). However, diversity in body size among nonhuman primate species creates difficulty in computation of energy needs and efficiencies. In comparing energy allocations with growth and homeothermy, McClure and Randolph (1980) found that the smaller cotton rat (*Sigmodon hispidus*) has a shorter gestation period, is weaned sooner, has larger litters, and reaches sexual maturation faster than the larger eastern wood rat (*Neotoma floridana*). Thus, it appears that young of the smaller species can allocate their energy preferentially to rapid development of physiologic functions rather than to growth. Conversely, young of the larger species can emphasize efficient growth and experience a long period of dependence on maternal investment in that growth. The authors advanced the hypothesis that, in general, large species defer onset of active thermoregulation until body masses of the young are greater (when mass-specific metabolic rates are lower) to permit more-efficient early growth. Small species sacrifice growth efficiency in favor of rapid attainment of early independence and consequently pay high energy costs to do so. If valid, that hypothesis might also apply to nonhuman primates, with species that range in adult weight from less than 100 g to more than 200 kg.

When daily intakes of semipurified diets by male and female squirrel monkeys (*S. sciureus*) weighing 846-1,552 g were measured for a 26-week period, the estimated ME requirement (mean ± SD) for maintenance was 179 ± 19 $kcal \cdot BW_{kg}^{-1} \cdot day^{-1}$. Sex, caloric density of the diet, and dietary fat content did not affect the maintenance requirement. After 24 weight gain or loss periods were measured, the cost of weight gain or loss was determined to be about 7.7 $kcal \cdot g^{-1}$ (only slightly higher than the previously discussed factor of 5.6 $kcal \cdot g^{-1}$). Body-composition changes were not determined (Ausman et al., 1981).

It has been proposed that energy requirements for infant New World monkeys are 300-500 kcal $GE \cdot BW_{kg}^{-1} \cdot day^{-1}$ compared with 200-300 kcal $GE \cdot BW_{kg}^{-1} \cdot day^{-1}$ for infants of the larger Old World species (NRC, 1978; Nicolosi and Hunt, 1979). However, the New World data were derived only from studies of very small species, and such a generalization seems unwise. Both Old World and New World monkeys were reported to have an adult energy requirement that was lower by 30-50% on a $kcal \cdot BW_{kg}^{-1} \cdot day^{-1}$ basis than requirements for growth (Nicolosi and Hunt, 1979). That is similar to the finding in humans that, although total daily EE increases between the age of 10 years and maturity (on the basis of BMR and activity estimates), daily EE per kilogram of BW decreases by about 34% and 30% for males and females, respectively (FAO/WHO/UNU, 1985).

Smaller primate species exhibit higher mass-specific energy requirements for growth than larger primate spe-

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cies. Ausman et al. (1970) reported that infant squirrel monkeys fed a commercial human infant formula consumed 450 kcal ME·BW_{kg}^{-1}·day^{-1}, a caloric intake greater, relative to weight, than that of physically larger, 8-week-old cebus monkeys that consumed 300 kcal ME·BW_{kg}^{-1}·day^{-1}. An average caloric intake of 200-250 kcal ME·BW_{kg}^{-1}·day^{-1} supported growth of healthy, young male squirrel monkeys (initial BW of 695 g) fed a dry commercial monkey diet (Ausman et al., 1985). When semipurified liquid and solid diets were fed to neonatal squirrel monkeys through adulthood, ME intakes approached 500 kcal·BW_{kg}^{-1}·day^{-1} during infancy and decreased to 208 kcal·BW_{kg}^{-1}·day^{-1} for lean adults (average BW, 788 g) and to 155 kcal·BW_{kg}^{-1}·day^{-1} for obese animals (average BW, 1,411 g) (Ausman et al., 1985). Growth patterns of infant squirrel monkeys fed semipurified diets (Ausman et al., 1979) are shown in Table 2-3. Both caloric intakes per kilogram BW and growth rate decreased with time and increasing body size to a final weight of 500 g. Weight gains of young male (104-156 weeks old) and young female (128-220 weeks old) squirrel monkeys (*S. sciureus*) fed a commercial monkey biscuit (3.1 kcal ME·g^{-1}) were 0.88 and 0.50 g·day^{-1}, respectively (Ausman et al., 1981). In contrast, weight gains of squirrel monkeys fed semipurified diets (21-31% of calories as coconut or corn oil, 13% as protein, and 25-35% each as sucrose and dextrin) were 2.89 and 0.89 g·day^{-1} for males and females, respectively. Data from those two studies suggest that the sources of energy in a diet play a role in the induction of spontaneous obesity. The markedly increased weight gain of squirrel monkeys fed the high-fat, purified diets indicates that dietary fat can be important in the regulation of body weight, as was found for rodents (Ausman et al., 1985). When the same diets were fed to *Cebus albifrons*, however, nutritional obesity did not develop before or during a 7-year period after sexual maturation (Ausman et al., 1981).

Infant baboons (*Papio* spp.) were fed similar volumes of two formulas with different caloric densities (0.92 and 0.49 kcal ME·g^{-1}) for an 18-week preweaning period (Lewis et al., 1984). Mean total ME intakes by males and females fed the high-calorie formula were 34.4 and 32.5 megacalories (Mcal), respectively. Both males and females fed the low-calorie formula consumed an average of 20.1 Mcal of ME. Males fed the high-calorie formula gained 145 g more lean mass than females, but fat-mass increases were similar in the two. When fed the low-calorie formula, males gained 150 g more lean mass than did females, but females gained 74 g more fat mass. Animals in another group fed a formula with an intermediate caloric density (0.67 kcal ME·g^{-1}) consumed an average of 24.9 Mcal of

TABLE 2-3 Biologic and Metabolic Parameters of the Young of Various Species Fed Liquid or Dry Diets

Species	Sex	n	Age (y)[a]	Weight (kg)	ME[b] (kcal·d^{-1})	ME[c] (kcal·BW_{kg}^{-1}·d^{-1})	Growth Rate (g·d^{-1})	Diet Type[d]	Reference
Saimiri sciureus									
	M/F	42	N	0.150	65	433	3.4	SP	Ausman et al., 1979
	M/F	42	I	0.200	81	405	2.5	SP	Ausman et al., 1979
	M/F	42	I	0.300	112	373	1.8	SP	Ausman et al., 1979
	M/F	42	J	0.400	123	308	1.3	SP	Ausman et al., 1979
	M/F	42	J	0.500	135	270	0.6	SP	Ausman et al., 1979
	M/F	6	J	0.788	166	210		SP	Ausman et al., 1981
	M/F	13	I	0.110	49.5	450		SP	Ausman et al., 1970
Cebus albifrons									
	M/F	9	I	0.300	97.5	325		SP	Ausman et al., 1970
Macaca fascicularis									
	M/F	10	I	0.400	116	290		SP	Ausman et al., 1970
Macaca mulatta									
	M/F	5	30d	0.65	178	272	6.6	SP	Kerr et al., 1975
	M/F	5	210d	1.71	375	219	5.1	SP	Kerr et al., 1975
	M/F	5	220d	1.76	386	219	5.0	SP	Kerr et al., 1975
	M/F	5	360d	2.37	539	226	3.8	SP	Kerr et al., 1975
	M/F	6	J	4.50	605	136		N	Hansen and Jen, 1979
	M/F	6	J	6.50	748	115		N	Hansen and Jen, 1979
	M/F	16	J	4.50	482	107		SP	Hansen and Jen, 1979
	M/F	16	J	6.50	546	84		SP	Hansen and Jen, 1979
Chimpanzee									
	M	1	2-mo	2.94	226_{GE}	76.8_{GE}		—	Bruhn and Benedict, 1936

[a] N = neonate, I = infant, J = juvenile.
[b] Daily metabolizable energy (ME) intake unless designated as gross energy (GE).
[c] Metabolizable energy intake·kg^{-1}·d^{-1} unless designated as gross energy (GE).
[d] Diet type: SP = semipurified, liquid, N = natural ingredient, liquid.

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ME, an intake that resulted in total body weight gains similar to those of breast-fed baboons. A semisynthetic diet that provided 4.00 kcal ME·g^{-1} (high fat and sugars) sustained good weight gains (an average of 110 g·wk^{-1}) in young male and female baboons (*Papio ursinus*) over a 70-week period (Du Bruyn and De Klerk, 1978).

At birth, male and female cynomolgus monkeys (*Macaca fascicularis*) weighed an average of 402 and 362 g, respectively (Willes et al., 1977). Nursery-reared infants were fed a lactose-fortified formula providing initial intakes of 140 kcal ME·BW_{kg}^{-1}·day^{-1} to both sexes and rising at 30 days to intakes of 325 and 290 kcal ME·BW_{kg}^{-1}·day^{-1} for females and males, respectively. Caloric intake declined to 200 kcal ME·BW_{kg}^{-1}·day^{-1} for males at the age of 140 days and to 250 kcal ME·BW_{kg}^{-1}·day^{-1} for females at the age of 100 days. Kerr (1972) reported declining daily ad libitum intakes of commercial milk products by infant rhesus monkeys between the ages of 1 month and 1 year, with energy intakes declining from 270 to 190 kcal ME·BW_{kg}^{-1}·day^{-1}. Starting at birth, *M. mulatta* weighing an average of 0.48 kg were fed a human liquid formula supplying 0.67 kcal ME·ml^{-1} (Kerr et al., 1975). These infant macaques exhibited decreasing caloric intakes per kilogram of BW with increasing age through 360 days and a decreasing rate of weight gain (Table 2-3).

At peak lactation, the suckling young of most mammalian species consume milk energy at about 225 kcal $BW_{kg}^{0.83}$ daily from milk (Oftedal, 1984). "Milk energy" refers to the GE concentration (kcal·g^{-1}) of the milk and does not account for the metabolic costs of milk production by the mother (Tilden and Oftedal, 1995). Diets in liquid form are essential for neonates, and commercially prepared human-infant formulas providing ME at about 0.67 kcal·ml^{-1} have been used as milk replacers for some nonhuman primates. However, these human milk replacers might have to be modified to meet the special nutritional requirements of some species (Ausman and Gallina, 1979; Lewis et al., 1984; Riopelle et al., 1986; Rutenburg and Coelho, 1988). Milk replacers with ME concentrations of 0.7 kcal·ml^{-1}, mineral salts at 0.68 g per 100 $kcal^{-1}$, and 38.5% of calories from lactose produced apparently normal growth in newborn squirrel monkeys (*Saimiri sciureus*) and cebus monkeys (*Cebus albifrons* and *apella*). Older monkeys (older than 3 months) tolerated substitutions of other carbohydrates for lactose and grew well on a liquid diet formulated to contain ME at 1 kcal ml^{-1}, increased mineral salts per 100 kcal (68% above infant diets), and 51% of calories from a mixture of equal concentrations of sucrose and dextrin (Ausman and Gallina, 1979).

Growth in clinically normal baboons (*P. cynocephalus anubis*) was observed during and after feeding of a control, medium-calorie (0.68 kcal ME·g^{-1}) liquid diet, a low-calorie (0.41 kcal ME·g^{-1}) liquid diet, or a high-calorie (0.95 kcal ME·g^{-1}) liquid diet (Rutenberg and Coelho, 1988). After 16 weeks, when the high- and low-calorie-fed baboons were returned to ad libitum feeding of the control diet, their growth patterns returned to normal by 26 weeks. The research data suggest that in the absence of substantial dietary stressors, growth rates appear to be controlled by a genetic component. "Catch-up" and "catch-down" growth adjustments occur in the same timeframe. However, the consequences of undernutrition and the resulting growth suppression were more negative in this study than those of overnutrition. Males generally resumed normal growth patterns, and females retained the effects of neonatal dietary manipulation throughout later studies (Lewis et al., 1986; Rutenberg and Coelho, 1988; Lewis et al., 1989).

Young, growing adolescent (over 4 kg) rhesus macaques (*Macaca mulatta*) were fed either a commercial dry diet with 4.18 kcal GE·g^{-1} or a highly digestible liquid diet formulated for human use with ME at 1.0-1.1 kcal·ml^{-1} (Hansen and Jen, 1979). Both diets provided sufficient energy. However, energy intakes on both diets decreased with increasing BW and age. Animals weighing 4-4.9 kg consumed 136 kcal ME·BW_{kg}^{-1}·day^{-1} on the dry diet versus 107 kcal ME·BW_{kg}^{-1}·day^{-1} on the liquid diet, whereas animals weighing 5-5.9 kg consumed 6.6% fewer calories from the dry diet and 13.1% fewer calories from the liquid diet per kilogram of BW. Heavier, young adult monkeys, weighing 6-8 kg, consumed the dry or liquid diet with ME at an average of 115 or 84 kcal BW_{kg}^{-1}·day^{-1}, respectively (Table 2-3).

Young, growing male and female pig-tailed macaques (*M. nemestrina*) weighing 4.5 kg initially and fed a commercial dry diet (15% protein) gained an average of 1 kg·$year^{-1}$ up to the age of 4 years (Walike et al., 1977). After the fourth year, females continued to gain 1 kg·$year^{-1}$, but males gained 2 kg·$year^{-1}$.

Energy intake and animal age are important considerations because overconsumption of calories by immature animals can result in excessive weight gain and obesity at or before normal adult weights are reached. Rate of gain of females early in life can markedly influence age and weight at sexual maturity (Steiner, 1987; Lee and Bowman, 1995). Increased calories from dietary fat, 31% versus 12%, fed to premenarchial rhesus monkeys from age 16 months to age 32 months resulted in earlier onset of perineal swelling and menarche despite lower BW. About 80% of the females consuming the high-fat diet exhibited an early first ovulation (at the age of 31-32 months), which was associated with significant differences in endocrine profiles (Schwartz et al., 1988).

In a study of the diets of 30- to 70-week-old, free-living female baboons (*Papio cynocephalus*), energy in the diets of all the animals fell short of their optimums during a 12-month period as determined by comprehensive statistical models developed with data from these animals (Altmann, 1991). Energy limitations during developmental periods of

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growth affect predictions of reproductive life span, survival traits of infants and juveniles, and probability of survival to adulthood. Periovulatory decreases of 10-35% in caloric intake have been reported for two baboon subspecies, *Papio* spp. (Wene et al., 1982) and *P. ursinus* (Bielert and Busse, 1983). Among macaques (*Macaca mulatta*), caloric intake is reduced during the preovulatory period by about 44% compared with all other phases of the estrous cycle. Increased estrogen has an apparent inhibitory influence on food intake during preovulation among both chacma baboons (*Papio ursinus*) (Bielert and Busse, 1983) and rhesus monkeys (Kemnitz et al., 1984, 1989).

Energy Requirements for Pregnancy and Lactation

Energy requirements for pregnancy and lactation remain undefined for nonhuman primates. The recommended dietary allowances for energy for healthy, active women in the first trimester are not different from those for nonpregnant women (National Research Council, 1989; Williams, 1997). However, some suggest an additional 285 or 200 kcal ME·day^{-1} (13% or 10% increase over 2,200 kcal·day^{-1}) for pregnant women with full or reduced activity, respectively (FAO/WHO/UNU, 1985). Those increases sustain the increase in BMR associated with the developing mass of active tissue (fetal, placental, and maternal) plus additional energy needs for new-tissue synthesis. ME increases of 300-350 kcal·day^{-1} (14-16%) for the second and third trimesters have been recommended (FAO/WHO/UNU, 1985; NRC, 1989; Williams, 1997).

The energy cost of lactation equals the energy content of the milk secreted plus the energy cost of milk production. The FAO/WHO/UNU Expert Consultation (1985) recommends that women have an additional energy allowance of 500 kcal ME·day^{-1} for the first 6 months of lactation on the basis of average milk production of 796 ml·day^{-1}.

The average energy concentration of human milk produced by well-nourished mothers is 0.70 kcal GE·ml^{-1} (FAO/WHO/UNU, 1985). The efficiency with which maternal energy is converted to milk energy in humans is about 80% (range 76-94%) compared with swine, in which conversion efficiency is about 72% (National Research Council, 1998). For humans, about 85 kcal of dietary ME are required for every 100 ml of milk produced (National Research Council, 1989).

Voluntary diet consumption tends to increase during gestation, as energy demand increases, although Kemnitz et al. (1984) reported little change in food intake of rhesus monkeys during early pregnancy and suggested that food energy was used more efficiently during pregnant than nonpregnant states. Clarke et al. (1977) estimated that the requirement for energy during pregnancy was 30% above the maintenance requirement. Free-living, lactating nonhuman primates are often severely constrained by dietary energy limitations and foraging distances that increase energy costs by 50-100% above maintenance. Lactating Gelada baboons spent 30% more time in foraging than their nonlactating counterparts, and 75% more time in foraging during peak lactation (Lee and Bowman, 1995). Free-living *P. cynocephalus* spent 45% more time in feeding when pregnant or lactating than a "semi-provisioned" group, including nulliparous females, that had access to human food refuse. Pregnant or lactating females also consumed more energy per day, 1,084 versus 826 kcal of ME (estimated from physiologic fuel values) (Muruthi et al., 1991). Maternal energy requirements for gestation for lemurs (*Eulemur fulvus* and *E. macaco*) and bushbabies (*Otolemur crassicaudatus* and *O. garnettii*), based on litter energy (number in litter x individual GE), have been estimated to be 301 and 256 kcal·$BW_{kg}^{0.75}$ for the respective lemur species and 790 and 393 kcal·$BW_{kg}^{0.75}$ for the respective bushbaby species (Tilden and Oftedal, 1995). Over the course of gestation, those values represented modest increases (2.5-3.0% for lemurs and 3-6.5% for bushbabies) above maintenance energy requirements—estimated to be 80, 83, 88, and 89 kcal·$BW_{kg}^{0.75}$·day^{-1} for *E. fulvus, E. macaco, O. crassicaudatus, and O. garnettii*, respectively. Average litter size was 1.3 young for the two species of lemurs and 1.35 young for the two species of bushbabies. Typical increases of 23-29% in energy requirements for lactation above nulliparous requirements appear to be linked to milk volume and numbers of offspring (Oftedal and Allen, 1996; Williams, 1997).

Maintenance requirements of Callitrichidae have been estimated to be roughly 2 × BMR to 2.5 × BMR (Kirkwood and Underwood, 1984). These researchers found that during the last 8 weeks of pregnancy, caged female cotton-top tamarins (*Saguinus oedipus oedipus*) gained 2 g·day^{-1}, but the increase in energy intake above maintenance was not significant (70.0 versus 66.9 kcal ME·day^{-1}, respectively). During lactation, however, their energy intake appeared to double (to 131 kcal·day^{-1}), although no differences in energy intake were noted for mothers with multiple versus single neonates.

Lactation is the most energetically demanding phase of reproduction for female mammals and can entail a several-fold increase in maternal food intake relative to consumption during nonreproductive periods (Tilden and Oftedal, 1995). Furthermore, both birth mass and milk output vary with body size, but not in direct proportion to maternal mass. When lactating baboons (*P. cynocephalus* and *P. anubis*) were fed 80% or 60% of ad libitum intake—1,052 vs 750 kcal ME·day^{-1}, respectively—the 20% restricted females exhibited a 17-25% increase in efficiency of energy use (Roberts et al., 1985). At 80% of ad libitum intake, milk output and body nutrient stores were protected; but at 60%, milk output was reduced by 20% and body-nutrient mobilization increased. Average energy intake for ad libi-

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tum-fed females was 1,375 kcal ME·day^{-1} throughout lactation. Energy intakes increased by 11% and 27% during initial and peak lactations, respectively, above the intake of 1,169 kcal ME·day^{-1} by nonreproductive females. Low maternal food intake clearly impairs lactation performance when severe enough to mobilize body energy stores.

Energy requirements for lactation often exceed those for rapid growth. Brody (1945) calculated that average daily output of energy in the milk of mammals is about 124 kcal·$BW_{kg}^{0.75}$. Milk-energy output and milk yields are proportional to a power function of body weight ($BW^{0.75}$), but milk yields exhibit a four-fold range among species (45-197 g·$BW_{kg}^{0.75}$ day^{-1}). Primates are at the low end of this range, with typical daily milk yields of 45-70 g·$BW_{kg}^{0.75}$ (Oftedal, 1984). At peak lactation, the metabolic mass of the litter (LLM)—(number in the litter) × (average littermate weight$^{0.83}$)—is a more reliable predictor of milk-energy yield than is maternal metabolic mass (maternal weight$^{0.75}$). It has been proposed that 225 × LLM is an estimate of peak milk energy yield (kilocalores of GE) for most mammalian species (Oftedal, 1984).

Primate milks are typically dilute (8.5-34.1% dry matter) with energy concentrations ranging from 0.5 to 0.85 kcal GE·g^{-1} for Lemuroidea and 1.1 to 1.8 kcal GE·g^{-1} for several prosimian species (Tilden and Oftedal, 1995; Tilden and Oftedal, 1997). Estimated GE outputs during a single lactation are 5,100-7,500 kcal·$BW_{kg}^{0.75}$ for bushbabies and 2,100-3,100 kcal·$BW_{kg}^{0.75}$ for lemurs. Thus, despite the shorter lactation in bushbabies than in lemurs, the estimated total milk-energy transfer of bushbabies is nearly twice that of lemurs relative to maternal metabolic size (Tilden and Oftedal, 1995). Differences in milk composition might be related to differences in maternal care. For example, prosimians that carry their young during lactation produce more dilute milks than do species that leave their young unattended for long periods (Tilden and Oftedal, 1997).

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3 Carbohydrates and Fiber

Carbohydrates are the most abundant of the compounds in living plants, other than water, and serve as a principal repository of photosynthetic energy. They are in aboveground parts (stem, leaves, flowers, fruits, and seeds) and belowground parts (roots and tubers); constitute about 50-80% of the dry matter in leaves, fruits, and seeds; and generally furnish 40% or more of the metabolizable energy in the diets of most primate species, including humans (Asp, 1994). Although their chemical structure and distribution in foods can be described, independently of the animals that eat them, information on the digestion and metabolism of carbohydrates is derived largely from studies of laboratory animals, domestic animals, and humans (Van Soest, 1994; Szepesi, 1996; Levin, 1999). The relevance of the information to nonhuman primates is uncertain, and it is reasonable to expect both similarities and differences among species.

CARBOHYDRATE CLASSIFICATION, CHARACTERISTICS, DIGESTION, AND METABOLISM

Carbohydrates are classified according to size as monosaccharides, disaccharides, oligosaccharides, or polysaccharides.

Monosaccharides

Monosaccharides, often called simple sugars, are single carbohydrate units that contain three to seven carbon atoms. The six-carbon monosaccharides (hexoses) that are particularly important in animal nutrition are glucose, fructose, and galactose.

Glucose is a moderately sweet simple sugar present in honey, ripe fruits, and some vegetables in free form and combined with fructose, forms the disaccharide sucrose (Matthews et al., 1987). It is the chief end-product of starch digestion in rats, pigs, and humans. It is absorbed through the intestinal wall, is transported via the portal vein to the liver, circulates in the blood, and is the primary carbohydrate used by the body's cells for energy. Amounts in excess of immediate need can be stored as glycogen or fat. Although glucose can be used for energy by all cells, it is essential for erythrocytes and brain cells. If unavailable in the diet or glycogen stores, glucose can be produced in small amounts from non-carbohydrate sources (gluconeogenesis). Thus, glucose—and carbohydrates in general—in the short term is not considered a dietary essential, but there are energetic costs associated with gluconeogenesis, and it is likely that minimum dietary concentrations of carbohydrates probably must be present for optimal health and metabolic efficiency. Acquisition of minimal amounts of carbohydrate does not pose a practical problem, because diet formulations designed to meet essential protein (amino acid), fatty acid, mineral, and vitamin requirements have adequate space for any conceivable carbohydrate need.

Fructose is a very sweet simple sugar present in honey, ripe fruits, and some vegetables in free form and combined with glucose in sucrose (Matthews et al., 1987). The enzymes in the mucosal cell brush border appear to adapt to increased intakes of sucrose or fructose, and fructose transport into plasma is accelerated by high intakes of fructose or sucrose in the rat (Mavrias and Mayer, 1973; Reiser et al., 1975) and baboon (Crossley and MacDonald, 1970). Limited amounts of fructose may be used directly for energy or converted into glucose by intestinal mucosal cells. Most of the fructose that reaches the liver via the portal vein is converted to glucose, lipid, or lactate.

Galactose is a simple sugar that is not very sweet and is seldom present free in foods (Matthews et al., 1987). It is usually bound with glucose in the disaccharide lactose, which is found in mammalian milks. Digestion of lactose releases glucose and galactose; after absorption, galactose is converted to glucose in the liver, although the kidney and erythrocyte may be involved in galactose metabolism to a minor extent.

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Disaccharides

A disaccharide consists of two monosaccharide units linked together, such as the disaccharide sucrose which is a plant energy reserve. Monosaccharides and disaccharides are known collectively as soluble sugars.

Sucrose (glucose + fructose) is present in high concentrations in sugar cane and sugar beets and in much lower concentrations in fruits, vegetables, seeds, and nuts (Matthews et al., 1987). Adults have no problem in digesting sucrose, but very young baby pigs show little ability to use dietary sucrose or fructose (Becker et al., 1954a, 1954b) unless gradually adapted to them (Manners and Stevens, 1972). Although apparently not studied in nonhuman primates, that finding suggests caution in the selection of carbohydrates for use in primate milk-replacers.

Lactose (glucose + galactose) is present in most mammalian milks. Some adult humans exhibit lactose intolerance associated with limited intestinal lactase activity; intolerance to lactose also has been reported in captive macaques (Hart et al., 1980; Streett and Jonas, 1980).

Maltose (glucose + glucose) is seldom present free in foods but is an intermediate formed during the digestion of starch to glucose.

Oligosaccharides

An oligosaccharide is a polymer of three or more monosaccharide units. Some are intermediates in the synthesis or degradation of polysaccharides. Oligosaccharides include **raffinose** (a trisaccharide: fructose + glucose + galactose), **stachyose** (a tetrasaccharide: fructose + glucose + two galactose molecules), and **verbascose** (a pentasaccharide: fructose + glucose + three galactose molecules) (Taiz and Zeiger, 1998). Raffinose and stachyose have been found, and their concentrations determined, in some grains, leguminous seeds, nuts, and vegetables (Matthews et al., 1987).

Polysaccharides

Polysaccharides are large, and often complex, polymers of multiple monosaccharide units. They can be divided into two categories, starch and starch-like compounds, which are the only polysaccharides directly digestible by mammals, and non-starch polysaccharides. Non-starch-polysaccharides can be further divided into two sub-categories, insoluble non-starch polysaccharides, also referred to as insoluble fiber, and soluble non-starch polysaccharides, or soluble fiber.

STARCH AND STARCH-LIKE POLYSACCHARIDES

Starch, a polymer of glucose, is a plant energy reserve and occurs in granules that consists of amylose and amylopectin in various proportions (Taiz and Zeiger, 1998). Amylose is primarily a straight-chain polymer of glucose units linked by α-1→4 glycosidic bonds. Amylopectin is a branched-chain polymer of glucose units linked by α-1→4 and α-1→6 glycosidic bonds. Starch solubility ranges from soluble to highly insoluble but tends to form a gel in water unless physical or enzymatic treatment is applied to promote dissolution (Lee et al., 1992; Van Soest, 1994). Starch digestion by endogenous mammalian enzymes involves salivary and pancreatic α-amylases and yields maltose, maltotriose, some glucose, and limit dextrin (three to five α-1,4-glucose units and one α-1,6-glucose unit). Further digestion to glucose is accomplished principally by maltase in the intestinal brushborder. Resistant starch escaping enzymatic digestion or foregut fermentation may undergo microbial fermentation in the hindgut. Starch concentrations in diets fed to captive primates are commonly higher than found in wild foods (Clutton-Brock, 1975; Hladik, 1977; McKey et al., 1981). When high-starch diets are fed, excessively rapid fermentation may lead to digestive upsets, characterized by signs of abdominal discomfort and poor stool quality. This is particularly serious when high-starch, low-fiber foods are consumed by foregut fermenting primates, and may result in death (Göltenboth, 1976).

Glycogen is an animal energy reserve consisting only of amylopectin and is of little quantitative significance in the diets of most nonhuman primates.

Dextrins are polymers of glucose and are intermediates in the digestion of amylopectin (principally from starch).

NON-STARCH POLYSACCHARIDES

Insoluble non-starch polysaccharides do not dissolve in water, nor do they generally swell in water to form a gel. Cellulose and hemicelluloses are structural polysaccharides making up the bulk of plant cell wall and also are referred to as insoluble fiber. They are commonly included in measures of fiber, along with non-carbohydrate components of cell wall, such as the highly complex phenylpropanoid lignin and the fatty substances cutin, suberin, and waxes. Other non-carbohydrate substances variously associated with cell wall (but not usually a part of fiber) are silica, calcium carbonate, tannins, resins, volatile oils, and crystalline pigments (Esau, 1965; Taiz and Zeiger, 1998).

Cellulose is a polymer of 1,000 or more glucose molecules bound together by β-1→4 linkages that cannot be broken (digested) by endogenous mammalian enzymes. Symbiotic gastrointestinal anaerobes can release the energy of cellulose through microbial fermentation and the production of volatile fatty acids, although digestion may not be complete. The principal volatile fatty acids are acetic, propionic, and butyric acids (in descending order of usual abundance) plus small and variable amounts of isobutyric, valeric, and isovaleric acids. Much of the butyric acid (and some acetic acid) can be used directly for energy by intesti-

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nal cells. The other volatile fatty acids are absorbed and enter metabolic pathways (Cummings, 1981; Cummings and Branch, 1986; Bourquin et al., 1992). Wheat bran is an example of a food source of cellulose.

Hemicelluloses are a heterogeneous group of single and mixed polymers of arabinose, xylose, mannose, glucose, fucose, galactose, and glucuronic acid closely associated with cellulose and lignin. Examples are xyloglucans, xylans, glucomannans, arabinoxylans, and glucuronoxylans (Taiz and Zeiger, 1998). Most hemicelluloses are water insoluble, but a few will form a viscous or gel-like solution (Gaillard, 1962). Like cellulose, hemicelluloses cannot be digested by endogenous mammalian enzymes, although they can be partially hydrolyzed in the acid stomach. Anaerobic fermentation is required for effective use of the energy that hemicelluloses contain, and the products of fermentation are essentially the same as those of cellulose. Humans and chimpanzees ferment hemicelluloses somewhat more completely than they do cellulose (Keys et al., 1970; Wiggens and Cummings, 1976; Milton and Dement, 1988).

Soluble non-starch polysaccharides do not dissolve in water completely but swell to form a gel or a gummy solution. Nevertheless, they are referred to as soluble fiber. They are nonstructural polysaccharides, some of which serve as plant energy reserves, but they are not as digestible as starch, although fermented quite completely by ruminal and intestinal bacteria (Salyers et al., 1977; Van Soest, 1994; Bourquin et al., 1996).

Included among the non-starch plant energy reserves are fructans, mannans, and galactans. **Fructans** (also known as fructosans, and including inulin) are polymers of fructose that are stored in grasses and composites (Smith, 1969), as well as in parts of some food crops (Ernst and Feldheim, 2000). Fructans are broken down in an acid environment (Smith, 1969), so passage through the acid stomach may result in release of some fructose monomers that can be absorbed in the small intestine (Ernst and Feldheim, 2000). **Mannans** are polymers of mannose found in sea weeds, algae, nuts, and seeds (Buckeridge et al., 2000; Sachslehner et al., 2000). **Galactans** are polymers of galactose found in sea weeds, algae, and with pectin in fruit pulps (Femenia et al., 1998).

Pectic substances are not plant energy reserves but are associated with the plant cell wall. Despite this association, their relative solubility results in their inclusion among the soluble non-starch polysaccharides along with soluble β-glucans and other gums. They are closely related to hemicelluloses, but have no covalent linkage with lignin, and occur as protopectin, pectin, and pectic acid. They are heterogeneous polysaccharides, characteristically containing galacturonic acid, rhamnose, galactose, and arabinose bound by α-1→4 linkages (Taiz and Zeiger, 1998), that cannot be digested by endogenous mammalian enzymes. Like cellulose and hemicelluloses, however, they can be degraded by fermentation, and microbial degradation of pectic substances is often quite complete (Cummings et al., 1979; Stevens et al., 1988).

Gums and mucilages are related to pectic substances, with which they share the property of swelling in water. Gums include β-glucans (soluble relatives of cellulose found in cereals, especially oats and barley), xyloglucans, and mannoglucans. Gums appear in plant exudates mainly as a result of physiologic or pathologic disturbances that induce breakdown of cell walls and cell contents. Mucilages occur in gelatinous or mucilaginous cell walls of aquatic plants and in seed coats. Sources are gum arabic, tragacanthic acid, locust bean gum, guar gum, xanthan, and tamarind. The algal polysaccharides are agar, alginates, and carrageenins. Psyllium or isopaghula is an indigestible mucilage used as a laxative by humans.

Fermentation of cellulose, hemicelluloses, and pectic substances is quantitatively important in meeting the energy requirements of herbivorous primates that have specialized pregastric (Colobinae) or postgastric (howlers) digestive compartments. Even in primates that have no specialized compartments, anaerobic fermentation of dietary carbohydrates in the colon and cecum can account for up to 28% or more of the total metabolizable energy supply, based upon natural dietary habits and analogies with simple-stomached animals, such as the pig (Parra, 1978). Many soluble fibers tend to ferment faster than do insoluble fibers and may be more energetically important to simple-stomached animals and hind-gut fermenters (Cork et al., 1999). Marmosets and tamarins may derive some of their nutrient and energy requirements by digesting or fermenting plant exudates, including gums, sap, and latex. Some callitrichids, notably the pigmy marmoset (*Cebuella pygmaea*) and *Callithrix* spp., have relatively large lower incisors adapted for tree-gouging and intestinal tract structure adapted for digesting the exudates released (Coimbro-Filho et al., 1980; Rylands and de Faria, 1993). Other callitrichids, such as *Saguinus* spp. and *Leontopithecus* spp., do not have specialized incisors for tree-gouging but feed on exudates opportunistically when they are available because of insect or mechanical damage to plants (Garber, 1993; Rylands, 1993).

Microbial fermentation of carbohydrates in the gastrointestinal tracts of some primates appears to support biosynthetic production of protein from recycled urea and some vitamins, such as vitamin B_{12} (Bauchop, 1978). On the basis of field observations by Jay (1965), it is probable that urea recycling and its associated water conservation contribute to colobines' tolerance of climates that include an extended dry season.

A classification of common dietary carbohydrates and associated digestive enzymes or digestive processes is shown in Table 3-1.

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TABLE 3-1 Common Dietary Carbohydrates and Their Digestion (Kronfeld and Van Soest, 1976)

Carbohydrate	Simple-Sugar Components	Digestion	Digestive Products
Maltose	Glucose	Maltase[a]	Glucose
Sucrose	Glucose, fructose	Sucrase[a]	Glucose, fructose
Lactose	Glucose, galactose	Lactase[b]	Glucose, galactase
Starch	Glucose	Amylases[a]	Glucose
Fructans	Fructose	Gastric acid[a]	Fructose
Galactans	Galactose	Fermentative	Volatile fatty acids
Mannans	Mannose	Fermentative	Volatile fatty acids
Pectins	Arabinose, galactose	Fermentative	Volatile fatty acids
Hemicelluloses	Arabinose, xylose, mannose, galactose, glucuronic acids	Fermentative	Volatile fatty acids
Cellulose	Glucose	Fermentative	Volatile fatty acids

[a] In primates with pregastric digestive compartments, digestion is primarily fermentative, yielding volatile fatty acids. Carbohydrates escaping digestion by endogenous enzymes in primates without pregastric digestive compartments may be digested fermentatively in the hindgut.

[b] Lactase activity declines after weaning in some species, and lactose may be digested fermentatively.

ANALYTIC PROCEDURES FOR CARBOHYDRATES AND FIBER

Analytic procedures for carbohydrates and for fiber are still under development despite a long history (DeVries et al., 1999). Their development is driven by the variability and complexity of carbohydrates and particularly of fiber and by recognition that some compounds in these categories have unique physiologic significance. Van Soest (1994) reviewed the relevant issues and described the limitations and advantages of various analytic techniques, emphasizing the characterization of fiber and pointing out that no protocol is appropriate for all samples. For other reviews of methodology, see Englyst and Cummings (1990) and Spiller (1992).

A basic challenge for the nutritional chemist is to place plant cell components in categories that have physiologic meaning for the plant consumer. One category might include plant components, such as cell contents, that have the potential to be completely available, depending on the rate of digestion and the rate of digesta passage. The category would be comprised of protein, lipids, organic acids, and nonstructural carbohydrates, such as sugars, starch, and fructans; pectic substances, normally associated with the plant cell wall, might be included because of their high availability through fermentation. A second category might include plant components that are incompletely available and that are refractory to hydrolysis by endogenous enzymes but subject to fermentation by gastrointestinal microbes; this category would comprise the structural carbohydrates, cellulose and hemicelluloses. The third category could include plant cell-wall components that are unavailable, such as lignin and cutin, plus indigestible Maillard products resulting from protein denaturation and condensations between denatured proteins and carbohydrates during excessive heat exposure.

Crude Fiber

Crude fiber (CF), as measured in the 19th century Weende procedure, is the insoluble organic residue remaining after sequential treatment of samples with acid and alkali to mimic digestion in the human stomach and intestine. Crude fiber was intended to represent the fibrous fraction of the plant cell that was indigestible. However, the Weende procedure results in substantial solubilization of hemicelluloses and lignin, thus seriously underestimating the structural fiber content (Englyst and Cummings, 1990; Spiller, 1992; Van Soest, 1994). As a consequence, variable proportions of these substances appear in the nonstructural carbohydrate fraction (or nitrogen-free extract [NFE]) by difference. Hemicelluloses, although they are carbohydrates, cannot be digested by endogenous enzymes and yield energy to the host only after gastrointestinal fermentation. Lignin is a noncarbohydrate phenolic polymer that cannot be digested by endogenous mammalian enzymes or fermented by gastrointestinal microorganisms. Thus, the placement of these compounds in NFE is a serious error. These errors in crude-fiber determination have been known for years, but crude fiber continues to be used by regulatory agencies in characterizing animal feeds, apparently because of lack of agreement on alternative procedures.

Total Dietary Fiber

DeVries et al. (1999) suggested that Hipsley in 1953 might have been the first to use the term dietary fiber for the indigestible constituents that make up the plant cell wall. The indigestible constituents were known to include cellulose, hemicelluloses, and lignin, and dietary fiber was intended to distinguish more clearly between the indigestible components and components being measured as crude fiber. The definition of dietary fiber was subsequently

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broadened to include "remnants of edible plant cells, polysaccharides, lignin, and associated substances resistant to (hydrolysis) digestion by the alimentary enzymes of humans." Included in dietary fiber were cellulose, hemicellulose, lignin, gums, modified celluloses, mucilages, oligosaccharides, and pectins and associated minor substances, such as waxes, cutin, and suberin.

After collaborative studies, AOAC Method 985.29 (1995) and AACC Method 32-05 (1995) were officially declared defining procedures for measuring dietary fiber. Modifications to separate total, soluble, and insoluble fiber were adopted as AOAC Method 991.43 (1995) and AACC Method 32-07 (1995). A reference standard with analytic values for those fractions is now available (Caldwell and Nelson, 1999). Total dietary fiber (TDF) (Prosky et al., 1985) is a more recent analytical method recognized as an official method of the AOAC, which has taken on an important role and is used extensively in human nutrition. Concentrations of TDF in human foods are included in the food composition tables in Chapter 12.

Despite that progress, analytic problems in defining dietary carbohydrates and fiber persist (Delcour and Eerlingen, 1996). Starch that is resistant to hydrolysis by digestive enzymes has physiologic effects in humans that make it comparable with dietary fiber. The formation, structure, and properties of enzyme-resistant starch have been reviewed (Eerlingen and Delcour, 1995), and its physiologic properties have been described (Annison and Topping, 1994). Type I resistant starch is trapped in the food matrix. For example, starch granules in cell contents can be physically separated from amylolytic digestive enzymes by an unbroken cell wall, and enzymatic digestion will proceed if the cell wall is ruptured by chewing or by food processing, such as grinding. Type II resistant starch is native granular starch that is resistant to enzymatic digestion because of its compactness and partially crystalline structure; this resistance can be overcome by gelatinization (heating in the presence of water to disrupt hydrogen bonding and destroy crystallinity). Type III resistant starch is formed during retrogradation (recrystallization), primarily of amylose, although retrogradation of amylopectin can also be involved.

The implications of the preceding paragraph for "accuracy" of the current AOAC and AACC methods depend on the intent to include or not include resistant starch in the dietary-fiber residue. Type I resistant starch generally *would not* be included in the residue, because type I resistance is destroyed during grinding of the sample in preparation for the analysis. Type II resistant starch *would not* appear in the residue, because the temperature to which it is exposed during the analysis (100°C) results in gelatinization, and it would be hydrolyzed by the added heat-stable α-amylase. Type III resistant starch consisting of retrograded amylopectin generally *would not* be included in the residue, because heating to 100°C would destroy most or all of the enzyme resistance. Retrograded amylose *would* be included in the residue because its enzyme resistance would not be destroyed until it reached a temperature of about 150°C, which is above the temperature used in the analysis.

Neutral-Detergent Fiber and Related Fractions

Progress is being made in defining the physiologically functional components of dietary fiber in human foods, but few TDF determinations have been made on the foods consumed by nonhuman primates in natural ecosystems or on the complete primate foods consumed in captivity. Except for crude-fiber values required by regulatory agencies on commercial feed labels, most measurements of fiber in the foods have been expressed as neutral-detergent fiber (NDF), acid-detergent fiber (ADF), and/or acid-detergent lignin (ADL), commonly using the procedures described by Van Soest et al. (1991) with the modifications described by Robertson and Horvath (1992). Although this detergent system of analysis does not quantify soluble fibers, quantification of insoluble fibers is comparable to that of the TDF system just described (Lee et al., 1992; Popovich et al., 1997), and soluble fiber concentrations may be estimated by subtracting NDF from TDF (Baer et al., 1997).

The scheme shown in Figure 3-1 illustrates plant cell components that one would expect to find in the various analytic fractions of the commonly used sequential detergent system devised by Robertson and Van Soest (1981). NDF includes the total insoluble fiber in plant cell wall, primarily cellulose, hemicelluloses, and lignin. ADF is primarily cellulose and lignin, and the quantity of hemicelluloses may be estimated by subtracting ADF from NDF. When ADF is treated with sulfuric acid, cellulose is dissolved, leaving a residue designated acid-detergent lignin (ADL) or acid lignin (AL). Lignins are polyphenols that not only are themselves indigestible and unfermentable but interfere with the fermentability of other fractions in the cell wall by physically and chemically entrapping them (Southgate and Englyst, 1985; Cummings and Branch, 1986; Van Soest, 1994), especially lignin-bound proteins (Pichard and Van Soest, 1977). The various fiber fractions also may include tannins, waxes (such as cutin and suberin), and latexes (Van Soest, 1994; Conklin and Wrangham, 1994).

Chitin (an unbranched polymer of β-1,4-linked N-acetyl-D-glucosamine), found in the cell walls of bacteria and fungi and in the exoskeletons of insects and crustaceans (Vonk and Western, 1984), is similar in structure and chemical behavior to cellulose and can be measured in the ADF fraction when analyzing chitin-containing foods of omnivorous or insectivorous primates (Allen, 1989). Chitin can be

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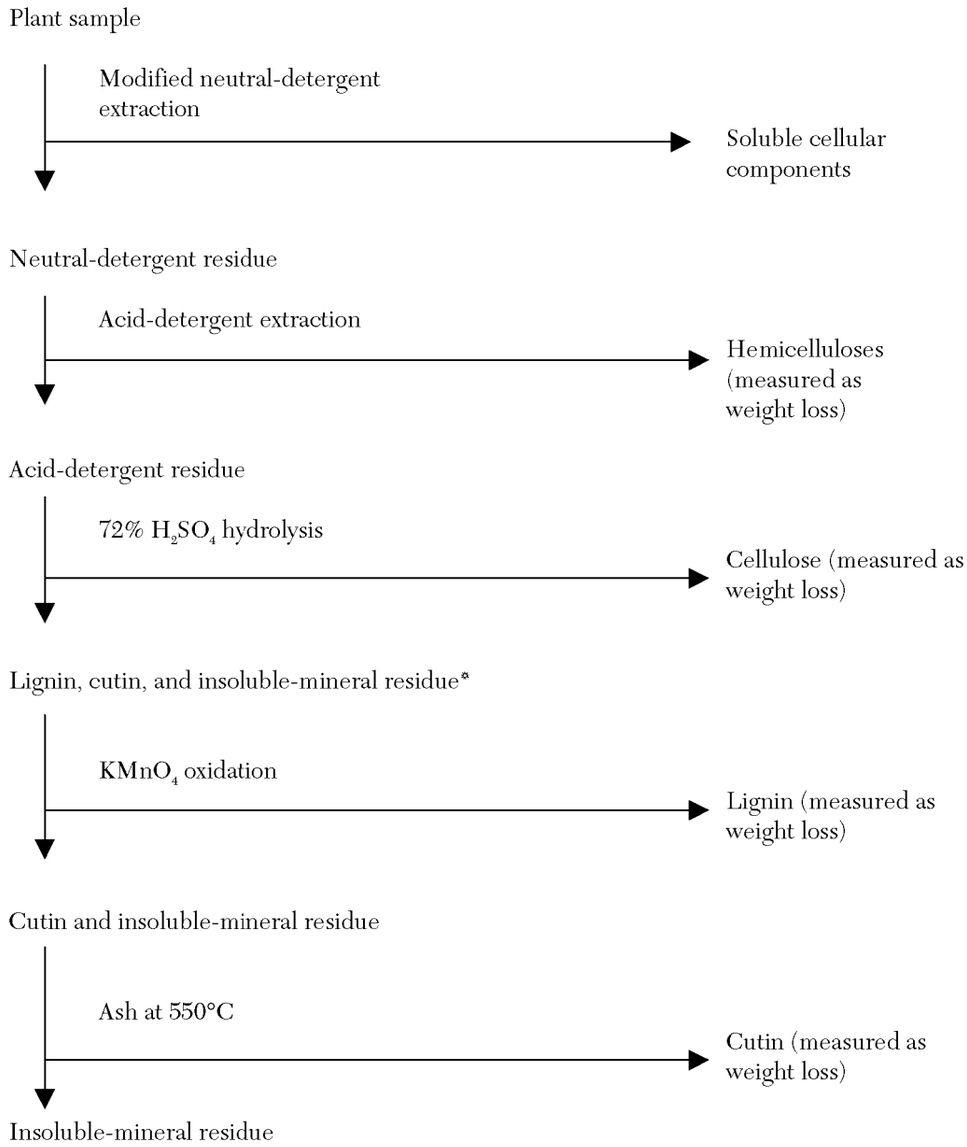

FIGURE 3-1 Plant cell components in the analytic fractions of the sequential detergent system of Robertson and Van Soest (1981). Alternatively, acid-detergent residue may be oxidized first with $KMnO_4$, leaving a cellulose, cutin, and insoluble-mineral residue, with lignin measured as weight loss. Subsequent hydrolysis of the cellulose, cutin, and insoluble-mineral residue with H_2SO_4 leaves a cutin and insoluble-mineral residue, with cellulose measured as weight loss. Ashing the cutin and insoluble-mineral residue at 550°C leaves an insoluble mineral residue, with cutin measured as weight loss.
*Acid-detergent lignin (or acid lignin) can be measured as weight loss after the lignin, cutin, and insoluble-mineral residue is ashed at 550°C and includes lignin + cutin.

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hydrolyzed to chitobiose by chitinase, and chitobiose can be hydrolyzed to N-acetyl-D-glucosamine by chitobiase (Stevens and Hume, 1995). Because these enzymes are found in many indigenous gut microorganisms, their presence in the gastrointestinal tract does not infer endogenous production. However, chitinase has been found in the gastric mucosa of a number of animal species (Jeuniaux, 1962), including the primates, *Cebus capucinus* (Jeuniaux and Cornelius, 1978) and *Perodicticus potto* (Beerten-Joly et al., 1974).

CARBOHYDRATES IN WILD FOOD PLANTS

Few studies of carbohydrates in wild food plants have identified or measured the specific carbohydrates found in plant parts consumed by free-ranging primates. In some instances, analytic procedures were used to measure concentrations of moisture, crude protein, ether extract, ash, NDF, ADF, and ADL in consumed plant parts (fresh basis). When the sum of moisture, crude protein, ether extract, ash, and NDF percentages was subtracted from 100% of fresh weight, the residual fraction was presumed to be mostly nonstructural carbohydrates, largely sugars, starch, and soluble fiber not included in NDF. NDF includes mainly cellulose, hemicelluloses, and lignin, so NDF minus ADL would approximate the structural-carbohydrate concentration; and NDF minus ADL plus nonstructural carbohydrates would yield an approximate measure of total carbohydrates. Of course, such estimates are subject to the errors associated with inaccuracies, imprecision, or lack of specificity in analyses of the other plant components. In addition, the category total carbohydrates combines carbohydrate fractions that differ tremendously in digestibility by endogenous alimentary enzymes. Carbohydrates in the insoluble fiber fraction (NDF-ADL) are relatively low in digestibility, those in the soluble fiber fraction (TDF-NDF) generally are moderately to highly digestible, whereas soluble sugars and starch are highly digestible.

Calvert (1985) collected 36 samples of stems, leaves, shoots, and fruits from 27 species of plants eaten by western gorillas (*Gorilla g. gorilla*) in Cameroon, West Africa. Mean nonstructural-carbohydrate concentrations (dry basis) were estimated to be 28, 5, 24, and 20% in leaves, shoots, stems, and fruits, respectively. Estimates of mean structural-carbohydrate concentrations (cellulose plus hemicelluloses) were 27, 62, 45, and 38%, respectively. Thus, total carbohydrate concentrations were about 55, 67, 69, and 58% in leaves, shoots, stems, and fruits, respectively. Edwards (1995) collected plant parts (representing 90% of feeding time) consumed by red howlers (*Alouatta seniculus*) in the central llanos of Venezuela. Mean dietary nonstructural-carbohydrate concentrations (dry basis) were 29% during the wet season and 37% during the dry season. Structural carbohydrate concentrations (dry basis) were 32% and 31% during the wet and dry seasons, respectively. Thus, total carbohydrate concentrations were 61% and 68%. Conklin-Brittain et al. (1997) analyzed 408 samples of 194 plant parts representing 94% of the plant-feeding time among chimpanzees (*Pan troglodytes*), gray-cheeked mangabeys (*Cercocebus albigena*), blue monkeys (*Cercopithecus mitis*), and redtail monkeys (*Cercopithecus ascanius*) in the Kibale Forest, Uganda. Reported mean concentrations (dry basis) of simple sugars were 10-15% and of total nonstructural carbohydrates from 34-39%. (Conklin-Brittain et al., 1998). Mean concentrations of structural carbohydrates (cellulose plus hemicelluloses) were 23-26%. Thus, total carbohydrate concentrations in the plant parts eaten were 57-65%.

Others have conducted nutrient analyses of the natural foods of gorillas in the Lopé Reserve, Gabon (Rogers et al., 1990), baboons (*Papio anubis*) on the Laikipia Plateau in Kenya (Barton et al., 1993) (Table 3-2), red colobus (*Colobus badius*) and black-and-white colobus (*C. guereza*) in the Kibale Forest in Uganda (Baranga, 1982), and silvered leaf monkey (*Trachypithecus auratus*) in the Pangandaran Nature Reserve, West Java (Kool, 1992) (Table 3-3). The proportions of items in wild diets that were analyzed are lower in Table 3-3 than in Table 3-2. The data generated do not permit estimates of total nonstructural carbohydrates or total carbohydrates, but measurements of ADF make it clear that fiber concentrations were variable in chosen foods and often high compared with those in fruits and vegetables cultivated for human consumption and in commercial primate diets.

Rogers et al. (1990) noted that plant diversity was high in the mature forest inhabited by gorillas in Gabon compared with the impoverished disturbed forest occupied by gorillas in Cameroon (Calvert, 1985). Fruit availability in Gabon was much greater, and Lopé Reserve gorillas eagerly consumed ripe fruits, particularly succulent flesh that tended to be more sugary and less fibrous than unripe fruit or the fruit parts that were uneaten. Mean water-soluble carbohydrate concentration in the dry matter of 46 fruits and fruit parts that were eaten was 35%, and mean ADF concentration 24%. Surprisingly, consumed fruit parts often were higher than nonconsumed fruit parts in condensed tannins and total phenols. Conklin and Wrangham (1994) analyzed nine fig species eaten by frugivorous primates in the Kibale Forest, Uganda, and found that water-soluble carbohydrates (free simple sugars) in the pulp organic matter (dry matter minus ash) were present at 7-23%, whereas NDF was present at 24-65%. For purposes of comparison, total sugar concentrations exceed 33% in the dry matter of the edible portion of raw figs consumed by humans when calculated by adding analytic

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TABLE 3-2 Fiber Concentrations in Wild-Primate Diets (% of Dry Matter) in Studies in Which over 70% of Items in Diet Were Analyzed

Species	Neutral-Detergent Fiber (NDF)	Acid-Detergent Fiber (ADF)	Acid-Detergent Lignin (ADL)	Crude Fiber (CF)	Cellulose	Reference	Notes
New World monkeys							
Alouatta palliata	34.0[a]	—	—	—	13.6	Hladik et al. (1971)	Weighted mean[d]—cellulose in many plant foods
Ateles geoffroyi	27.5[a]	—	—	—	11.0	ibid.	ibid.
Cebus capucinus	19.0[a]	—	—	—	7.6	″	″
Saguinus geoffroyi	18.2[a]	—	—	—	7.3	″	″
Alouatta palliata	50.8[b]	40.8	—	—	—	Glander (1981)	Mean—fruit
	47.5[b]	37.5	—	—	—	ibid.	Mean—mature leaves
	43.7[b]	33.7	—	—	—	″	Mean—young leaves
	47.3[b]	37.3	—	—	—	″	Mean—all items
Alouatta seniculus	50.6	35.8	17.1	—	—	Oftedal (1991)	Mean—flowers
	53.8	35.2	16.6	—	—	ibid.	Mean—fruit
	57.2	40.5	20.4	—	—	″	Mean—mature leaves
	54.4	36.4	21.1	—	—	″	Mean—young leaves
	54.0	37.0	18.8	—	—	″	Mean—all items
Prosimians							
Avahi laniger	53.3	—	—	—	—	Ganzhorn et al. (1985)	Mean—all items
Daubentonia madagascariensi	28.9	22.5	16.8	—	—	Sterling et al. (1994)	Mean—diet items
Old World monkeys							
Macaca fuscata	45.4[c]	—	—	22.7	—	Iwamoto (1982)	Mean—leaves-shoots
	41.8[c]	—	—	20.9	—	ibid.	Mean—fruit-seeds
	23.0[c]	—	—	11.5	—	″	Mean—invertebrates
	36.8[c]	—	—	18.4	—	″	Mean—all diet items
Cercocebus torquatus	33.2[b]	23.2	—	—	—	Mitani (1989)	Weighted mean[e]—diet items
Papio anubis	27.1[b]	17.1	—	—	—	Barton et al. (1993)	Mean—foliage
	37.2[b]	27.2	—	—	—	ibid.	Mean—fruit
	24.8[b]	14.8	—	—	—	″	Mean—seeds
	29.7[b]	19.7	—	—	—	″	Mean—all diet items
Lophocebus albigena	33.0	20.4	8.2	—	—	Conklin-Britain et al. (1998)	Weighted mean[e]—annual diet
Cercopithecus ascanius	31.5	19.4	8.1	—	—	ibid.	Weighted mean[e]—annual diet
Cercopithecus mitis	32.8	20.0	8.1	—	—	ibid.	Weighted mean[e]—annual diet
Cercopithecus mitis	40.2[b]	30.2	—	—	—	Beeson (1989)	Mean—dry-season diet
	35.3[b]	25.3	—	—	—	ibid.	Mean—wet- and dry-season diet
Colobines							
Colobines (several)	44.1[b]	34.1	—	—	—	Waterman and Kool (1994)	Weighted mean[e]—leaves
Presbytis senex	[67.4]	—	—	—	—	Hladik (1988)	Estimated diet NDF
Presbytis entellus	[61.8]	—	—	—	—	ibid.	Estimated diet NDF
Procolobus badius	36.0[b]	26.0	—	—	—	Mowry et al. (1996)	Mean—young leaves
	40.0[b]	30.0	—	—	—	ibid.	Mean—mature leaves
	35.6[b]	25.6	—	—	—	″	Mean—flowers
	62.2[b]	52.2	—	—	—	″	Mean—fruit
	43.5[b]	33.5	—	—	—	″	Mean—all diet items
Apes							
Hylobates lar	33.8[c]	—	—	16.9	—	Vellayan (1981)	Estimated mean—low-fiber diet
	51.2[c]	—	—	25.6	—	ibid.	Estimated mean—high-fiber diet

(continues)

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TABLE 3-2 *(continued)*

Species	Neutral-Detergent Fiber (NDF)	Acid-Detergent Fiber (ADF)	Acid-Detergent Lignin (ADL)	Crude Fiber (CF)	Cellulose	Reference	Notes
Gorilla g. gorilla	46.0	42.6	19.4	—	—	Calvert (1985)	Mean—leaves
	55.9	44.4	11.4	—	—	ibid.	Mean—stems
	73.2	52.0	11.3	—	—	″	Mean—shoots
	64.6	44.8	26.9	—	—	″	Mean—fruit
	59.9	46.0	17.3	—	—	″	Mean—all diet items
	38.8[b]	28.8	—	—	—	Rogers et al. (1990)	Mean—foliage
	33.7[b]	23.7	—	—	—	ibid.	Mean—fruit
	34.6[b]	24.6	—	—	—	″	Mean—seeds
	54.9[b]	44.9	—	—	—	″	Mean—stems-bark
	40.5[b]	30.5	—	—	—	″	Mean—all diet items
Pan troglodytes	33.6	19.6	7.8	—	—	Conklin-Brittain et al. (1998)	Weighted mean[e]—annual diet
Pongo pygmaeus	17.0	—	—	—	—	Knott (1999)	Weighted mean[f]—high fruit
	69.0	—	—	—	—	ibid.	Weighted mean[f]—low fruit

[a] NDF estimated by multiplying analyzed cellulose by 2.5.
[b] NDF estimated by adding 10 to analyzed ADF.
[c] NDF estimated by multiplying analyzed crude fiber by 2.
[d] Weighting coefficient based on proportions of plant foods in stomach.
[e] Weighting coefficient based on time spent in feeding on each food item.
[f] Weighting coefficient based on calculated mass of each food item eaten.

values of 17.7%, 13.4%, and 1.9% for glucose, fructose, and sucrose, respectively (Matthews et al., 1987). Galactose, trioses, and tetroses also were known to be present but were unmeasured. Assuming that the unmeasured sugars were present in low concentrations, failure to consider them should produce only a minimal error in the estimate of total sugar concentrations. Total carbohydrate (including the water-soluble sugars) concentration was reported to be 90.2%, and fiber concentration 5.3% (Watt and Merrill, 1963). Because the latter figure was determined with the Weende crude-fiber procedure, it is probably too low; and because the total carbohydrate value was determined by difference from 100% after analysis of moisture, crude protein, ether extract, crude fiber, and ash, it is probably too high. Nevertheless, the domesticated fig is appreciably lower in fiber and higher in nonstructural carbohydrates than the wild figs consumed by free-ranging primates.

SIGNIFICANCE OF FIBER

Among primate species, acceptable concentrations of fiber in the diet and the ability to digest it tend to be highest in Colobinae (with pregastric fermentation similar to that in ruminants). Human diets are generally low in fiber and elevated levels may decrease fat and protein digestibility, although apparent digestibility of TDF has been shown to range from 67 to 82% (Baer et al., 1997). Certain fibers have a high cation-exchange capacity and may influence mineral metabolism by reducing absorption of iron, calcium, copper, and zinc (Schneeman, 1990). That is not to say that fiber in the diet is an entirely adverse factor. In humans, dietary fiber is useful in managing obesity (Burley and Blundell, 1990; Rytigg et al., 1990). Some fiber appears to lower plasma lipid and cholesterol (Anderson et al, 1990; Sugano et al., 1990), modulate the postprandial glycemic and insulinemic response (Trowell, 1990; Wolever, 1990), and improve large bowel function (Stephan, 1985) in humans. Soluble fiber that undergoes fermentation may contribute little to laxation (Stephen and Cummings, 1980; Southgate and Englyst, 1985), and insoluble fibers of cereal brans are more effective than fiber in domestic fruits and vegetables for increasing fecal bulk (Stephen, 1985). However, fine grinding of cereal brans may greatly reduce this laxation effect (Brodribb and Groves, 1978; Floch and Fuchs, 1978; Wrick et al., 1983; Van Soest, 1994). The risk of diverticular disease (Painter, 1985) and colon cancer (Hill and Fernandez, 1990; Lanza, 1990) in humans may be reduced by increased fiber intake from fruits and vegetables, but the data are not conclusive (Schatzkin et al., 2000). It is difficult to separate the effects of fruit and vegetable fiber from other potentially beneficial components of these foods or from the decrease in relative intake of other foods that may have components that increase disease risk (Gallaher and Schneeman, 1996).

Whether fiber in the diet of nonhuman primates promotes the health benefits proposed for humans has not been sufficiently studied. It has been shown that some fiber or fiber sources may be associated with increases, decreases, or no change (depending on fiber type) in serum lipid and cholesterol concentrations and the incidence of atherosclerosis and colonic mucosal damage in rhesus (*Macaca mulatta*) and vervet or green (*Chlorocebus aethiops*) monkeys (Heine et al., 1984; Kritchevsky et al., 1986,

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TABLE 3-3 Fiber Concentrations in Wild-Primate Diets (% of Dry Matter) in Studies in Which under 70% of Items in diet Were Analyzed

Species	Neutral-Detergent Fiber (NDF)	Acid-Detergent Fiber (ADF)	Acid-Detergent Lignin (ADL)	Crude Fiber (CF)	Total Dietary Fiber (TDF)	Reference	Notes
New World monkeys							
Alouatta palliata	27.5	—	—	—	—	Milton (1979)	Mean—young leaves
	36.4	—	—	—	—	″	Mean—mature leaves Leaves 48.2% of diet
Alouatta palliata	34.4[a]	—	—	17.2	—	Estrada (1984)	Mean—young leaves (39.3% of diet)
	53.6[a]	—	—	26.8	—	″	Mean—mature leaves (10% of diet)
Alouatta palliata	42.8[a]	—	—	21.4	—	Estrada & Coates-Estrada (1986)	Mean—young leaves (36% of diet)
	53.2[a]	—	—	26.6	—	″	Mean—mature leaves (10% of diet)
Prosimians							
Avahi laniger	63.0	46.2	—	—	—	Ganzhorn (1988)	Mean—leaves (folivore)
Cheirogaleus major	63.1	43.0	—	—	—	″	Mean—leaves (frugivore)
Eulemur fulvus	58.7	49.0	—	—	—	″	Mean—leaves (frugivore)
Hapalemur griseus	70.4	29.7	—	—	—	″	Mean—leaves (folivore)
Indri indri	61.4	47.5	—	—	—	″	Mean—leaves (folivore)
Lepilemur mustelinus	62.1	45.1	—	—	—	″	Mean—leaves (folivore)
Old World monkeys							
Macaca fuscata	49.6[c]	—	—	—	—	Hill & Lucas (1996)	Mean—petioles
	66.4[c]	—	—	—	—	″	Mean—leaf midrib
	42.0[c]	—	—	—	—	″	Mean—leaf lamina
Colobines							
Colobus guereza	34.8	20.2	—	—	—	Oates (1978)	Mean—eight foods (68% of diet)
Presbytis johnii	38.1	30.0	13.6	—	—	Oates et al. (1980)	Mean—young leaves (35.4% of diet)
	41.6	32.6	15.3	—	—	″	Mean—mature leaves (26.8% of diet)
Colobus badius	49.4[b]	39.4	—	—	—	Waterman & Choo (1981)	Mean—leaves
Colobus satanas	65.2[b]	55.2	—	—	—	″	Mean—leaves
Presbytis johnii	52.1[b]	42.1	—	—	—	″	Mean—leaves
Colobus badius	48.4[b]	38.4	—	—	—	Choo et al. (1981)	Mean—mature leaves
	38.8[b]	28.8	—	—	—	″	Mean—young leaves
Colobus satanas	70.8[b]	60.8	—	—	—	McKey et al. (1981)	Mean—mature leaves
	58.6[b]	48.6	—	—	—	″	Mean—young leaves Leaf 43%, seeds 57% of diet
Colobus badius,	44.0[b]	34.0	10.2	—	—	Baranga (1982)	Favored foliage (mean of two)
C. guereza	48.4[b]	38.4	17.0	—	—	″	Less-favored foliage (6)
Trachypithecus auratus	40.0[b]	30.0	—	—	—	Kool (1992)	Mean—mature leaves
	45.0[b]	35.0	—	—	—	″	Mean—fruit
Presbytis entellus	34.6[b]	24.6	—	—	—	Kar-Gupta & Kumar (1994)	Mean—winter foliage
	32.6[b]	22.6	—	—	—		Mean—spring foliage
Nasalis larvatus	63.9	34.7	16.5	—	—	Yeager et al. (1997)	Mean—mature leaves
	44.4	31.4	16.0	—	—	″	Mean—young leaves
Rhinopithecus brelichi	46.2	37.0	18.9	—	—	Bleisch et al. (1998)	Mean—leaves
Apes							
Pan troglodytes	50.5	33.7	4.5	—	—	Wrangham et al. (1991)	Mean—pith (nine species)
Pan troglodytes	35.6	—	—	—	—	Wrangham et al. (1993)	Mean—pulp (eight fig species)
	63.7	—	—	—	—	″	Mean—seeds (eight fig species)

(continues)

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TABLE 3-3 *(continued)*

Species	Neutral-Detergent Fiber (NDF)	Acid-Detergent Fiber (ADF)	Acid-Detergent Lignin (ADL)	Crude Fiber (CF)	Total Dietary Fiber (TDF)	Reference	Notes
Pan troglodytes	55.7[b]	45.7	—	—	—	Conklin & Wrangham (1994)	Mean—26 fig species from literature
	41.3	34.3	15.3	—	—	″	Mean—8 fig species from Uganda
Pongo pygmaeus	36.0[b]	26.0	—	—	—	Leighton (1993)	Mean—nonfig pulp
	34.0[b]	24.0	—	—	—	″	Mean—nonfig seeds
	60.4[b]	50.4	—	—	—	″	Mean—nine favored fig species
Pongo pygmaeus	51.3[b]	41.3	—	—	—	Hamilton & Galdikas (1994)	Weighted mean—8 items
Pongo pygmaeus	28.7	—	—	—	—	Knott (1999)	Mean—five favored fruits (high abundance)
	62.2	—	—	—	—	″	Mean—five typical fruits (low abundance)
Gorilla g. gorilla	64.2	47.7	—	—	65.5	Popovich et al. (1997)	Mean—16 leaves
	80.4	54.5	—	—	86.9	″	Mean—eight stems
	79.5	64.6	—	—	66.5	″	Mean—two vines
	78.7	65.4	—	—	83.8	″	Mean—five fruits
							Analyzed 15% of items eaten

[a] NDF estimated by multiplying analyzed CF by 2.
[b] NDF estimated by adding 10 to analyzed ADF.
[c] NDF estimated from wet weight assuming 25% DM.

1988; Paulini et al., 1987). There is strong evidence of beneficial roles for dietary fiber in the diets of several orders of herbivorous animals (Salley and Bryson, 1957; Cummings et al., 1978; Edwards, 1995), including nonhuman primates, particularly those whose gastrointestinal tracts are specialized for foregut or hindgut fermentation by symbiotic microorganisms (Stevens and Hume, 1995). In fact, the occurrence of morbidity associated with gastrointestinal disease in captive specimens of these specialist primates has been attributed to the low concentrations of fiber in their diets (Göltenboth, 1976; Griner, 1977, 1983; Janssen, 1994). The more fermentable (soluble) fraction of dietary fiber may be energetically important for some simple-stomached or hindgut-fermenting nonhuman primates (Cork et al., 1999). Some callitrichid species show evidence of high use of gum arabic included in captive diets, on the basis of measures of dry-matter digestibility (Power and Oftedal, 1996).

PROPOSED FIBER INTAKES BY NONHUMAN PRIMATES

Minimal required dietary concentrations of specific kinds of fiber, such as cellulose, or of a broad fiber category, such as NDF, have not been—and perhaps cannot be—established in the same sense as minimal requirements for essential nutrients. However, adverse effects of inappropriate fiber intakes have been reported in nonhuman primates, particularly in species with specialized foregut or hindgut fermentation, and it might be helpful to draw analogies with other well-studied species.

Fiber Recommendations for Other Species

The National Research Council has recommended that the dietary DM of the dairy cow (a foregut fermenter) should contain no more than 30-40% nonstructural carbohydrate to avoid acidosis and other metabolic problems (National Research Council, 2001). Minimum recommended NDF concentrations for dairy cattle of various ages and productive states range from 25-33% of dietary DM (National Research Council, 2001). When expressed as ADF, the recommended minimal range is 17-21%.

The National Research Council has recommended that the horse (a hindgut fermenter) receive sufficient forage to minimize digestive dysfunctions attributable to sudden dietary change and the feeding of excessive concentrate (inadequate fiber) (National Research Council, 1989). Depending on age and activity, recommended proportions of forage in the total dietary dry matter fed to horses range from 30-100%. Corresponding values for dietary NDF or ADF were not provided.

Fiber in Wild Food Plants as Guides for Captive-Diet Fiber Concentrations

Fiber concentrations in the diets of free-ranging nonhuman primates can serve as guides for fiber in the diets of captive species, and data on fiber concentrations in wild-

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TABLE 3-4 Fiber Levels (% of Dietary Dry Matter) Fed to Primates in Captivity

Species	Neutral-Detergent Fiber (NDF)	Acid-Detergent Fiber (ADF)	Acid-Detergent Lignin (ADL)	Crude Fiber (CF)	Total Dietary Fiber (TDF)	Reference	Notes
Macaca mulatta							
	4.4[a]	—	—	2.2	—	Morin et al. (1978)	Commercial extruded diet; 20.8% intestinal disorders
	4.8[a]	—	—	2.4	—	″	Baked experimental diet; 11.1% intestinal disorders
	14.0[a]	—	—	7.0	—	″	Baked experimental diet; 1.4% intestinal disorders
	19.6[a]	—	—	9.8	—	″	Baked experimental diet; 12.5% intestinal disorders
Alouatta palliata	40.6	25.7	11.4	—	—	Milton et al. (1980)	Wild-fruit diet; AD[b] of NDF = 23%
	39.7	22.7	10.6	—	—	″	Wild-leaf diet; AD of NDF = 41%
Colobus guereza							
	25.1	—	—	—	—	Watkins et al. (1985)	Commercial extruded diet; AD of NDF = 81.3%
Pan troglodytes							
	34.5	10.0	2.8	—	—	Milton & Demment (1988)	Commercial extruded diet; AD of NDF = 54.3%, AD of ADF = 32.9%
	15.3	5.2	1.1	—	—	″	Commercial extruded diet; AD of NDF = 70.6%; AD of ADF = 57.2%
Macaca fuscata, M. mulatta	37.5	15.1	—	—	—	Sakaguchi et al. (1991)	Commercial extruded diet; AD of NDF = 48.3%; AD of ADF = 34.5%
	18.0	4.7	—	—	—	″	Commercial extruded diet; AD of NDF = 78.0%; AD of ADF = 60.7%
Semnopithecus cristatus	37.5	15.1	—	—	—	″	Commercial extruded diet; AD of NDF = 68.9%; AD of ADF = 61.8%
Nasalis larvatus							
	14.0	—	—	—	—	Dierenfeld et al. (1992)	Commercial extruded diet; AD of NDF = 86.4%
	14.5	—	—	—	—	″	Commercial extruded diet; AD of NDF = 86.2%
Callithrix jacchus	—	—	—	—	16.0	Power & Oftedal (1996)	Gel diet; AD of DM = 77.2%
Cebuella pygmaea	—	—	—	—	16.0	″	Gel diet; AD of DM = 83.7%
Leontopithecus pithecus	—	—	—	—	16.0	″	Gel diet; AD of DM = 85.4%
Saguinus fusicollis	—	—	—	—	16.0	″	Gel diet; AD of DM = 74.3%
Saguinus oedipus	—	—	—	—	16.0	″	Gel diet; AD of DM = 83.0%
Varecia variegata							
	24	15	—	—	—	Edwards & Ullrey (1999a)	Experimental extruded diet; AD of NDF = 20.4%; AD of ADF = 9.4%
	42	30	—	—	—	″	Experimental extruded diet; AD of NDF = 20.7%; AD of ADF = 12.6%
Alouatta caraya							
	24	15	—	—	—	Edwards & Ullrey (1999b)	Experimental extruded diet; AD of NDF = 46.5%; AD of ADF = 40.5%;
	42	30	—	—	—	″	Experimental extruded diet; AD of NDF = 45.8%; AD of ADF = 37.7%
Alouatta seniculus							
	24	15	—	—	—	″	Experimental extruded diet; AD of NDF = 43.3%; AD of ADF = 43.1%;
	42	30	—	—	—	″	Experimental extruded diet; AD of NDF = 44.8%; AD of ADF = 39.5%
Alouatta villosa							
	24	15	—	—	—	″	Experimental extruded diet; AD of NDF = 43.7%; AD of ADF = 43.8%
	42	30	—	—	—	″	Experimental extruded diet; AD of NDF = 52.6%; AD of ADF = 46.2%
Colobus guereza							
	24	15	—	—	—	″	Experimental extruded diet; AD of NDF = 77.0%; AD of ADF = 80.1%
	42	30	—	—	—	″	Experimental extruded diet; AD of NDF = 74.3%; AD of ADF = 56.2%
Pygathrix nemaeus							
	24	15	—	—	—	″	Experimental extruded diet; AD of NDF = 66.5%; AD of ADF = 66.6%
	42	30	—	—	—	″	Experimental extruded diet; AD of NDF = 69.8%; AD of ADF = 67.6%
Trachypithecus francoisi							
	24	15	—	—	—	″	Experimental extruded diet; AD of NDF = 79.3%; AD of ADF = 82.3%
	42	30	—	—	—	″	Experimental extruded diet; AD of NDF = 75.7%; AD of ADF = 76.9%

[a] NDF estimated by multiplying analyzed CF by 2.
[b] AD = apparent digestibility.

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TABLE 3-5 Proposed Fiber Concentrations in Total Dietary Dry Matter of Extruded Diets for Primate Species Grouped by Relative Ability to Utilize Plant Cell Wall[a]

Fiber Form and Percentage	Species
Group I	
NDF 10	*Callithrix* spp.
ADF 5	*Cebuella* spp.
	Leontopithecus spp.
	Macaca spp.
	Saguinus spp.
Group II	
NDF 20	*Pan troglodytes*
ADF 10	*Varecia variegata*
Group III	
NDF 30	*Alouatta* spp.
ADF 15	*Colobus* spp.
	Nasalis larvatus
	Propithecus spp.
	Pygathrix nemaeus
	Semnopithecus entellus
	Trachypithecus spp.

[a] These concentrations were reported to have desirable effects on gut health and fecal consistency. Complete diets with higher fiber concentrations are difficult to extrude with present technology, and waste is unacceptably high.

primate foods are presented in Tables 3-2 and 3-3. However, it is questionable whether field studies are sufficient for deducing optimal dietary fiber concentration, in that the foods consumed in the wild depend on what foods are available, both regionally and seasonally. It might be necessary for primates to consume higher-fiber foods in a degraded habitat, and a number of studies have noted a tendency for primates to select against highly fibrous plant parts when less-fibrous foods are available. Of course, concentrations of other components—such as protein, sugars, and tannins—in these plant parts might influence food choices in the wild. Primate populations that appear healthy and that are reproducing at an expected rate are probably not harmed by a seemingly high fiber intake. At some field sites and sampling times, however, certain primates appear to be just maintaining a viable population. Consequently, fiber levels consumed in the wild may represent maximum levels that still allow for growth and reproduction but may not be optimal.

Fiber Digestion by Nonhuman Primates as a Guide for Captive-Diet Fiber Concentrations

The digestive capabilities of several primate species have been studied with multiple fiber concentrations in controlled studies (Table 3-4). Animal response was, as one would expect, related to the gastrointestinal adaptations of the species involved. In one study, the relative digestibility of NDF by primates with foregut fermentation (colobines), hindgut fermentation (howlers), and a simple gastrointestinal tract (ruffed lemurs) was comparable with that seen in domestic mammalian species that have similar digestive tract adaptations (Edwards, 1995).

Proposed NDF and ADF Concentrations in Captive Nonhuman-Primate Diets

On the basis of the data in Table 3-4, we propose NDF and ADF in total dietary dry matter as shown in Table 3-5 for three groups of primate species that have various demonstrated abilities to use plant cell wall. These concentrations are not intended as minimal requirements for fiber, but represent guidelines for diet formulation that are rational and achievable and appear to be consistent with primate health.

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4 Protein

Protein and the element nitrogen (N) have been known as essential dietary components since before the 20th century. In all animals, protein and many of its constituent amino acids are required for maintenance of body tissues, for growth, and as a source of nonprotein N-containing bioactive compounds. Dietary requirements are increased during pregnancy and lactation, stress, and illness and are also influenced by the quality and digestibility of the protein consumed.

PROTEIN SOURCES

Protein can be obtained from a wide variety of foodstuffs. In highly controlled research studies, protein is often provided by purified or semipurified ingredients, such as lactalbumin, casein, and isolated soy protein. In diets composed of natural ingredients, protein is commonly supplied by grains, grain byproducts, legume meals, leafy vegetables, seeds, and seed processing byproducts. Animal products—such as meat meal, fish meal, milk and milk-processing byproducts, and processed eggs—are sometimes used in dry or canned complete diets, and insects can be provided separately as protein sources or as "treats." There are excellent data demonstrating that the nitrogen in the protein in most animal and cereal protein sources varies between 14% and 18% (Jones, 1931), with a mean of 16%. Conversion from nitrogen to protein values is conventionally accomplished by multiplying by 6.25. Based upon amino acid analyses, it has been proposed that the appropriate factor for converting nitrogen concentrations (by Kjeldahl analysis) to protein in the pulp of the tropical fruits *Cecropia peltata, Chlorophora tinctoria, Ficus ovalis,* and *Piper amalogo* may be 4.13, 3.28, 3.67, and 3.12, respectively (Herbst, 1986). Alternatively, nitrogen bound to acid-detergent residue has been subtracted from nitrogen in the whole plant before multiplication by 6.25 to estimate available crude protein concentration (Van Soest, 1994). Conklin-Brittain and colleagues (1999) showed that in some wild tropical vegetation, substantial nitrogen is bound to lignin, making nitrogen bound to acid-detergent residue correction particularly important. For the purposes of the present review, the protein data in Table 4-1 were estimated by using 6.25 to multiply measured nitrogen concentrations in the plant or animal protein sources commonly used in diets for nonhuman primates.

ASSESSMENT OF PROTEIN REQUIREMENTS

Methods

The earliest information on protein requirements of nonhuman primates was derived empirically; that is, concentrations of protein in the diet that appeared to maintain nonhuman primates satisfactorily in active colonies in zoos and research laboratories were considered "adequate." Needs of nonhuman primates also were extrapolated from well-defined requirements for other laboratory, domestic, and wild animals and for humans. Later, several researchers conducted studies of protein requirements, using dose-response experiments in which graded concentrations of dietary protein were evaluated with respect to selected dependent variables, including weight change or growth, urinary and fecal nitrogen, nitrogen balance, and serum albumin. In studies in which multiple dietary protein concentrations were chosen strategically from below to slightly above the expected requirement, a regression analysis could be used to predict the requirement necessary to support the tested outcome variables. In any experiment, the estimate of the dietary protein requirement would, by definition, be the average amount needed to produce a given result. In setting dietary protein requirements for humans, this "average" amount is commonly increased by factors to account for variability in digestibility, protein

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TABLE 4-1 Estimated Protein Requirements for Primates Using High-Quality Reference Proteins

Species	Age	BW Kg	Protein % of DM[a]	Protein Intake g·BW$_{kg}^{-1}$·day^{-1}	Protein Intake % of ME[b]	Protein Source	Dependent Variable	Reference
Saguinus fuscicollis	Adult	0.452	7.3	2.80	6.2	Casein	Weight change	Flurer and Zucker, 1985
Callithrix jacchus	Adult	0.408	6.6	2.50	6.0	Soy concentrate	Nitrogen balance	Flurer et al., 1988
Saimiri sciureus	2-3 wk, infant	0.150	20.8	17.70	14.8	Casein	Weight change	Ausman et al., 1979
	2-3 m, infant	0.300	10.0	7.30	7.1	Casein	Weight change	Ausman et al., 1979
	9 m, juvenile	0.500	8.1	4.30	5.8	Casein	Weight change	Ausman et al., 1979
Cebus albifrons	5 wk	0.400	9.8	5.30	7.0	Lactalbumin	Weight change	Samonds and Hegsted, 1973
	3 m	0.600	8.9	4.20	6.4	Lactalbumin	Weight change	Samonds and Hegsted, 1973
	5 m	0.800	8.1	3.60	5.8	Lactalbumin	Weight change	Samonds and Hegsted, 1973
	7 m	1.000	7.2	3.30	5.2	Lactalbumin	Weight change	Samonds and Hegsted, 1973
	Adult	2.000	7.1	1.80	7.5	Lactalbumin	Weight change	Ausman and Hegsted, 1980
Macaca mulatta	1-7 m, infant	0.500	7.3	4.00	1.7	Milk protein	Weight change	Kerr et al., 1970
	Adult	5.000	7.6-15.1[c]	2-4[c]	6.7-13.4[c]	Casein	Weight change	Riopelle et al., 1974
	Adult	4-12	<16.4[d]	<2.60[d]	<18.9[d]	Mixed	Nitrogen balance	Robbins and Gavan, 1966
Macaca fascicularis	Infant	0.5	9.3	3.8	6.6	Lactalbumin	Weight change	Ausman et al, 1979
	Young	1.000	6.4	2.50	4.6	Lactalbumin	Weight change	Ausman et al., 1979
Pan troglodytes	Young	10-24	<14.2[d]	<4[d]	<14.4[d]	Mixed	Weight change	Hodson et al., 1967
Homo sapiens	3-5.9 m	6.000	—	1.38	5.1	Egg or milk protein	Factorial	NRC, 1989
	6-11.9 m	9.000	—	1.21	4.9	Egg or milk protein	Factorial	NRC, 1989
	1 yr	9-13	—	0.97	3.8	Egg or milk protein	Factorial	NRC, 1989
	9 yr	28.000	—	0.80	4.6	Egg or milk protein	Factorial	NRC, 1989
	Adult female	58.000	—	0.59	6.3	Egg protein	Nitrogen balance	NRC, 1989
	Adult male	70.000	—	0.59	5.8	Egg protein	Nitrogen balance	NRC, 1989

[a] DM = dry matter. Calculations assume 10% moisture content in ingredients in typical diet. All calculations based on crude protein (6.25 × N) or, if not possible, reported protein value in citation.
[b] ME = metabolizable energy.
[c] Insufficient data between 7.6% and 15.1% protein diet to determine actual requirement.
[d] Above requirement. Lower dietary protein concentrations were not tested.

quality, and need within the population. Usually, an extra 30% is added to meet average needs of the population ± 2 standard deviations.

Digestibility

Digestibility of a protein is easily measured over a period of a few days. To determine apparent digestibility, one subtracts fecal nitrogen from ingested nitrogen, divides the result by ingested nitrogen, and multiplies by 100 to express digestibility in percent. Note that estimates of apparent digestibility do not take into account obligatory fecal nitrogen losses that would have occurred (from sloughed mucosal cells, bacterial cells, and enzymes) even if the diets contained no nitrogen. Estimates of true digestibility are always higher and are corrected for this bias by subtracting obligatory fecal nitrogen losses from measured fecal nitrogen before calculating nitrogen disappearance (presumably

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absorbed). Differences between estimates of true and apparent digestibility are larger when dietary protein concentrations are low, because obligatory fecal losses make up a larger proportion of total fecal nitrogen loss. Very few data on protein digestibility (apparent or true) are available for protein sources fed to nonhuman primates.

Robbins and Gavin (1966) fed a commercial monkey diet containing ground wheat and corn, soybean meal, alfalfa meal, and lactalbumin as protein sources to rhesus monkeys and found that the apparent digestibility of total dietary protein was 83.8%. Hodson et al. (1967), using chimpanzees, estimated the apparent digestibility of protein in diets containing ground wheat, dehydrated alfalfa meal, ground corn, dried skim milk, and soybean meal, and providing 12-18% protein. Apparent digestibility was 63-66%. Liquid diets (1.5-8.5% protein) formulated primarily with purified casein and fed to infant capuchin monkeys had an apparent protein digestibility of about 88.3% (Gallina and Ausman, 1986). Protein in diets fed to *Saguinus fuscicollis* had an apparent digestibility varying from 72.9% to 87.1% as dietary protein concentration increased. When fed in increasing percentages to *Callithrix jacchus*, apparent digestibility of dietary proteins increased from 76.6 to 86.8% (Flurer and Zucker, 1985). Thus, the apparent digestibilities of dietary proteins (purified or natural sources) fed to five species of monkeys were found to be 63-88%.

Requirements

Protein requirements of primates do not appear markedly different from those predicted from studies of other mammals. Table 4-1 summarizes the estimated protein requirements of several species of primates, including humans.

Requirements for juvenile to adult primates, expressed as grams of protein per kilogram of body weight (BW) per day, range from 0.59 $g \cdot BW_{kg}^{-1} \cdot day^{-1}$ for adult humans to 4.3 $g \cdot BW_{kg}^{-1} \cdot day^{-1}$ for juvenile squirrel monkeys; most adult primates (when there were sufficient data) required less than 3 $g \cdot BW_{kg}^{-1} \cdot day^{-1}$. When the daily energy intakes of the species were considered, protein concentrations needed to support requirements were 4.6-7.5% of ME calories or 6.4-8% of dietary dry matter. There were insufficient data on adult rhesus macaques and chimpanzees to fix requirements exactly.

Five primate species have been studied from infancy through adulthood: a squirrel monkey, a cebus monkey, two species of macaques, and humans. In each species, protein requirements, expressed as above, decreased as growth rates declined and animals matured.

PROTEIN QUALITY

The nutritional quality of a protein is heavily influenced by its amino acid composition. Mitchell and Block (1946) suggested that the quality of a protein is inversely proportional to its percent deficit in essential amino acids; that is, "limiting" amino acids determine the quality amino acid score of the protein. Given the chemically determined pattern of amino acids in a reference protein, such as that of whole egg, and in a test protein, the amino acid score of the test protein can be calculated without using live animals. Later, other measures of protein quality such as biologic value (BV), net protein utilization (NPU), and protein efficiency ratio (PER) were popularized in studies with humans or rodents (Pellett and Young, 1980; Rand et al., 1981). The most accurate measure, relative nutritive value (RNV), relies on feeding both a reference protein (or standard) and a test protein at several different growth-limiting concentrations in the same experimental paradigm and comparing animal responses to the test protein and the standard (Hegsted and Worcester, 1966; Rand et al, 1981). The result is expressed as potency (test-protein response as a percentage of reference-protein response). Tests of the RNV of proteins have been conducted with squirrel and cebus monkeys and with humans (Table 4-2). The degree to which an essential amino acid becomes limiting is thought to depend, in part, on the growth rate of the test subject; rapidly growing animals require more amino acids for new tissue growth than do adults.

Proteins Limiting in Sulfur Amino Acids

Data from studies of infant and young squirrel monkeys (Ausman et al, 1979) and cebus monkeys (Samonds and Hegsted, 1973; Ausman et al., 1986) indicate that soy protein, limiting in the essential amino acid methionine, has a lower potency than a standard of casein or lactalbumin. It is noteworthy that the addition of methionine in appropriate amounts provided a dietary protein mixture that was not different from the reference protein as judged by nitrogen balance (Ausman et al., 1986). In a final set of experiments, growth and nitrogen-balance assays with growing cebus monkeys indicated that the potency of casein with respect to lactalbumin was 60-70%, reflecting its relative paucity of cysteine. The results were consistent with the lower potency of the same lots of soy protein and casein when assayed with growing rats (Ausman et al., 1986). In comparison, nitrogen-balance experiments with adult humans fed soy protein yielded potencies less than 100% but often not significantly different from the reference protein (Rand et al., 1981). Experiments in which protein quantity and quality are limiting cannot ethically be conducted with infants or children.

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TABLE 4-2 Potency of Common Proteins Measured by Bioassay in Primates

Species	Age	Potency[a] Growth/Weight Maintenance	Potency[a] Nitrogen Balance	Protein Source	Reference
Saimiri sciureus	Infant	100.0	N.D.	Casein	Ausman et al., 1979
	Infant	86.7 ± 13.4[b]	N.D.	Lactalbumin	
	Infant	69.4 ± 13.3[c]	N.D.	Soy protein isolate	
Cebus albifrons	Infant	100.0	N.D.	Lactalbumin	Samonds and Hegsted, 1973
	Infant	46.1 ± 5.6[c]	N.D.	Soy	
	Infant	15.3 ± 2.5[c]	N.D.	Gluten	
	Infant	48.2 ± 5.1[c]	N.D.	Gluten + lysine	
Cebus albifrons	Adult	100.0	N.D.	Lactalbumin	Ausman and Hegsted, 1980
	Adult	46.3	N.D.	Bread + gluten + lysine	
Cebus albifrons	Infant	100.0	100.0	Lactalbumin	Ausman et al, 1986
	Infant	40.6 ± 8.1[c]	46.8 ± 9.4[c]	Soy isolate	
	Infant	72.1 ± 12.7[c]	62.2 ± 12.9[c]	Casein	
	Infant	52.5 ± 8.8[c]	69.0 ± 11.6[c]	Soy concentrate	
	Infant	72.2 ± 13.0[c]	90.7 ± 16.7	Soy isolate + methionine	
Homo sapiens	Adult males	N.A.	100.0	Egg or beef protein	Rand et al, 1981
		N.A.	78.8	Soy isolate	
		N.A.	54.0[c]	Wheat protein	

[a] ND = not done; NA = not applicable.
[b] Mean ± SD.
[c] Significantly different from reference values ($P < 0.05$).

Proteins Limiting in Lysine

The potency of gluten, the major protein in wheat, for infant cebus monkeys was extremely poor—about 15% (Samonds and Hegsted, 1973). It was improved by adding lysine to the diet in an amount equal to that in the reference protein, but performance was still substantially lower than that of the standard. The same situation was found in studies with adult cebus monkeys fed diets containing bread protein and gluten with various amounts of added lysine. Doubling the lysine concentration in the diet was necessary to allow the monkeys to attain their pre-experimental body weights. Additions of threonine and methionine also were helpful in promoting body-weight gain (Ausman and Hegsted, 1980). Experiments with adult humans commonly indicate that the potency of wheat protein, unsupplemented with lysine, is less than 50% of the standard (see the experiment cited in Table 4-2).

Humans rarely consume a diet containing only a single protein source. The exception might be infants that are fed diets containing only milk or soy proteins for the first few weeks of life. Ordinarily, the amino acid composition of the proteins in the diet complement each other. Indeed, the latest edition of *Recommended Dietary Allowances* (National Research Council, 1989) suggests that no correction for protein quality need be made in protein-requirement values for humans in the United States in as much as the biologic value of a typical mixed-protein diet is not distinguishable from that of reference protein.

Given that both young and adult monkeys are sensitive to protein quality, it is extremely important that semipurified and natural-product diets contain nutritionally balanced amino acid mixtures. Combining grain and legume proteins (limiting in lysine and methionine, respectively) or animal and plant proteins generally accomplishes this. Of course, to be satisfactory, commercial monkey biscuits should be formulated to contain adequate concentrations and appropriate proportions of essential amino acids.

AMINO ACID REQUIREMENTS

The essential amino acid requirements of monkeys appear to be similar to those of humans. Although data are insufficient to fix the amino acid requirements absolutely, results of experiments in which essential amino acids were limiting produced results as predicted from studies with humans and with growing and adult mammals of other species.

In primate species with significant foregut fermentation, dietary amino acid requirements may vary. The extent of amino acid degradation and microbial protein synthesis in foregut fermenting species are unknown. Research, similar to the extensive studies that have been conducted in ruminants, is needed to elucidate the effect of foregut fermentation on amino acid bioavailability and requirements.

Lysine and Methionine

The preceding sections have established that lysine and methionine are essential amino acids needed in appropriate

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amounts for normal growth and development of primates. A report by Stegink and colleagues (1980) conclusively showed that D-methionine is poorly used by monkeys. That is in agreement with data from humans but in contrast with data from rats, chickens, pigs, and rabbits, in which D-methionine may be converted to L-methionine by an oxidase. Although no studies have used a pure amino acid mixture to titrate the exact lysine or methionine requirement, the addition of lysine to gluten or bread diets and of methionine to soy-isolate diets markedly improved protein potency (Table 4-2). In the case of methionine-supplemented soy protein, potency was not distinguishable from the reference. That addition of lysine alone to wheat protein did not make its potency equivalent to the reference suggests that a secondary and perhaps tertiary amino acid was limiting (Samonds and Hegsted, 1973; Ausman and Hegsted, 1980).

Phenylalanine

Human infants with phenylketonuria have a deficiency of the hepatic enzyme phenylalanine hydroxylase, which converts phenylalanine to tyrosine. Treatment for this condition is life-long restriction of dietary phenylalanine. Kerr et al. (1969a) fed a commercial formula low in phenylalanine to infant rhesus monkeys. Those maintained on the formula up to the age of 70 days developed lethargy, anemia, anorexia, diarrhea, hair depigmentation, dermatitis, and edema. Supplementation of the formula with phenylalanine ameliorated all the signs except dermatitis. The experiments suggest how difficult it might be to restrict phenylalanine in the diet of a phenylketonuric without producing evidence of protein deficiency.

Tryptophan

Experimental studies with the vervet monkey (*Cercopithecus aethiops*) focused on the role of tryptophan and its neurotransmitter, 5-hydroxytryptamine, in aggression (Chamberlain et al., 1987). Monkeys were given amino acid mixtures that contained no tryptophan (T−), were nutritionally balanced (B), or had tryptophan in excess (T+). During competition for food, the T− solution increased aggression in male vervet monkeys whereas the T+ solution decreased aggression in both males and females. In a second study with these monkeys, Young et al. (1989) were able to show that the change in behavior (aggression) was inversely correlated with the amount of tryptophan and 5-hydroxyindoleacetic acid in the cerebrospinal fluid, adding further support to the idea that altered behavior in humans could be due to a decrease in 5-hydroxytryptamine. Of the common proteins fed, maize has the lowest ratio of tryptophan to total protein.

Taurine

Taurine was first isolated in 1827 from ox bile (Hayes, 1985). Taurine (γ-aminoethanesulfonic acid) is synthesized in liver and brain of all animals studied, but the synthetic system might be poorly developed in young or preterm infants of any species (Hayes, 1985), thereby necessitating an exogenous supply. Taurine is found in most cells, and it is suggested that it performs a wide variety of functions (Gaull, 1989). Initial observations centered on stabilization of the membranes of the central retinal tapetum (Hayes, 1985). It is also thought to play a role in the developing nervous system, conjugation of bile acids, brain osmoregulation, and platelet and muscle function. Infant monkeys fed soy-based human-infant formulas (lacking supplemental taurine) showed a depression in growth and an alteration in the ratio of glycine to taurine in conjugated bile acids (Hayes et al., 1980; Stephan et al., 1981). Indeed, in this latter study, infant cynomolgus monkeys showed no change in bile acid pool size during taurine depletion whereas bile acid pool size dropped from 89.0 to 73.0 $\mu mol \cdot BW_{kg}^{-1}$ in the infant capuchin monkey under the same conditions. It is noteworthy that cynomolgus monkeys normally conjugated 84% of their bile acids with taurine, and taurine depletion decreased this value to 64%. In contrast, capuchin monkeys obligatorially conjugated 97% of their bile acids with taurine, independent of taurine status. Infant rhesus macaques fed a taurine-free diet exhibited a loss of visual acuity and retinal degeneration (Sturman et al., 1984; Neuringer and Sturman, 1987; Imaki et al., 1987). In a further study, Sturman et al. (1988) compared monkeys fed a liquid soy diet with those fed one supplemented with taurine at 70 $\mu mol \cdot dl^{-1}$, the amount in rhesus monkey milk. Taurine concentrations in 28 of 31 tissues measured were significantly increased (by 50-75%) over nonsupplemented concentrations. Further studies showed that by 12 months of age, infant rhesus monkeys were no longer dependent on an exogenous source of dietary taurine (Sturman et al., 1991; Neuringer et al., 1992). Collectively, those results suggest that it is important to provide an exogenous source of taurine for primates for the first year of life.

EFFICIENCY OF PROTEIN USE

Given a high-quality "reference" protein, the efficiency of protein use in the growing rat is greater than 90%. That is to say, given 1 g of dietary protein, a growing rat will deposit more than 0.9 g in its carcass (Rand et al., 1981). Humans are not nearly as efficient; their efficiency of protein use is 50-70% (Rand et al., 1981). Cynomolgus monkeys (*Macaca fascicularis*) fed lactalbumin protein have an efficiency of 65% (Ausman et al., 1979). In one study, infant cebus monkeys fed lactalbumin were reported to

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have an efficiency of 65% (Samonds and Hegsted, 1973) measured by weight gain. In a second study, lactalbumin-fed monkeys showed efficiencies of 43% measured by weight gain or 47% measured by nitrogen balance (Ausman et al., 1986). Finally, when infant squirrel monkeys were fed lactalbumin or casein, their efficiencies of protein use were 28.8 and 37.4%, respectively; this suggests that the animals were extremely inefficient users of the protein provided (Ausman et al., 1979). In all species, efficiency drops as protein quality is decreased.

PROTEIN DEFICIENCY

Beginning in the 1960s, several laboratories worldwide were engaged in studies of protein and calorie malnutrition, using the monkey as a model in which to produce the human diseases of kwashiorkor and marasmus (Oftedal, 1991). Protein deficiency and its sequelae are easily produced in several primate models. The studies have been reviewed by Knapka et al. (1995). Biochemical and clinical signs of protein deficiency include decreased total serum protein and albumin concentrations, decreased plasma amino acid concentrations, decreased serum transferrin concentrations, alopecia, anemia, edema, altered hormone and enzyme concentrations, abnormal neural cytochemistry, and pathologic alterations in several organs.

In some of the studies, the investigators studied pure protein deficiency, pure caloric deficiency, or a combination of the two. Samonds and Hegsted (1978) found that a 33% caloric restriction in the face of an otherwise adequate diet with added proteins, minerals, and vitamins produced a small but otherwise apparently "healthy" monkey. When the caloric restriction was combined with a protein-deficient diet, the resulting animals appeared no worse than either group alone; that suggests that in the face of an energy deficit protein was not "burned" for calories, as implied by several short-term studies in humans (Calloway, 1981; Garza et al., 1976; Calloway and Margen, 1971). The same experimental paradigm was repeated in infant squirrel monkeys fed protein-deficient, calorie-deficient, and protein and calorie-deficient diets (Gallina et al., 1987; Ausman et al., 1989). Again, the double-deficient animals appeared no worse than the others. The observations made on these squirrel and cebus monkeys appeared to be restricted to serum biochemical measurements, food intake, body weight, and appearance. The authors could make no judgments about body composition; rates of protein synthesis, turnover, or degradation; or any other index of protein and calorie metabolism. See Chapter 9 for further discussion of caloric restriction and health.

Alopecia and weight loss in a colony of western lowland gorillas over a 3-year period was ascribed to a dietary protein deficiency, based on findings of hypoalbuminemia, low serum amino acid and protein concentrations, and the positive response to dietary protein supplementation (Mundy et al., 1998).

PROTEIN FOR PREGNANCY AND LACTATION

Protein requirements for pregnancy and lactation have not been systematically studied. The protein requirement for infant monkeys is presumed to be the amount provided in the mother's milk. The protein concentration in mature nonhuman-primate milk is 7-22% of GE (Oftedal, 1984, 1991). Studies of infant squirrel monkeys show that mean protein requirements for maximal growth approximate 18% of ME calories (Ausman et al., 1985b), which is similar to what is found in squirrel monkey milk (Buss and Cooper, 1972).

It is clear that protein deficiency in the pregnant nonhuman primate can have untoward effects on the offspring. When pregnant rhesus monkeys were fed diets containing 3.4% ME calories as protein, neonatal mortality was 40-50% (Riopelle et al., 1975a, 1976; Kohrs, 1976). If the diet provided protein at 0.4-0.5 $g \cdot BW_{kg}^{-1} \cdot day^{-1}$, infants had reduced birth weights (Kohrs 1976; Novy, 1981) and decreased head circumferences for several months after birth (Kohrs et al., 1980). Maternal protein intakes of at least 1 $g \cdot BW_{kg}^{-1} \cdot day^{-1}$ were associated with normal prenatal linear growth; normal birth weight; normal skeletal maturity and measurements; and normal post-natal food intake (Riopelle et al., 1975b, 1976; Cheek et al., 1976; Riopelle and Favret, 1977).

PROTEIN-CALORIE MALNUTRITION IN YOUNG PRIMATES

Nutritional requirements per unit body weight are highest for the young of any species, and growing children or growing animals exhibit the most serious clinical and biochemical evidence of malnutrition when fed diets deficient in essential nutrients. Studies of malnutrition conducted with young rats and pigs have not proved relevant to the pathogenesis of the malnourished human child, primarily because the animals grow more rapidly and have shorter periods between weaning and puberty (Coward and Whitehead, 1972). A closer relationship between higher primates and humans in growth patterns suggests that nonhuman primates would be more realistic experimental models.

Nonhuman-primate models of protein-calorie malnutrition (PCM) could provide a means to study biochemical and physiologic responses to a primary deficiency of either protein or energy and could replicate the related clinical

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syndromes, kwashiorkor and marasmus (Whitehead, 1980). In kwashiorkor, characterized by edema, there is a deficiency in the quantity and quality of dietary protein, whereas energy intake can be adequate; other clinical signs include hypoalbuminemia and consequent fatty liver, growth retardation, loss of weight and muscle mass, and dermal and hair changes (Wilgram et al., 1958; Whitehead, 1980; Coward and Lunn, 1981; Ausman et al., 1989; Murray et al., 1996). Marasmus is most commonly associated with energy-deficient diets, but there can be generalized wasting due to severe and prolonged restriction of both energy and protein and characterized by severe muscle and body-fat loss. To serve as valid models, the pathologic effects manifested in those two disorders should be produced under dietary and environmental circumstances (often including infection) as similar as possible to those of the human population that typically develops these syndromes (Whitehead, 1980). Furthermore, persons conducting animal studies designed to reproduce clinical signs of kwashiokor and marasmus in children should recognize that there are likely to be other essential-nutrient deficits coincidental with the protein and energy deficiencies.

Nonhuman primates (*Macaca mulatta*) have served as models of undernutrition in the study of prepubertal and pubertal reproductive events as related to nutrition and the neuroendocrine system (Steiner, 1987). Young rhesus macaques (*M. mulatta*) with a body mass of 1.5-2.0 kg exhibited PCM after only 45 days when energy (undefined) and protein intake were restricted to an intake of 55 kcal·BW_{kg}^{-1}·day^{-1} and 2.42 g·BW_{kg}^{-1}·day^{-1}, respectively (Mehta et al., 1980). Ad libitum intakes were 90 kcal·BW_{kg}^{-1}·day^{-1} and 3.0 g·BW_{kg}^{-1}·day^{-1}, respectively. The degree of restriction proved severe, and 70% of the monkeys died during acclimatization or during different phases of the study, whereas the monkeys fed ad libitum thrived. PCM was induced in male rhesus macaques 1-12 months old, when 50% of the allotted control diet was fed per day for 10-12 weeks. That restriction provided undefined energy at 55 kcal·BW_{kg}^{-1}·day^{-1} and protein at 2.32 g·BW_{kg}^{-1}·day^{-1} and resulted in a 36% loss in BW, decreased serum albumin concentrations, hair loss, easily peeled skin, muscular wasting, and decreased physical activity (Chopra et al., 1987).

During a study spanning several years, young rhesus macaques (*M. mulatta*) were subjected to various degrees of protein or calorie malnutrition to evaluate effects on physical growth (Kerr et al., 1970), organ size and skeletal growth (Kerr et al., 1973), cerebral lipids (Kerr and Helmuth, 1973), growth failure and "catch-up" growth (Kerr et al., 1975), and biochemical and cytochemical composition of major organs (Kerr et al., 1976). Nutritional rehabilitation of surviving monkeys produced responses comparable with those seen in rehabilitated undernourished children; 2 years later, the external dimensions of the monkeys were within the range of normal controls (Kerr et al., 1973). The study design included feeding the young monkeys (from 1 to 7 months of age) various combinations of five diets: a commercial human-infant milk preparation (ME at about 0.67 kcal·ml^{-1}, protein at 0.0182 g· ml^{-1} [Kerr et al., 1969b]); a 1:1 milk:water dilution of the commercial milk; a 1:3 milk:water dilution of the commercial milk; and the commercial milk with 50% or 25% of normal protein concentration made isocaloric by lactose additions. Mortality of 44-54% was reported in monkeys fed the diet made isocaloric with lactose and containing only 25% of the normal protein level (Kerr et al., 1970; Kerr et al., 1973). Monkeys fed this adequate-energy, low-protein diet exhibited evidence of malnutrition: gastrointestinal distention, diarrhea, enteric infections, lymphoid hypoplasia, anemia, muscular wasting, reduced organ mass, and extensive fatty metamorphosis of the liver. It was noted that, whereas total intake by monkeys fed the low-protein diet was reduced below that appropriate for age, total intake per kilogram of body mass was comparable with that of the controls, owing primarily to weight loss in the protein-restricted monkeys (Kerr et al., 1970). However, during 5 months of rehabilitation, energy and protein deficits (expressed as intake of diet volume in liters, kilocalories of energy, and grams of protein) continued to increase in these animals compared with normal-weight controls (Kerr et al., 1975). A mortality of 17% was reported for monkeys fed the 1:3 diet, in which all nutrients were diluted (Kerr et al., 1970). These monkeys also exhibited marked growth failure despite satisfactory intake (they consumed 3-4 times the usual volume) of all nutrients except for an excess of water. Monkeys that did not consume enough of the dilute diet to provide a normal intake of nutrients had a nutrient deficit of about 20-30% in terms of kilograms of body mass (Kerr et al., 1973). By the age of 7 months, the monkeys fed the 1:3 dilute diet were consuming 217% of the volume of control animals, providing only 54% of the normal energy and protein intake (Kerr et al., 1975). Monkeys fed the dilute diet accumulated nutrient deficits that were not restored during nutritional rehabilitation, but the deficits did not continue to increase. Young (10-28 months old), pigtail macaques (*M. nemestrina*) were fed 400 g of synthetic diet per day, containing either 20% or 2% casein and ME at 3.96 or 3.24 kcal·g^{-1}, respectively, for about 3 months to determine biochemical and morphologic alterations in response to PCM (Enwonwu et al., 1973). In a preliminary study, the protein content of the diet was gradually reduced over a period of 9 months from 8% through 6% to 2%. Monkeys fed the 8% or 6% casein diets ad libitum gained BW and showed no clinical or biochemical signs suggestive of PCM. After 3 months of the 2% casein diet, however, serum albumin concentration was reduced by 25%, plasma corticosteroid had increased by 132%, and impairment of liver-protein biosynthesis resulted in extensive fatty liver metamorphosis.

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Four infant crab-eating macaques (*M. fasicularis)*, 5-7 months old, also were fed a 2% casein diet over 14 weeks (Worthington et al., 1979) and exhibited significant decreases in plasma essential amino acids (especially the branched-chain group), whereas plasma nonessential amino acids tended to rise (especially glycine and alanine). The peak response was noted within 3-4 weeks of protein restriction.

Nine 6- to 9-month-old male crab-eating macaques (*M. nemestrina*) from the study of Enwonwu et al. (1977) were later further diet-restricted and fed the 20% and 2% casein diets at 200 $g \cdot day^{-1}$ for 20 weeks to examine hepatic alterations associated with PCM. Mean initial BW of both groups was 1.4 ± 0.13 kg. Control monkeys fed the 20% casein diet showed a 40% net gain of BW during the 20-week study. Monkeys receiving the 2% casein diet showed a 4% net gain of BW, which was consistent with marked accumulation of extracellular fluid. Severe disturbances of the structure and function of the liver were noted.

Female rhesus macaques (*M. mulatta*), 12-24 months old and weighing 2.1 to 3.0 kg, were fed either 2% or 0% protein diets (isocaloric to 20% casein diet) to provide undefined energy at 100 $kcal \cdot BW_{kg}^{-1} \cdot day^{-1}$. Structural changes were observed in the liver, myocardium, and striated muscle. There also was extensive cytoplasmic necrosis of the pancreas, the organ most severely affected; and cellular injury was evident in pancreatic secretions that were enzyme-deficient (Racela et al., 1966). In kwashiorkor, pancreatic enzymes have been described as deficient at a very early stage of the disease before fatty change of the liver is evident. During a 6-week interval, six 4-kg rhesus macaques (*M. mulatta*) were fed a diet deficient in protein but providing undefined energy at 100 $kcal \cdot BW_{kg}^{-1} \cdot day^{-1}$. They developed carbohydrate intolerance attributed to diminished insulin production, hepatic dysfunction, and decreased glucose disposal as a consequence of protein deprivation (Khardori et al., 1980).

Young squirrel monkeys (*Saimiri sciureus,* Leticia) have been used as pediatric models in malnutrition studies because they share several physiologic characteristics with human infants. They were fed diets restricted in protein, in energy, or in both (Gallina et al., 1987; Ausman et al., 1989) from the age of 2 to 8 weeks, or were only protein-restricted from the age of 4 to 24 weeks (Gallina et al., 1987) to support maintenance of BW without significant weight gain. The earlier study was designed to investigate the effects of particular nutritional deficiencies on plasma concentrations of albumin and transferrin, proteins used as biochemical indexes of nutritional status. Imposition of severe energy restriction (less than 250 kcal $ME \cdot BW_{kg}^{-1} \cdot day^{-1}$) with adequate protein intake (23% of calories) did not lower serum albumin concentrations in four animals—a finding similar to that observed in another ceboidea species (*Cebus albifrons*) fed similarly (Samonds and Hegsted, 1978). Plasma albumin levels were decreased only when dietary protein (6.82% or 3.41% of calories), but not energy, was low (Gallina et al., 1987). Plasma transferrin in the control animals was significantly higher than in animals that were diet-restricted in protein, energy, or both. Sixteen monkeys exhibited an adaptive response to dietary manipulation in which energy restriction (288 ± 30 kcal $ME \cdot BW_{kg}^{-1} \cdot day^{-1}$ vs control 449 ± 71 kcal $ME \cdot BW_{kg}^{-1} \cdot day^{-1}$) coupled with protein restriction (4.9 ± 0.3 $g \cdot BW_{kg}^{-1} \cdot day^{-1}$ vs control 14.6 ± 2.3 $g \cdot BW_{kg}^{-1} \cdot day^{-1}$) provided no evidence of a more severe protein deficiency than protein restriction alone (Ausman et al., 1989).

The effects of PCM on early growth of 8- to 28-week-old, 520-g cebus monkeys (*Cebus albifrons*) were studied when they were fed a synthetic liquid control diet (13% of calories as lactalbumin protein and undefined energy at 135 $kcal \cdot day^{-1}$), a low-protein diet (2.8% of calories), or a low-calorie diet (90 $kcal \cdot day^{-1}$) (Fleagle et al., 1975). By week 4 of the 20-week study, significant body-size differences were apparent. By 20 weeks, both protein- and calorie-restricted animals had developed a thin, emaciated appearance associated with marasmus, not from continuous loss of tissue but from redistribution of tissue over a slowly expanding skeleton that differed in proportion and shape from that of control monkeys. Fatty liver also was associated with a low protein concentration or dietary amino acid imbalance in cebus and rhesus *(M. mulatta)* monkeys (Wilgram et al., 1958).

Sucrose, when provided as the primary carbohydrate—20% of the total energy in a low-protein diet—potentiated the development of fatty liver, a rapid fall in serum albumin concentration to 1 $g \cdot dl^{-1}$, edema, and other signs of kwashiorkor among young baboons (*Papio* spp.). These baboons were diet-manipulated (low-protein, high-carbohydrate staples: banana, cassava, and matooke) and periodically stressed with acute energy restriction to produce models of PCM (Coward and Whitehead, 1972). Average protein and undefined energy intakes of control baboons were 6.1 $g \cdot BW_{kg}^{-1} \cdot day^{-1}$ and 290 $kcal \cdot BW_{kg}^{-1} \cdot day^{-1}$, respectively. Average serum albumin concentrations in the controls were maintained at 4.05 $g \cdot dl^{-1}$. When starch was the primary carbohydrate, there was a notable absence of fatty liver infiltration among similar baboons (Coward and Whitehead, 1972; Whitehead, 1980). Suppressed immune response in three baboons with signs of kwashiorkor also has been reported (Qazzaz et al., 1981).

Marmosets and tamarins, members of the family Callitrichidae, also have served as nonhuman-primate models of human disease. In research laboratories, they have suffered reproductive inefficiencies and high mortality due to the occurrence of "wasting marmoset syndrome" (WMS), a protein-calorie deficiency that is characterized by weight loss, alopecia, chronic diarrhea, muscle atrophy, chronic

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colitis, and often anemia (Barnard et al., 1988). Seventeen male and 22 female adult *Saguinus mystax* were offered a commercial canned (60.3% moisture) marmoset diet at 120 g·day^{-1}. The diet contained 23.4% crude protein (CP, dry basis) and 4.74 kcal gross energy (GE) per g of dry matter (DM), and was supplemented 3 days per week (20 ml per supplemented day) with a preparation (78.7% moisture) containing 14.2% CP (dry basis) and GE at 4.11 kcal·DM$_g^{-1}$. Ingredients in the commercial diet included water, ground wheat, whole egg, soy grits, sucrose, brewer's rice, dried skimmed milk, vegetable oil, dehydrated alfalfa meal, dicalcium phosphate, iodized salt, and brewer's dried yeast. The supplement contained water, wheat germ, honey, grape juice, and Biozyme®. On those days when only the commercial canned product was offered, average consumption was 172 g·BW$_{kg}^{-1}$·day^{-1}, providing 12.0 g of protein and 290 kcal GE·BW$_{kg}^{-1}$·day^{-1}. When the supplement was available, consumption of the commercial diet decreased to 110 g·BW$_{kg}^{-1}$·day^{-1}, providing 10.2 g of protein and 185 kcal GE·BW$_{kg}^{-1}$·day^{-1}. The tamarins preferred the supplement and, when offered, consumed it prior to consumption of the canned diet. The tamarins lost weight and exhibited alopecia and chronic diarrhea.

During 3 months of feeding a pelleted diet (10.3% moisture), formulated to contain 26.2% protein (dry basis) and 4.78 kcal GE·DM$_g^{-1}$, mean food intake was 82 g·BW$_{kg}^{-1}$·day^{-1}, providing protein at 19.3 g and GE at 335 kcal·BW$_{kg}^{-1}$·day^{-1}, and the marmosets gained an average of 56 g. The pelleted diet contained rice gel, glucose, soybean meal, dried apple pomace, high fat milk solids, casein, beet pulp, soy oil, soy lecithin, and mineral and vitamin premixes. Evidence of WMS abated, and hematologic and serum-biochemistry profiles were no longer consistent with those of protein-calorie deficiency. The authors concluded that the tamarins appeared physically unable to consume sufficient amounts of the high-moisture canned diet and supplement to meet apparent protein and energy requirements for prevention of WMS. Because some of the pathophysiologic signs exhibited during consumption of the commercial diet and supplement resemble those of gluten intolerance, and these signs disappeared when the pelleted diet containing no gluten source was fed, it may be appropriate to consider the possibility of a multifactorial nutritional disease. The issue of callitrichid nutrition and food sensitivity has been explored further by Gore et al. (2001).

PROTEIN EXCESS

Although pathologic protein excess is more rare in monkeys than in other species, such as the rat, monkeys can develop pathologic changes in the kidney, which sometimes lead to terminal renal failure (Burek et al., 1988). It is common practice in all species, including humans, to limit protein intake to prolong the preterminal period in renal disease (Bourgoignie, 1992). It has not been shown in humans that a high-protein diet will compromise an otherwise healthy kidney.

Bourgoignie et al. (1994) monitored renal function in 14 baboons that had been subjected to right nephrectomy and 20-30% infarction in the left kidney and that had been fed either 8% or 25% protein diets. Hemodynamic and metabolic characteristics were measured every 4 months for 5 years. Modest proteinuria developed after the kidney infarction, and hypertension after the nephrectomy. There was no difference in these measures between the monkeys fed 8% and 25% protein diets and no progression of the proteinuria or hypertension during the 60 months. Inulin clearance and glomerular filtration rate were significantly greater in baboons fed the 25% than the 8% protein diet throughout the study. The results suggest that within the 5-year experimental period excess protein was not detrimental to kidney function in the absence of other disease.

In humans, it has been clearly shown that excess dietary protein increases urinary calcium loss (see Chapter 6) and thus calcium requirements. There are no data on calcium requirements of nonhuman primates relative to different dietary protein intakes. Therefore, the conservative approach is to keep dietary protein within reasonable bounds.

NON-AMINO-ACID EFFECTS OF PROTEIN SOURCES

Soy protein can have biologic effects other than those that depend strictly on protein quality. Fitch et al. (1964) reported reduced iron absorption and later anemia in rhesus monkeys fed a diet of soy isolate. Ausman et al. (1977) also reported anemia when infant squirrel monkeys were fed a protein-limiting diet based on soy isolate but not when they were fed lactalbumin. It was unclear which aspect of the soy protein was responsible for the anemia, although phytic acid in soybean meal has been shown to chelate iron and reduce its availability. A slightly lower digestibility of soy-protein was observed when diets containing soy-protein concentrate, casein, or lactalbumin were fed to *Callithrix jacchus* and *Saguinus fuscicollis* (Flurer et al., 1985).

Protein sources are often carriers of potentially harmful or beneficial non-amino-acid components in the primate diet. Examples are saturated fat and cholesterol in red meat and fiber in grains. Raw soybeans have harmful concentrations of trypsin inhibitor, which, when incorporated into the diet, interfere with protein digestion in all species and are associated with pancreatic hypertrophy and cancer in rodents (McGuinness et al., 1980, 1982). Heat treatment of soybean meal or isolating soy protein decreases trypsin

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inhibitor several fold, decreasing risk of an adverse effect. Cebus monkeys fed diets based on soy isolate or soy concentrate for 4 years showed no differences from controls in tests strategically chosen to examine pancreatic function and disease (Harwood et al., 1986; Ausman et al., 1985a). Chacma baboons showed no untoward pancreatic effects of raw soy protein (Robbins et al., 1988).

Consumption of diets based on soy protein has been associated with a reduction in plasma LDL-cholesterol concentrations in humans and nonhuman primates (Anderson et al., 1995; Anthony et al., 1996). Although early research suggested that the amino acid pattern of soy protein was responsible for the hypocholesterolemic effect, the latest evidence suggests that the isoflavonoid phytoestrogens genistein and diadzein may be the active compounds (Anthony et al., 1997).

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5 Fats and Fatty Acids

Fats have the highest energy density among dietary components. Fatty acids are basic chemical units of fat, and the names and structural features of several are shown in Table 5-1. The fatty acids most commonly found in primates and in primate diets have 16 and 18 carbon atoms; those found less commonly have 12, 14, 20, and 22 carbon atoms. All are straight carbon chains that have zero to six double bonds in the *cis* conformation. Fatty acids with double bonds in the *trans* conformation are rare in nature and are unlikely to have an important presence in natural foods of primates. Multiples of double bonds typically occur in series, with a double bond beginning every fourth carbon. Essential fatty acids are those which cannot be made by the body; and for primates, these include the n-3 and n-6 fatty acids (Innis, 1991).

The designations n-3 and n-6 (sometimes written ω-3 and ω-6) refer to the number of carbons from the methyl end of the fatty acyl chain to the first double bond. The fatty acid that is the building block for the n-6 series is linoleic acid, an 18-carbon fatty acid containing two double bonds, the first between the sixth and seventh carbons. The building block for the n-3 fatty acids is α-linolenic acid, an 18-carbon fatty acid with three double bonds, the first between the third and fourth carbons. A short-form designation for fatty acids lists the number of carbons, a colon, the number of double bonds, and identity of the n series, for example, C18:2 n-6 for linoleic acid (Lin, et al., 1994; Buss and Cooper, 1970). The liver and, to a lesser extent, other tissues have enzymes needed to elongate and further desaturate linoleic and α-linolenic acid to make other fatty acids in these series. However, the primates that have been studied have no enzymes that can desaturate fatty acids at the third or sixth carbon. Thus, the basic fatty acids with these double bonds are termed essential and must be consumed in the diet.

Most dietary fats of animal or vegetable origin are triacylglycerols (TAGs; formerly called triglycerides); they have three fatty acids esterified to a glycerol molecule in one of three stereochemically distinct bonding positions: sn-1, sn-2, and sn-3. To a lesser extent, phospholipids also are parts of primate diets, typically with two fatty acids esterified to a glycerol phosphate molecule and an acidic or basic adduct attached to the phosphate residue.

The classification of a fatty acid as essential means that the fatty acid is not synthesized by the body. A recent article presents a proposal to reclassify essential fatty acids into categories of "conditionally indispensable" and "conditionally dispensable" (Cunnane, 2000). This proposal was made recognizing that the requirement for each of the n-3 and n-6 fatty acids is not the same throughout the life span of the animal. Adult animals do not need the same level of dietary intake as young, growing animals in part because they have well-developed body stores of each of the essential fatty acids. Further, the number of longer chain derivatives of either linoleate or α-linolenate with additional double bonds is recognized as large and each may sometimes be classified as essential by some individuals. However, the bulk of the evidence is that with the dietary precursor 16 or 18 carbon fatty acids with either the n-3 or n-6 double bond in place, the remainder of the n-3 or n-6 fatty acid series, respectively, can be generated in the body by the appropriate elongases and desaturases. While there is some evidence that not all of these enzymes for fatty acid modification are present in equivalent abundance, apparently all are available to the extent needed to provide for normal function. Some have suggested that the fatty acids in the n-3 and n-6 series will compete for access to one or more of the desaturases; however, the likelihood that such competition could lead to a deficiency has not been demonstrated. In addition, the efficiency of utilization of α-linolenate for making docosahexaenoic acid (22:6 n-3) for use in body functions is less than direct utilization of exogenous docosahexaenoic acid, due to the many energy requiring elongation and desaturation steps used in deriving the latter from the former. However, this does not change the fact that the body cannot generate either the n-3 or n-6 double bond in any fatty acid. We have used the term essential fatty acid to indicate this fact. We con-

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TABLE 5-1 Common names, scientific names, and short-form designations of fatty acids

Common Name	Scientific Name	Short-Form Designation
Butyric acid	butanoic acid	C4:0
Caproic acid	hexanoic acid	C6:0
Caprylic acid	octanoic acid	C8:0
Capric acid	decanoic acid	C10:0
Lauric acid	dodecanoic acid	C12:0
Myristic acid	tetradecanoic acid	C14:0
Palmitic acid	hexadecanoic acid	C16:0
Stearic acid	octadecanoic acid	C18:0
Palmitoleic acid	9-hexadecaenoic acid	C16:1 n-7 *cis*
Oleic acid	9-octadecaenoic acid	C18:1 n-9 *cis*
Elaidic acid	9-octadecaenoic acid	C18:1 n-9 *trans*
Linoleic acid	9,12-octadecadienoic acid	C18:2 n-6,9 all *cis*
α-Linolenic acid	9,12,15-octadecatrienoic acid	C18:3 n-3,6,9 all *cis*
γ-Linolenic acid	6,9,12-octadecatrienoic acid	C18:3 n-6,9,12 all *cis*
Arachidic acid	eicosanoic acid	C20:0
Behenic acid	docosanoic acid	C22:0
Eicosenoic acid	11-eicosenoic acid	C20:1 n-9 *cis*
Erucic acid	13-docosaenoic acid	C22:1 n-9 *cis*
Brassidic acid	13-docosaenoic acid	C22:1 n-9 *trans*
Nervonic acid	15-tetracosaenoic acid	C24:1 n-9 *cis*
Dihomo-γ-linolenic acid	8,11,14-eicosatrienoic acid	C20:3 n-6,9,12 all *cis*
Arachidonic acid	5,8,11,14-eicosatetraenoic acid	C20:4 n-6,9,12,15 all *cis*
Timnodonic acid	5,8,11,14,17-eicosapentaenoic acid	C20:5 n-3,6,9,12,15 all *cis*
Clupanodonic acid	7,10,13,16,19-docosapentaenoic acid	C22:5 n-3,6,9,12,15 all *cis*
Docosahexaenoic acid	4,7,10,13,16,19-docosahexaenoic acid	C22:6 n-3,6,9,12,15,18 all *cis*

sider the most common dietary n-6 and n-3 fatty acids, linoleate and α-linolenate, as truly essential since these fatty acids must be ingested. Additional long chain polyunsaturated fatty acids can be constructed from these fatty acids, but ingestion of fatty acids with the n-3 and n-6 double bonds is a true requirement.

FAT ABSORPTION

In response to entry of fat into the intestine during digestion of a meal, the liver secretes bile into the gut; with the help of intestinal peristalsis, food fats are emulsified. Simultaneously, the pancreas secretes digestive enzymes, including lipases and esterases, into the small intestine. Fat digestion begins at the surface of emulsion particles with pancreatic lipase-catalyzed hydrolysis of triacylglycerol molecules into two fatty acids and a monoacylglyceride. These products of initial lipolytic activity and bile salts are active in further breakdown of emulsion particles and, with phospholipid and cholesterol bile micelles, form the micellar phase from which lipid absorption is maximal. In most laboratory studies of nonhuman primates, fat digestion and absorption were essentially quantitative, with less than 5% of dietary fat lost in the feces; this was true in a wide array of types and amounts (up to 40% of ME) of fat ingested (L. Rudel and P. Huth, unpublished). The processes of fat digestion and absorption also facilitate the absorption of cholesterol and fat-soluble vitamins from the intestine. These molecules are incorporated into emulsion particles and micelles, from which they pass into the enterocyte. However, only about 50% of cholesterol is absorbed from the intestine (Rudel et al., 1994; Wilson and Rudel, 1994), though some of the molecular processes involved are different for sterols and fatty acids.

Once inside the intestinal enterocyte, fatty acids and glycerides are reassembled into triacylglycerol molecules and incorporated into newly forming chylomicrons that include a protein, apolipoprotein B48. Nonhuman primates and humans share the characteristic presence of only apolipoprotein B48 in the intestine for transport of TAGs in chylomicrons, in contrast with the liver, where only apolipoprotein B100 is used for TAG secretion in very-low-density lipoproteins (VLDLs) (Klein and Rudel, 1983). Newly absorbed cholesterol is also esterified and incorporated into chylomicrons, although it makes up only about one percent (by mass) of these particles.

Capture of high-energy fatty acids from chylomicrons is efficient. The chylomicron particles are secreted by the enterocytes into basolateral spaces, where they cross into the lymphatic lacteals and enter the body via the thoracic lymph duct. This pathway of entry into the bloodstream directs fats first to the peripheral tissues, where interactions with lipoprotein lipase (LPL), attached to the endothelial cells of most tissues, can occur. Removal of TAG molecules from chylomicrons then proceeds with the LPL-catalyzed hydrolysis of TAGs into two fatty acids and a monoacylglyceride. In this form, the molecules pass across cell membranes and enter cells. In adipose tissue, TAG molecules are reassembled and stored for later use. In most other

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tissues, the fatty acids are either oxidized for energy or used for assembly of the phospholipid molecules that are the primary building blocks of cell membranes. After the bulk of the TAGs are removed, the remainder of the chylomicron particle, termed a remnant lipoprotein and still containing absorbed cholesterol and fat-soluble vitamins, travels to the liver, where it is quantitatively removed from the bloodstream.

MILK FATS

The position of the three fatty acids on the three-carbon glycerol backbone of fats is not random, but appears to depend on fatty acyl specificities of enzymes involved in TAG synthesis and to some extent in TAG hydrolysis. These molecules are taken apart and resynthesized several times during their movement into the body, so it is important to recognize that fatty acids in the sn-1 and sn-3 positions are the most labile and most readily available for use in the tissues. The fat in milk gives perhaps the best indication of the relative importance of different fatty acids. The breast milk of most primates that have been studied contains a TAG concentration of about 4 $g \cdot dl^{-1}$, which represents about 50% of the GE provided by milk (Wolfe et al., 1993).

Milk fats of several Old World nonhuman primates (including five different macaque species, African green monkeys, Talapoin monkeys, and the sooty mangabey) have been reported to have a fatty acid composition similar to that of the fat in human milk (Buss and Cooper, 1970; Jensen et al., 1980; Smith and Hardjo, 1974a; Smith and Hardjo, 1974b; Wolfe et al., 1993). In the work of Smith and Hardjo (1974b), caprylic (C8:0), stearic (C18:0), oleic (C18:1), and linoleic (C18:2) acid were found predominantly in the sn-1 and sn-3 positions, and lauric (C12:0), myristic (C14:0), palmitic (C16:0), and palmitoleic (C16:1) acids were found in the sn-2 position of the TAG molecule. Linoleic acid made up about 12-13% of the fatty acids, and 80% of this was in the sn-1 and sn-3 positions. The most abundant fatty acid was oleic acid (25-30%), and over 80% of it was found in the sn-1 and sn-3 positions. Palmitic acid was about 20% of total fatty acids and was the most abundant fatty acid in the sn-2 position, representing about 40% of total sn-2 fatty acids. Long-chain polyunsaturated fatty acids were not reported in this study.

Buss and Cooper's (1970) examination of the milk of Talapoin monkeys revealed a fatty acid composition that differed somewhat from that of milk of the other primate species. Linoleic acid made up about 40% and palmitic and oleic acids about 20% of total fatty acids. The Talapoin monkeys were fed commercial monkey biscuits, a diet low in fat (about 10% of ME) with about 44% of the fatty acids as linoleic acid. Talapoin milk fat contained about 5% more palmitic acid and 5% less oleic acid than the fat in the diet. α-Linolenic acid was found to be 2.5-5.5% of milk fatty acids compared with 7% of fatty acids in the diet.

African green monkeys were fed two fat-enriched diets (40% of ME) containing isocaloric amounts of polyunsaturated or saturated fat (Wolfe et al., 1993). Milk analyses revealed that the dietary fat of the mothers was a major factor in determining the fatty acid composition of their milk, as previously shown in humans (Potter and Nestel, 1976). Linoleic acid was 14% of the total milk fatty acids when dietary fat was enriched in saturated fatty acids and 42% of total milk fatty acids when the diet was enriched in linoleic acid. The increase in linoleic acid in the milk of mothers fed polyunsaturated fat was at the expense of the other major fatty acids in the milk of the saturated fat group. Monounsaturated fatty acids (primarily oleic acid) were 45%, and saturated fatty acids (primarily palmitic acid) 40% of the fatty acids in the milk of the saturated-fat group. Concentrations of both monounsaturated and saturated fatty acids decreased to 28% of total fatty acids in the milk of the polyunsaturated fat group. Birth weight and growth and development of infants in both diet groups were comparable. Thus, the fatty acid shift in the mothers' diet and in later milk fatty acid composition had no obvious detrimental effects on normal growth of the monkeys (Wolfe et al., 1993). From the perspective of milk fatty acid composition, the data suggest that the types of fatty acids acceptable for primate diets can vary widely, and they provide no support for the contention that linoleic acid levels above 20% of total dietary fatty acids might be harmful (discussed by Innis, 1991).

ESSENTIAL n-3 FATTY ACIDS

Primate diets should contain sufficient concentrations of both n-3 and n-6 fatty acids to support normal growth and development. In a study of African green monkeys (Wolfe et al., 1993), dietary ME was present as long-chain n-3 fatty acids (docosahexaenoic acid and eicosapentaenoic acid) at about 0.25%. Another 0.2% of dietary ME was present as α-linolenic acid. That was sufficient to provide the long-chain n-3 fatty acids needed for normal growth and development. Other studies have shown that if all of the n-3 fatty acids in the diet are to be provided in the form of α-linolenic acid, it can take as much as 1% of dietary ME to maintain normal brain and retinal development (Innis, 1991). Those findings are consistent with the observations of Greiner et al (1996) indicating that the efficiency with which docosahexaenoic acid is incorporated into brain and retinal lipids of fetal and infant rhesus monkeys is about 10 times higher than that of α-linolenic acid and the data from Su et al (1999b) showing a 7-fold higher efficiency in neonatal baboons. A large body of literature

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indicates that the amount of long-chain n-3 polyunsaturated fatty acids required in the diet is less than the requirement for α-linolenic acid alone (reviewed by Innis, 1991; Greiner et al., 1997; Su et al. 1999a).

The patterns of brain development in rhesus monkeys show a growth spurt in the last trimester of fetal development; the brain of a newborn weighs nearly 70% as much as that of an adult (Venkatraman et al., 1992). The presence of n-3 fatty acids, and particularly the long chain docosahexaenoic and eicosapentaenoic acids, in the diet of pregnant females (Greiner et al., 1996), is therefore critical for sustaining normal brain development. The work of Conner and associates (Connor et al., 1984; Neuringer et al., 1984; Neuringer et al., 1986; Lin et al., 1990; Reisbick et al., 1991; Lin et al., 1994; Reisbick et al., 1994) has demonstrated that a deficiency of n-3 fatty acids in diets of rhesus monkeys can result in demonstrable abnormalities in brain and retinal function. In a series of studies, two diets were fed to pregnant and lactating females, one with about 1% of dietary ME as α-linolenic acid (control) and one with less than 0.1% of dietary ME as α-linolenic acid (deficient). The infants raised on the n-3 fatty acid-deficient diet showed reduced visual acuity by the age of 4 weeks (Neuringer et al., 1984). Deficient monkeys also showed a tendency toward increased intake of water and other fluids (Reisbick et al., 1991) and more stereotypical behavior than the control monkeys (Reisbick et al., 1994).

Observed biochemical changes included reduced docosahexaenoic acid levels in the phospholipids of brain and retina and replacement with long-chain n-6 fatty acids, principally 22:5 n-6 (Lin et al., 1990). Replenishment of the deficient diet with long-chain n-3 fatty acids from fish oil for 14 months resulted in complete reversal of the patterns of n-6 and n-3 fatty acids in brain phospholipids. The remodeling of brain phospholipids appeared to occur normally without significant loss of n-3 fatty acids (Innis, 1991). Furthermore, observations of Kanazawa et al. (1991) in cynomolgus monkeys and in Japanese macaques showed that the ability of the brain tissue to convert α-linolenic acid into docosahexaenoic acid is age-dependent, being essentially zero in newborn primates and increasing maximally in young adults. Nevertheless, apparently adequate amounts of docosahexaenoic acid are deposited in the brains of monkeys fed diets in which essentially the only n-3 fatty acid is α-linolenic acid (Lin et al. 1990). That indicates that other tissues, predominantly the liver, have the desaturases and elongases needed for conversion of α-linolenic acid to the docosahexaenoic acid required for lipid deposition in the gray matter of developing brain and in the retina. In the case of monkeys, in which much of brain development occurs *in utero*, the transfer of n-3 fatty acids across the placenta into the fetus supplies a major portion of the requirements for early life (Innis, 1991).

The amounts of n-3 fatty acids that must be consumed for adequate deposition of docosahexaenoic acid in the developing nonhuman primate brain can be estimated by extrapolation (Kanazawa et al., 1995) from human data (Clandinin et al., 1980a, 1980b). However, it is difficult to define an exact dietary requirement because much of the needed n-3 fatty acid will be derived *in utero* from the mother, and the efficiency of this transfer process is unknown (Greiner et al., 1996). Subsequent studies by the same group (Greiner et al., 1997) gave the estimate of the requirement as 0.45% of ME as α-linolenic acid or 0.30% of ME as docosahexenoic acid (22:6 n-3) in fetal baboons for normal brain development. Other data show that diets of rhesus monkey mothers with 1% of ME as α-linolenic acid were adequate to maintain normal fetal brain development, as were infant diets that contained about 2% of ME as α-linolenic acid (Lin et al., 1990; Neuringer et al., 1984). Furthermore, the data derived from studies of African green monkeys showed that diets for mothers and infants containing about 0.25% of ME as long-chain n-3 fatty acids (eicosapentaenoic and docosahexaenoic acids), with another 0.2% of α-linolenic acid, resulted in normal development (Wolfe et al., 1993). In the mother's milk, about 0.6% of ME was found as 22:5 n-3 and 22:6 n-3 fatty acids, and 0.2% as α-linolenic acid. Therefore, in the absence of dose-range studies, those data form the basis of the minimal amounts of n-3 fatty acids recommended for nonhuman primate diets. It is recommended that 0.5% (by weight) of dietary dry matter (about 1% of ME) be present as n-3 fatty acids to support normal development and maintenance of the brain and nervous system.

ESSENTIAL n-6 FATTY ACIDS

Research showing that n-6 fatty acids are dietary essentials for nonhuman primates was published by Greenberg and Moon (1961), who documented changes in blood fatty acids in rhesus monkeys fed a linoleic acid-deficient diet. Subsequently, Greenberg (1970) showed that diets containing corn oil at about 2% by weight (about 4% of ME) prevented the deficiency. Portman et al. (1959, 1961) demonstrated linoleic acid deficiency in cebus monkeys and described the changes in physical appearance of the animals and many biochemical changes in fatty acid composition and concentration in their tissues. Substantial pathophysiologic changes in cebus monkeys fed a fat-free diet for 19 months were limited to scaly skin, hyperplastic bone marrow, erythrophagocytosis by the reticuloendothelial system, and undersized gonads. The link between requirements for polyunsaturated fatty acids and vitamin E was studied in rhesus monkeys made vitamin E-deficient (Fitch et al., 1961, 1963). It was shown that vitamin E deficiency could be induced by using diets either unsupplemented

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or supplemented with fat, but the level of vitamin E required for normalcy was higher in fat-supplemented diets, presumably because of the involvement of vitamin E in preventing lipid peroxidation. When dietary fats were more saturated, the requirements for vitamin E were lower. When monkeys are fed fat-deficient diets, the simultaneous occurrence of fatty acid deficiency and vitamin E deficiency is of concern because absorption of fat-soluble vitamins is limited in the absence of sufficient quantities of dietary fat, and some of the documented pathologic changes might have been due to vitamin E deficiency.

The minimal amount of linoleic acid required in the diet of nonhuman primates is not known with certainty. The milk fat of many of the primate species described above contained about 10-15% linoleic acid, or a minimum of about 5% of GE. It should be noted that nonhuman-primate milk fat also typically contains 1-1.5% arachidonic acid, the bioactive metabolite of linoleic acid, which is the most prominent precusor of eicosanoids, bioactive molecules used in many signal transduction processes within and among cells. Linoleic acid and its metabolites (arachidonic acid (20:4 n-6), di-homo-γ-linolenic acid (20:3 n-6) and docosapentaenoic acid (22:5 n-6) are a significant part of the fatty acids in the developing brain, and to a lesser extent in membrane lipids in other tissues. Thus, for normal growth and development, it is essential that adequate linoleic acid or its products such as arachidonic acid be consumed in the diet. Su et al. (1999b) studied the kinetics of conversion of linoleic acid to its bioactive products in pregnant and fetal baboons fed a diet with 2% ME as linoleic acid and 0.2% α-linolenic acid, possibly a less than maximal dose of n-3 fatty acid as discussed above. The data suggest that the fetus derives about half of its arachidonate from conversion of linoleic acid and half from the diet, with the amount in the brain plateauing by 21 days after dosing. The ratio of n-6 to n-3 fatty acids in the diet was 10:1, a dose considered representative of the normal for human adults. The authors point out that this ratio might have affected the outcome, depending on the competition among n-3 and n-6 fatty acids for the desaturases and elongases required for conversion.

From the available data, we can only infer that the minimal requirements of infant monkeys for linoleic acid and its metabolites may be in the range of 5% of dietary GE. Greenberg (1970) replaced about 2% of dietary ME with linoleic acid in young adult rhesus monkeys and appeared to reverse the signs of n-6 fatty acid deficiency, so the requirement in older animals may be somewhat less than in infant monkeys, perhaps 1-2% of dietary ME. Therefore, it is recommended that the dry matter in diets for nonhuman primates contain 2% of linoleic acid by weight to avoid a deficiency of n-6 polyunsaturated fatty acids.

A separate issue is the upper limit of acceptable concentrations of n-6 polyunsaturated fatty acids in the diet. The value would appear to be high, on the basis of laboratory experiments with African green monkeys in which n-6 fatty acids in milk made up 42% of total fatty acids or about 20% of ME, and a n-6:n-3 ratio of >50 with no demonstrable ill effects on infant growth and development (Wolfe et al., 1993). Maintaining an optimal ratio of dietary n-3 to n-6 fatty acids has been proposed so that interactions among desaturase and elongase enzymes, involved in synthesis of long-chain polyunsaturated fatty acids, do not exacerbate any deficiency (Innis, 1991). However, data are insufficient to know where that is a concern. Normal development has been observed over a wide range of n-3:n-6 ratios.

DETRIMENTAL FATTY ACIDS

Fatty acids that could cause harmful effects in primates include the long-chain, monounsaturated docosaenoic acids—22 carbons with one n-9 or n-11 double bond (Loew et al., 1978; Schiefer et al., 1978). Diets studied contained very high concentrations (25% by weight or about 50% of ME) of rapeseed oil or partially hydrogenated herring oil. The *Cebus* monkeys in the studies had very high intakes of 22-carbon fatty acids with one double bond (constituting up to 25% of total fatty acids in rapeseed oil and 24% of the herring oil used in the experiments). Laboratory-reared animals were fed the diets for 120-170 days and were then killed and their hearts examined. A mild degeneration of cardiac and skeletal muscle with lipid infiltration was noted, although the pathophysiologic changes were mild compared to that seen in rats. It should be mentioned that the rapeseed now used for making canola oil has been genetically modified so that concentrations of docosaenoic acid are no longer increased.

CHOLESTEROL

A minimal dietary cholesterol concentration has not been established. Monkey milk has cholesterol at 10-20 $mg \cdot dl^{-1}$, which is equivalent to about 0.06 $mg \cdot GE_{kcal}^{-1}$ (Wolfe et al., 1993). That would provide an infant with milligram quantities of cholesterol that could be used for brain development or incorporated into cell membranes of many tissues. However, commercial monkey biscuits that have essentially no cholesterol and have been shown to be hypocholesterolemic (Rudel, 1997) have been fed to many mothers during *in utero* development of the fetus and during nursing of infants with no obvious ill effects. Thus, a dietary requirement for cholesterol seems unlikely. If cholesterol is not available in the diet, it is synthesized in tissues that require it or is transported into those tissues from plasma via LDL receptor after synthesis in the liver or intestine (Brown and Goldstein, 1986). Dietschy and

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Wilson (1968) showed essentially all tissues in the body of the squirrel monkey have the capacity to synthesize cholesterol.

PRIMATES AS CARDIOVASCULAR DISEASE MODELS

The typical diet of Western humans is rich in fat and cholesterol, and both constituents are believed to contribute to the coronary heart disease (CHD) epidemic in Western societies. Many studies have been conducted in nonhuman primates (reviewed in Strong, 1976) using diets imitating the Western diet to identify the nutritional factors important in development of atherosclerosis (hardening of the arteries), the disease process underlying CHD and the leading cause of death in Western societies (Marmot, 1992). When diets are fed containing 35-40% of ME as fat of different types, nonhuman primates do not develop significant atherosclerosis. However, when cholesterol is added to such diets, most species develop a degree of hypercholesterolemia that is species-specific (Rudel, 1997). Studies of the sensitivity of *Macaca* to dietary induction of atherosclerosis have included the rhesus monkey (*Macaca mulatta*), cynomolgus monkey (*Macaca fascicularis*), and pigtailed macaque (*Macaca nemestrina*) (Strong, 1976). Macaques, in general, are highly diet responsive, with cynomolgus monkeys and pigtailed macaques being particularly sensitive. Vervet monkeys (*Cercopithecus aethiops*) and patas monkey (*Erythrocebus patas*) are less so and require more dietary cholesterol to induce hypercholesterolemia and atherosclerosis (Rudel, 1997). The baboon (*Papio* spp.) has been extensively studied, is among the most diet-resistant primate species, and requires a dietary cholesterol concentration of 1.7 $mg{\cdot}ME_{kcal}^{-1}$ for atherosclerosis to develop (McGill et al., 1981). If nonhuman primates are maintained on a hypercholesterolemic diet long enough, usually several years, coronary artery atherosclerosis will develop (Rudel et al., 1995a), and the coronary artery lesions will show essentially all of the characteristics seen in atherosclerosis in humans (Rudel et al., 1995b). Nonhuman-primate diets enriched in n-3 and n-6 polyunsaturated fatty acids appear to protect against coronary arterial atherosclerosis, whereas diets enriched in saturated and monounsaturated fatty acids appear to promote the disease, as demonstrated in several studies (Rudel et al., 1995a; Rudel et al., 1995b; Rudel et al., 1998; Wolfe et al., 1994). The phytoestrogen content of soy is protective, and the primate model has been useful in clarifying these effects (Anthony et al., 1997; Clarkson et al., 2001).

The lesson to be taken from those studies is that many species of nonhuman primates have a diet-related susceptibility to atherosclerosis similar to that of humans and so can constitute good models for studying the mechanisms of atherosclerosis. In general, these man-prepared diets are well tolerated; and in some studies in which offspring were born and raised, body weight and size were normal to large relative to those of comparable animals from the wild (Wolfe et al., 1993). However, the likelihood that such diets would be encountered in the wild by nonhuman primates is nil.

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6 Minerals

Animals, plants, and microorganisms all require minerals. In animals, minerals function as structural components of organs and tissues, as cofactors or activators in enzyme and hormone systems, as constituents of body fluids and tissues (where they maintain osmotic pressure, acid-base balance, membrane permeability, and tissue irritability), and as regulators of cell replication and differentiation (Underwood and Suttle, 1999). If tissues and foods are burned, the mineral content is the fraction that remains; it is termed ash. The inorganic elements in ash exist principally as oxides, carbonates, and sulfates, so the percentage of total ash is higher than the sum of the individually determined inorganic elements. Some of the elements in ash are essential nutrients, but few definitive studies have been conducted in nonhuman primates to determine quantitative requirements.

The essential macrominerals include calcium, phosphorus, magnesium, potassium, sodium, chlorine, and sulfur. Concentrations of macrominerals in animal diets are usually expressed in percentages.

Trace elements known to be required include iron, copper, manganese, zinc, iodine, selenium, chromium, and cobalt (as a part of vitamin B_{12}, cobalamin). Other trace elements (such as fluorine, molybdenum, silicon, boron, nickel, and tin) might be required (Underwood, 1977; Nielson, 1994), although little research on the qualitative or quantitative needs of nonhuman primates for these elements has been conducted. Trace element requirements are usually expressed in parts per million (ppm) or parts per billion (ppb), equivalent to milligrams per kilogram ($mg \cdot kg^{-1}$) or micrograms per kilogram ($\mu g \cdot kg^{-1}$), respectively.

In the wild, primates obtain minerals mostly from plant and animal tissues, depending on dietary habits, although geophagia (dirt-eating) has been observed in moustached tamarins (*Saguinus mystax*) (Hartmann and Hartmann, 1991), howlers (*Alouatta seniculus*), spider monkeys (*Ateles belzebuth*) (Izawa, 1993), mountain gorillas (*Gorilla gorilla beringei*) (Mahaney et al., 1990, 1995a), and rhesus macaques (Mahaney et al., 1995b; Marriott et al., 1996), and sometimes this practice supplements the dietary mineral supply. Green leaves and bones are usually good sources of calcium and magnesium; some gums are high in calcium, magnesium, and potassium (Bearder and Martin, 1980); and seeds, nuts, bones, muscle, and invertebrates are usually good sources of phosphorus. Primates in laboratories or zoos fulfill many of their mineral requirements from specific mineral additions to diets containing ingredients that would otherwise be nutritionally incomplete. Browse (fresh or dried foliage) offered to captive primates can also contribute to the dietary supply of essential minerals.

Quantitative mineral requirements of nonhuman primates are poorly defined, but proposed minimal dietary concentrations are presented in Chapter 11. Mineral concentrations in foods and feedstuffs commonly used in feeding captive primates are presented in Chapter 12.

The bioavailability of minerals in foods (Ammerman et al., 1995) for nonhuman primates has not been studied, but bioavailability of many minerals for many other species is less than 100%, compared with highly bioavailable standards. For example, calcium bound to oxalate and phosphorus bound to phytate appear to be largely unavailable to simple-stomached animals. Spinach contains appreciable calcium, but most is bound to oxalate, so only about 5% is available to humans (Heaney et al., 1998). The mineral concentrations in foods might require interpolation when diets are being formulated to ensure that requirements for minimal *available* nutrients are met.

Some mineral elements, such as cadmium, lead, and antimony, are of concern because of their potential toxicity. Primate research on this subject is sparse, although some clinical reports might contribute to definitions of lead tolerance (Zook and Paasch, 1980), and the effects of different lead intakes and low or normal dietary calcium concentrations upon chromosomal abnormalities in lymphocytes have been studied in cynomolgus *(Macaca irus)* monkeys (Deknudt et al., 1977). Dietary cadmium intake and its

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effects upon serum thyroxine and triiodothyronine concentrations have been studied in rhesus monkeys (Mehta et al., 1986), and chronic cadmium poisoning has been induced in cynomolgus monkeys as a model of human itai-itai disease (Umemura, 2000). The publication *Mineral Tolerances of Domestic Animals* (National Research Council, 1980) provides information on the toxicity of specific minerals in diets for farm animals, pets, and some laboratory animals.

Interactions of minerals with each other and with other nutrients have been fairly well studied in laboratory and domesticated animals (Underwood, 1981; Mertz et al., 1986, 1987; National Research Council, 1995). For example, in rats, calcium absorption decreases in the presence of high dietary phosphorus (Schoenmakers et al., 1989); this relationship may be affected by magnesium intake (Bunce et al., 1965). In humans, long-term calcium supplementation did not adversely affect iron status as assessed by plasma ferritin concentrations in one study (Minihane and Fairweather-Tait, 1998), but other studies demonstrated a short-term reduction in iron absorption as dietary calcium increased (Cook et al., 1991; Hallberg et al., 2000).

For many years, salt mixes (mineral premixes of published composition) have been successfully used in laboratory primate diets (Hegsted et al., 1941; Hayes et al., 1980; Hawk et al., 1994). This information has been used to formulate commercial primate biscuits or pellets that appear to meet the mineral requirements of nonhuman primates. It is important to note that substantial deviations in mineral concentrations have been found among primate diets produced by different manufacturers, and between manufacturers' published specifications and the mineral concentrations found by analysis (Wise and Gilburt, 1981).

MACROMINERALS

Calcium and Phosphorus

The skeleton and teeth of mammals contain over 98% of the body's calcium (Ca) and about 80% of the body's phosphorus (P). Because of the relative mass and density of bones and teeth, Ca and P are required in large amounts, relative to other macrominerals. In addition to their critical structural role, Ca and P are essential for normal cellular communication and modulation.

Calcium binds to many cellular proteins, resulting in their activation. The functions of the proteins are diverse and include cell movement, muscle contraction, nerve transmission, glandular secretion, blood clotting, and cell division (Weaver and Heaney, 1999). When a cell, such as a muscle fiber, receives a nerve stimulus to contract, Ca channels in the plasma membrane open to admit a few Ca ions from the cytosol. The ions bind to an array of intracellular activator proteins that release a flood of Ca from intracellular storage vesicles (sarcoplasmic reticulum in the case of muscle). The increase in cytosolic Ca concentration leads to activation of the contraction complex. Troponin c, after binding Ca, initiates a series of steps leading to muscle contraction. Another Ca-binding protein, calmodulin, has many secondary messenger functions, one of which is to activate the enzymes that break down glycogen. Thus, Ca ions both trigger muscle contraction and fuel the process.

P is widely distributed in soft tissue and is required to drive multiple metabolic and energy reactions within and between cells. As phosphate, it helps to maintain osmotic and acid-base balance. As a component of deoxyribonucleic and ribonucleic acids, P is involved in cell growth and differentiation. As a phospholipid, it contributes to cell-membrane fluidity and integrity. Through involvement in creatine phosphate, adenosine triphosphate (ATP), and other phosphorylated compounds, P plays a vital role in energy transfer and use, gluconeogenesis, fatty acid transport, amino acid and protein synthesis, and activity of the sodium-potassium pump (Knochel, 1999).

Short-term, moderate inadequacies in Ca intake are modulated by skeletal reserves and cause few signs of deficiency, particularly in adults. However, rapidly growing young animals might exhibit hypocalcemia, hypercalciuria, and increased plasma alkaline phosphatase activity. Chronic, long-term dietary Ca deficiency can result in retarded growth and rickets in the young and osteomalacia and osteoporosis in adults.

Early responses to low dietary P include a decline in plasma inorganic P concentration and an increase in plasma alkaline phosphatase activity. If the deficiency is sufficiently severe or prolonged, abnormalities of the bones and teeth can be expected, growth will slow in the young, and appetite will be depressed; and pica (depraved appetite) will be seen in some domestic animals (Underwood and Suttle, 1999).

An early study of Ca metabolism in rhesus macaques concluded that a growing 3-kg monkey requires Ca at 150 $mg \cdot BW_{kg}^{-1} \cdot d^{-1}$ (Harris et al., 1961). In later studies with rhesus macaques, feeding a diet containing 0.15% Ca (equivalent to Ca at 150 $mg \cdot BW_{kg}^{-1} \cdot d^{-1}$ for 2- to 3-kg animals) resulted in osteoporosis (Griffiths et al., 1975). Fluoride added to such a diet at 50 ppm prevented osteoporosis by reducing bone growth rate and resorption, resulting in bones with normal density, but the added fluoride interfered with mineralization of osteoid, and led to osteomalacia.

When diets containing 0.32% Ca were fed to young cynomolgus monkeys for about 3½ years, motor neuron damage resulted; the damage was exacerbated by addition of aluminum and manganese to the diet (Garruto et al., 1989).

The minimal dietary Ca concentration of 0.5% (air-dry basis) previously recommended (National Research Coun-

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cil, 1978) should be sufficient to support maintenance of adult nonhuman primates, assuming appropriate P and adequate vitamin D consumption or sufficient ultraviolet B (UVB) exposure. When expressed on a dietary dry matter (DM) basis, this estimated Ca requirement would be 0.55% (assuming 10% moisture in the air-dry diet). Lactation can be expected to increase the demand for Ca, particularly in mothers with more than one offspring, but bone reserves and increased food intake during lactation can compensate to some extent in the short term. With proper diet, at least partial postweaning restoration of bone Ca reserves (depleted by lactation) has been seen in humans (Prentice, 2000).

Although juveniles of the larger primate species grow relatively slowly, compared with the young of many other mammals, the period of growth will probably raise the requirement for both Ca and P over maintenance requirements. Furthermore, the growth of small species, such as marmosets and tamarins, is sufficiently rapid that Ca and P requirements will increase.

Dietary protein and sodium concentrations can influence requirements for Ca. High sodium intakes result in higher sodium concentrations in glomerular filtrate, competing with Ca for renal tubular reabsorption (Nordin et al., 1993). In humans, increased Ca excretion occurs when protein and sodium intakes are high (Heaney and Recker, 1982; Matkovic et al., 1995; Nordin, 1997). The negative Ca balance associated with high protein intakes might be due to increased glomerular filtration and decreased renal Ca reabsorption as end-products of protein metabolism, such as phosphate and possibly sulfate, complex Ca in the renal tubules and carry it out in the urine (Johnson et al., 1970; Spencer et al., 1978; Nordin, 1997). However, Grynpas et al. (1993) found that free-ranging rhesus monkeys from the Caribbean Primate Research Center that had been provisioned with either a 15% or a 25% protein extruded diet for most of their lives were not different in vertebral mineral concentrations, as determined by neutron activation analysis. Calcium concentrations were 0.90% in the lower-protein diet and 1.00 to 1.15% in the higher-protein diet, as fed. Heaney (1998) argued that if Ca intake is sufficiently high, excessive dietary protein will not result in bone loss; he contended that the ratio of dietary Ca to protein is more important than the absolute dietary concentration of Ca. A ratio that was proposed as adequate to prevent bone loss was about 20 mg of dietary Ca per gram of dietary protein, although the suitability of that ratio has not been experimentally confirmed in nonhuman primates. In any case, it is likely that Ca requirements of nonhuman primates will vary to some extent with dietary habits and composition of the diet, as they do in humans (Nordin, 2000).

A diagnostic distinction between protein-calorie malnutrition and Ca deficiency was noted when cadmium was administered to rhesus macaques. Metallothionein (MT) production was induced, but the major liver isoform was MTc in protein-calorie malnourished monkeys and MTb in Ca-deficient monkeys (Nath et al., 1987).

As early as 1957, a relationship of bone loss, a decrease in effective Ca use, and restricted physical activity in humans was reported (Whedon and Shorr, 1957). Physical restriction of *Macaca nemestrina* also increased Ca excretion (Pyke et al., 1968). Osteoporosis and osteoarthritis might be more common in chronically physically restricted primates (DeRousseau, 1985a,b; Pritzker et al., 1985; Rothchild and Woods, 1992), although some authors question the occurrence or incidence of osteoarthritis in nonhuman primates (Ford et al., 1986; Jurmain, 1989; Chateauvert et al., 1990; Sokoloff, 1990). When over 1,500 nonhuman-primate skeletons of 29 species were examined, osteoarthritis was more prevalent in captive animals (presumably physically restricted) than in wild animals (Rothschild and Woods, 1992). Eaton and Nelson (1991) have proposed that Ca intakes of humans living at the end of the Stone Age were twice those of contemporary humans, and their physical exertion was greater than at present. Skeletal remains suggest that Stone Age humans developed a greater peak bone mass and experienced less age-related bone loss than 20th Century humans.

Many of the diets fed to captive nonhuman primates comprise mixtures of nutritionally complete biscuits or pellets, fruits, vegetables, browse, and insects. However, given the opportunity for free choice among such an assortment of foods, the likelihood of Ca deficiency is real. With the exception of primate biscuits and some green, leafy vegetables, most of those foods are inadequate sources of Ca. In spinach, much of the Ca is bound to oxalate and unavailable. Sprinkling on Ca supplements does not necessarily prevent Ca deficiencies that might appear when mixed diets are fed. That practice was attempted with two species of lemurs (*Lemur catta* and *L. variegatus*) at the Cincinnati Zoo, but much of the supplement did not adhere to the foods; signs of nutritional secondary hyperparathyroidism were seen, including hyperphosphatemia, hypocalcemia, increased alkaline phosphatase activity, impaired mobility, bowing of the long bones, poorly mineralized skeleton, and soft tissue mineralization (Tomson and Lotshaw, 1978).

Nursing neonatal New World and Old World primates, with presumably adequate Ca intakes from milk, presented signs of abnormal Ca status (Ullrey, 1986; Morrisey et al., 1995). Responses to UVB exposure or to intramuscular vitamin D injections made it look as though vitamin D supplies were inadequate to support normal Ca absorption and metabolism. The milk of species that have been examined is low in vitamin D; if solid food containing vitamin D is not consumed in sufficient amounts or if there is no UVB exposure, absorbed Ca might be inadequate to meet tissue needs. Because of solar UVB exposure, that is proba-

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bly not a problem in nursing wild primates. In humans, if infant formula thickened with an indigestible carbohydrate, such as locust bean gum, replaces mother's milk, Ca availability is reduced compared with that in unthickened infant formula or formula thickened with a digestible carbohydrate, such as pregelatinized rice starch (Bosscher et al., 2000). Further, it has been shown that the Ca in fortified soy milk is absorbed at only 75% of the efficiency of Ca in cow's milk (Heaney et al., 2000).

Tarsiers held at the National Zoological Park were fed crickets exclusively, a particularly poor calcium source (see Chapter 12). Repeated breeding failures were experienced until a high-Ca (8%) cricket diet was made available to the free-ranging crickets in the tarsier enclosure (Roberts and Kohn, 1993). Although the Ca concentrations in cricket tissues were unchanged, the residue of high-Ca diet in the cricket gut supplied sufficient Ca to meet tarsier needs. Successful births and weanings were observed regularly after that dietary change was made.

Mineral mixes (salt mixes) historically used in diets for laboratory primates appear to have provided about 0.2% of available (non-phytate) P in the diet. When they were combined with the P in food ingredients (those furnishing protein tending to be richer in P), available P concentrations (air-dry basis) in formulated diets were about 0.3-0.4% and appeared to be adequate (National Research Council, 1978). When the lowest National Research Council (1978) value is expressed on a DM basis, the estimated dietary available P requirement would be 0.33% (assuming 10% moisture in the air-dry diet). Total P requirements in natural-ingredient diets are generally higher because the bioavailability of P tends to be less than that in inorganic P sources, particularly when associated with phytate in commonly used cereals and oil-seed meals. P bioavailability studies have not been conducted with nonhuman primates, but P bioavailability values have been reported for feed ingredients fed to pigs (National Research Council, 1998). Phytate P is believed to be only slightly available or totally unavailable to non-ruminants. In ruminants, the phytase activity of ruminal microorganisms renders nearly all of the phytate P available for absorption (National Research Council, 2001). Whether this would be true for microorganisms in the complex stomach of the Colobinae has not been established.

Provision of a dietary Ca:P ratio between 1:1 and 2:1 has been emphasized in setting Ca and P requirements in the past. However, it has been shown in the pig that inorganic P, added to the diet to maintain a particular Ca:P ratio, will lower use of phytate P, and phytate lowers use of Ca (Underwood and Suttle, 1999). Furthermore, excess Ca lowers P absorption (National Research Council, 1998). Thus, it might be important to consider the Ca and P concentrations in diets used in defining Ca and P requirements and the effects of phytate on requirement estimates.

In practical diet formulations for nonhuman primates, the addition of stable phytases might increase phytate P availability, on the basis of studies with other species (Cromwell et al., 1995). However, the choice of phytase, and its resistance to the heat and pressure of food processing, will influence its effectiveness (National Research Council, 1998).

Magnesium

It has been said that about 70% of the body's magnesium (Mg) of ruminants is in the skeleton (Todd, 1969), although Shils (1999) has stated that bone contains about 53% of the Mg in the adult human body. Mg is a component of regulatory enzymes and enzyme systems, and over 300 essential metabolic reactions involving Mg have been identified (Shils, 1999). Mg helps to regulate muscle and nerve function and influences the metabolism of protein, carbohydrate, fat, and nucleic acids. ATP exists in all cells primarily as MgATP, and the complex plays a central role in many of these reactions. Cyclic adenosine monophosphate (cAMP), formed from MgATP and adenylate cyclase, is involved in the secretion of parathyroid hormone (PTH), and PTH exerts some of its physiologic effects through the formation and actions of cAMP. That role of Mg might partially explain the hypocalcemia seen in Mg-depleted rhesus monkeys, humans, calves, sheep, dogs, and pigs (Dunn, 1971).

Studies of the effects of dietary calcium, phosphorus, or vitamin D on absorption and retention of Mg in humans have produced equivocal results (Shils, 1999). Long-term balance studies with healthy adults generally suggest that increased calcium intakes do not substantially influence Mg absorption or retention. Some reports indicated that high phosphorus intakes decreased Mg absorption, whereas others did not. Some patients, but not others, with impaired calcium absorption and both osteomalacia and osteoporosis showed improvement in Mg absorption when given vitamin D or calcitriol orally. Increased intakes of Mg have been associated with decreased calcium absorption or no effect.

Signs of Mg depletion in humans include neuromuscular, gastrointestinal, and cardiovascular changes (Shils, 1999). Tremor and muscle fasciculations are seen; anorexia, nausea, and vomiting can be experienced; and in severe Mg depletion, there can be electrocardiographic changes compatible with hypokalemia or hypocalcemia.

In only 4 weeks, rhesus monkeys fed a diet containing Mg at 3 mg·100 g^{-1} (0.003%, air-dry basis) (Dunn, 1971) exhibited hyperirritability associated with hypomagnesemia, whereas monkeys fed a control diet containing Mg at 102 mg·100 g^{-1} (0.1%, air-dry basis) did not. Affected macaques fed additional Mg (33% of control concentrations, equivalent to 0.034% of the diet on an air-dry basis)

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returned to normal. Thus, it would appear that a Mg concentration of 0.04% in dietary DM should support maintenance requirements when dietary calcium and phosphorus concentrations are relatively low. However, few studies of Mg requirements of nonhuman primates have been reported, and higher dietary concentrations of calcium and phosphorus have been shown to elevate the Mg requirements of some other species (Underwood and Suttle, 1999). Examination of natural-ingredient diets for primates and other mammals, with their higher Ca and P concentrations, indicates that 0.08% Mg is more likely to be a consistently adequate dietary level. Thus, the recommendation in Table 11-2 reflects a presumed adequate dietary level of 0.08%, whereas the estimates of 0.04 to 0.074% Mg in Table 11-1 are minimum requirements.

Mg concentrations in the milk of rhesus monkeys are 32.9 ± 3 $\mu g \cdot ml^{-1}$ compared with 49.6 ± 12.1 $\mu g \cdot ml^{-1}$ in colostrum (Lonnerdal, et al., 1984). Formulas for artificial rearing should contain supplemental sources of this essential nutrient.

Potassium

Potassium (K) is usually found in high concentrations in plant and animal tissue. Concentrations over 3% are typical in plant DM, and deficiencies are rare. K helps to regulate tissue turgidity of plants; in animals, K is the major intracellular cation and is largely responsible, with sodium and chloride, for the maintenance of osmotic pressure and acid-base balance. A K concentration of 0.24-1.1% in dietary DM appeared to support maintenance in baboons (Hummer, 1970). However, studies with other species using natural-ingredient diets suggest that minimum K requirements may be 0.4% or more of dietary DM, and may depend upon species, life stage, and diet composition (Underwood and Suttle, 1999). Thus, recommendations in Table 11-2 reflect the higher concentrations reported to be adequate with natural-ingredient diets. In rhesus monkeys, Lonnerdal et al. (1984) found that K is higher in colostrum (367 $\mu g \cdot ml^{-1}$) than in milk expressed after 30 days of lactation (260 $\mu g \cdot ml^{-1}$).

Sodium

The major extracellular cation in mammals is sodium (Na). Thirst and total body water are regulated by dietary Na. Na thirst has been identified in a number of mammal species. Natural diets usually contain adequate supplies of Na, although strict herbivores might be at risk for Na deficiency. Depending on soil and environmental characteristics, plants might be poor sources of Na or phosphorus. The influence of Na on blood pressure has been extensively studied in primates because of the high incidence of hypertension in Western human populations. Increasing dietary sodium chloride (NaCl) concentrations to 3-6% increased systolic and diastolic blood pressure in African green monkeys, spider monkeys, and hamadryas baboons. Rhesus monkeys, however, failed to show an increase in blood pressure under the same conditions over a 6-week period (Srinivasan et al., 1980, 1984). The rhesus monkeys expressed a distaste for the high-NaCl diet, and a decline in body weight was associated with increasing dietary NaCl.

Diets containing 0.25-0.65% Na appear to support maintenance of nonhuman primates, but are likely to exceed minimum needs (Hummer et al., 1970; National Research Council, 1978). The milk of rhesus monkeys contains Na at about 171 $\mu g \cdot ml^{-1}$ in the first week of lactation, but milk Na appears to decline to about 90 $\mu g \cdot ml^{-1}$ after a month (Lonnerdal et al., 1984). Apparently female rhesus monkeys ingest more NaCl than do males when presented the opportunity (Shulkin, 1992). However, ovarian hormones do not appear to be involved in this sex difference (Krecek et al., 1972; Krecek, 1973).

Chloride

The major digestive chemical in gastric secretions is hydrochloric acid. With the exception of foregut-fermenting primates, the acid stomach is the first and the major organ responsible for processing feedstuffs. Chloride (Cl) is also critical (with sodium and potassium) in the osmotic regulation of cells and tissues. Hummer (1970) fed diets containing 0.27-0.62% Cl to baboons, and they appeared to support maintenance but probably exceeded minimum requirements. The lower of the previous National Research Council (1978) recommendations of 0.2-0.55% dietary Cl would be expected to be sufficient, based on comparisons with the Cl requirements of other species.

Sulfur

Important compounds in the diets of primates that contain sulfur (S) include biotin, thiamin, cystine, cysteine, methionine, and taurine. A frank deficiency of S in primates has not been described, although taurine deficiency may occur in neonates (Hayes, 1980). Excessive intakes of protein high in S-containing amino acids (cystine, methionine, and taurine) might exacerbate problems of renal calcium loss.

TRACE MINERALS

Iron

Iron (Fe) is an essential component of such proteins as hemoglobin, myoglobin, and ferritin; and some enzymes require Fe as a cofactor (Fairbanks, 1999). Iron in heme

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allows the transport of oxygen to tissues (hemoglobin), transitional storage of oxygen in tissues (myoglobin), and the transport of electrons through the respiratory chain (cytochromes). Biologic functions that depend on Fe include energy metabolism, neurotransmitter synthesis, connective tissue metabolism, immune function, thyroid hormone metabolism, and thermogenesis. Recently, Fe has been found to bind to proteins, forming transcription factors that can affect the expression of other proteins. Thus, impaired Fe status can affect the metabolism of several nutrients.

Fe is present in many natural ingredients. The biologic availability of such Fe has been studied mostly in chickens and rats, and the results might not be completely applicable to nonhuman primates. Generally, the biologic availability of Fe in natural ingredients is about 40-60% (Henry and Miller, 1995). Iron is a substantial contaminant of most sources of dicalcium phosphate, and this makes it difficult to reduce the Fe concentration of natural diets.

Ferrous sulfate is customarily used as the standard in bioavailability studies and is usually assigned an Fe bioavailability of 100%. Ferrous sulfate and ferrous carbonate are the usual sources of Fe added to commercial diets, but various Fe sources are used in purified diets. Fe in ferrous sulfate, ferric chloride, ferric citrate, and ferric ammonium citrate has high biologic availability for several species. Bioavailability of Fe in ferrous carbonate and reduced iron varies with source and possibly particle size. The Fe in ferric oxide, which is occasionally added to feed as a coloring agent, is virtually unavailable (Henry and Miller, 1995). Fe absorption has been studied extensively in humans. Absorption is enhanced by the presence of ascorbic acid in the diet. Meat, fish, and chicken also enhance the absorption of Fe, whereas polyphenols, such as are found in tea and leaves, seem to inhibit absorption (Yip and Dallman, 1996; Zijp et al., 2000). An algorithm has been developed for calculating absorption and bioavailability of Fe in a number of human foods, and concentrations of phytate phosphorus and Fe-binding polyphenols in foods used in human and some nonhuman-primate diets have been published (Hallberg and Hulthén, 2000).

There are a number of nutritionally significant interactions of Fe with other minerals, although few of these have been studied in nonhuman primates. Dietary concentrations of calcium, copper, manganese, and zinc may influence Fe absorption. Plasma concentrations of chromium and manganese may influence Fe transport. Tissue concentrations of copper and zinc may influence cellular Fe uptake, and tissue concentrations of chromium, copper, and zinc may influence the size and mobility of Fe stores (O'Dell and Sunde, 1997)

Fe absorption from infant formulas has been determined in infant rhesus monkeys and was found to be 20-30% from milk-based and soy-based formulas (Davidson et al., 1990; Lonnerdal et al., 1999). The effect of various dietary factors on Fe absorption has not been studied extensively in primates, but the rhesus monkey has been used as a model to study the effect of lactoferrin, a major Fe-binding protein in the milk of rhesus monkeys (Davidson and Lonnerdal, 1986) and in human milk, on Fe uptake from milk and milk-replacers (Davidson et al., 1990). It appears that a unique receptor-mediated mechanism in the small intestine facilitates the uptake of Fe from lactoferrin (Davidson and Lonnerdal, 1988, 1989). Removal of phytate from soy in a soy-based formula appeared to have little effect on Fe absorption in infant rhesus monkeys (Lonnerdal et al., 1999). Young rhesus monkeys fed a soy protein diet were found to be anemic after 2-7 months, and Fe absorption from this diet was lower than from a casein diet (Fitch et al., 1964). The diet was baked, however, and both the heat treatment and the addition of baking soda (pH) might have affected Fe bioavailability.

Adequate Fe status is needed for normal hematologic characteristics. Age-related changes in hematologic measures have been described in infant rhesus monkeys (Martin et al., 1973). Packed cell volumes were high at birth, declining during the first 2 post-natal weeks. Proportions of neutrophils were high at birth and declined with age, whereas proportions of lymphocytes were low at birth but rose rapidly to adult values. Proportions of eosinophils were low at birth, increasing to adult values during the first post-natal month. Total leukocyte counts were essentially constant from birth to 2 years. The consequences of impaired Fe status on such hematologic measures as hemoglobin, hematocrit, MCV, transferrin saturation, and serum iron have been described in rhesus macaques (Wolcott et al., 1973; Mandell and George, 1991; Bicknese et al., 1993; Sreeramulu et al., 1994; Kriete et al., 1995) and cynomolgus macaques (Giuletti et al., 1991). When 30-70% of blood volume was withdrawn from adult (6.5- to 10-year-old) nonpregnant female rhesus monkeys over a long period (5-10% per week), anemia developed (Mandell and George, 1991).

No firm indices for the identification of anemia or Fe deficiency have been established for nonhuman primates, and indices for human subjects are usually used. Results of a study in which dietary Fe deficiency was induced in rhesus monkeys suggest that serum ferritin is not a good indicator of Fe status in this species (Sreeramulu et al., 1994). The assay used, however, might not have recognized rhesus monkey ferritin, which is necessary if commercially available kits for assay of serum ferritin in humans are to be useful in measuring the response to dietary Fe intake in rhesus infants (Lonnerdal et al., 1996). The effect of transferrin polymorphism on total iron-binding capacity has been examined in rhesus monkeys, and it has been suggested that different types of transferrin (genotypes) affect fertility and growth of offspring (Smith, 1982).

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Fe-deficiency anemia has been produced in rhesus monkeys (Wolcott et al., 1973; Mandell and George, 1991). Weanling rhesus monkeys (3 months old) were found to be less Fe-deficient if they were raised in the nursery than if they were mother-reared (Bicknese et al., 1993), and multiparous dams were more likely to have Fe-deficient weanlings than primiparous dams. Formula-fed infant rhesus monkeys have been shown to develop Fe-deficiency anemia at the age of 3-5 months even if the formula was fortified with Fe (Kriete et al., 1995). Another study, however, showed no anemia at that age in infant rhesus monkeys fed Fe-fortified formula exclusively from birth (Lonnerdal et al., 1999). Differences in Fe endowment at birth, growth rate, number of bleedings, and Fe concentration in the formulas used might explain the disparate findings. Fe deficiency has also inadvertently been produced in monkeys fed diets low in protein (Sood et al., 1965).

The Fe requirements of nonhuman primates have not been well established. Infant rhesus monkeys fed infant formula exclusively up to 5.5 months of age showed no signs of anemia (Lonnerdal et al., 1999). The formula contained Fe at 12 $mg{\cdot}L^{-1}$, and average consumption was 400 $ml{\cdot}d^{-1}$, so it appears that an Fe intake of about 5 $mg{\cdot}d^{-1}$, or about 3-10 $mg{\cdot}BW_{kg}^{-1}{\cdot}d^{-1}$, given in formula meets the Fe requirement during infancy. Rhesus milk contains Fe at about 1.1-1.8 $mg{\cdot}L^{-1}$ during the first month of lactation and slightly less after that (Lonnerdal et al., 1984). Assuming that milk intake by nursed rhesus infants is similar to that by formula-fed infants, the "true" Fe requirement might be substantially lower than that estimated for formula-fed infants.

Fe-deficiency anemia has been produced in adult female baboons (*Papio* spp.) (Huser et al., 1967) and newborn squirrel monkeys *(Saimiri sciureus)* (Amine et al., 1972), and an Fe-deficient diet developed for 4-year-old capuchins *(Cebus albifrons)* produced a negative Fe balance (Wolfe et al., 1989). But the minimal Fe requirement for those species cannot be deduced from the studies.

Although Fe-deficiency anemia is of concern in most colonies, it should be recognized that giving primates high-Fe diets can result in Fe overload. Hemosiderosis has been observed in lemurs in captivity (Gonzales et al., 1984); signs were most pronounced in the black lemur (*Eulemur macaco*) and least in the ring-tailed lemur (*Lemur catta*). It was later found that all 49 lemurs in the colony that had been necropsied during a 10-year period had hemosiderosis and that severity increased with age (Spelman et al., 1989). A suggested explanation was that captive lemurs received diets high in Fe (commercial monkey diets) and in ascorbic acid (citrus fruits), which enhanced Fe absorption, while they received few inhibitors of Fe absorption, such as tannins (polyphenols), that are constituents of the diet consumed in the wild (leaves, fruits, and bark). Because hemosiderosis can lead to liver and kidney disease, the authors suggested that lemur diets should be modified to reduce this risk. Marmosets (*Callithrix jacchus*), too, develop hemosiderosis in captivity; it is also believed to be caused by high-Fe diets (Miller et al., 1997). When a diet lower in Fe (100 $mg{\cdot}kg^{-1}$) was fed, liver Fe was only one-tenth that of animals fed a high-Fe diet (500 $mg{\cdot}kg^{-1}$), demonstrating that lowering the Fe content of the monkey diet can reduce the risk of hemosiderosis. Experimental hemosiderosis has been induced in rhesus monkeys by injections of Fe dextran (Nath et al., 1972). Cebus monkeys, loaded with Fe dextran, were found to be a useful model for study of the effectiveness of Fe chelators in Fe overload. Desferroxamine, administered intramuscularly, and desferrithiocin, administered intramuscularly or orally, were found to significantly promote Fe excretion (Wolfe et al., 1989). To test new orally active Fe chelators, marmosets (*Callithrix jacchus*) have been Fe-overloaded by intraperitoneal injections of Fe hydroxide polyisomaltose (Sergejew et al., 2000).

Copper

Copper (Cu) is associated with a number of proteins, including many important enzymes. The Cu-containing enzymes are commonly divided into amine oxidases, ferroxidases, cytochrome *c* oxidase, dopamine β-hydroxylase, superoxide dismutases, and tyrosinase. The known Cu-binding proteins are metallothionein, albumin, transcuprein, and blood-clotting factor V (Turnlund, 1999).

Cytochrome *c* oxidase might be the most important enzyme in the mammalian cell because it is the terminal link in the mitochondrial electron-transport chain and regulates the formation of ATP. Other Cu-containing enzymes are part of the body's antioxidant defense system, are involved in melanin formation, and function in the cross-linking of collagen and elastin during formation of connective tissue (Linder, 1996). In studies of the development of age-related macular degeneration in elderly (20 years old and older) rhesus macaques, monkeys with diagnosed drusen (hyaline excrescences in the basal choroid layer of the eye) exhibited alterations in concentrations and activities of the free-radical defense system, particularly of enzymes associated with Cu (Olin et al., 1995b). Cardiovascular defects in Cu deficiency include weakened heart and blood-vessel structure, impaired use of energy by the heart, reduced ability of the heart to contract, altered ability of blood vessels to grow and regulate their diameter, and altered structure and function of the blood cells. Those defects result principally from impaired effectiveness of the enzymes that are Cu-dependent (Saari and Schuske, 1999).

Copper is usually added to manufactured feeds in the form of cupric sulfate, $CuSO_4$, a form that is highly bioavailable. Cupric carbonate, $CuCO_3$, a form sometimes used in rations, is intermediate in Cu bioavailability. Copper in

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cupric oxide, CuO, is absorbed very poorly by most species (Baker and Ammerman, 1995a). However, no studies on the biologic availability of Cu in these compounds have been conducted with nonhuman primates.

Excessive dietary zinc can lead to Cu deficiency in a number of mammalian species (Baker and Ammerman, 1995a). That could be important in infant primates raised with their mothers in breeding colonies in galvanized cages, such as corncribs. Under such circumstances, depigmentation of the hair (achromotrichia), alopecia, weakness, and microcytic anemia were observed in infants of rhesus (*Macaca mulatta*) mothers fed commercial diets but not in the adults. The achromotrichia was described as development of a steel-gray hair coat. Serum zinc was increased, and serum Cu decreased. Animals raised in stainless-steel cages and fed the same diet did not develop the syndrome. High intakes of zinc from the galvanized caging apparently induced a Cu deficiency in the infant animals (Stevens et al. 1977; Obeck, 1978; Wagner et al., 1985). Stevens et al. (1977) and Wagner et al. (1985) gave no details on diet composition. Obeck (1978) reported that the commercial diet contained zinc at 34 $mg \cdot kg^{-1}$ and Cu at 10 $mg \cdot kg^{-1}$, an insufficient amount of Cu to prevent the syndrome. Higher concentrations were not evaluated, so it is not known whether the effect of galvanized caging on infant rhesus can be overcome by increasing the Cu in rations consumed mostly by the mothers. Hypocupremia, sideroblastic anemia, leukopenia, and neutropenia were observed in an adolescent human who ingested excessive amounts of zinc (Porea et al., 2000).

Low Cu status in infant rhesus monkeys also has been induced by feeding a commercial canned infant liquid formula designed for human infants (Lonnerdal et al., 2001). Information on the form of Cu in the liquid formula and the heat treatment to which it was subjected were not revealed by the manufacturer of the product. However, the Cu concentration was described to be comparable to that in other commercial products tested at the same time. The researchers speculated that the conditions of heat processing might have reduced Cu availability, thereby inducing a Cu deficiency. Besides hypocupremia, low serum ceruloplasmin, and low erythrocyte Cu, Zn-superoxide dismutase activity, the monkeys became anemic and had a change in hair color.

Fischer and Giroux (1987) fed a specially formulated commercial type of monkey diet containing zinc at 30 $mg \cdot kg^{-1}$ and Cu at 6 $mg \cdot kg^{-1}$ to cynomolgus *(Macaca fascicularis)* monkeys. The diet was supplemented with 10 or 24 mg of zinc each day. The 10-mg zinc supplement was given to the control group to meet the nutritional requirement and compensate for zinc bound to dietary phytate. The male and female animals weighed about 3.5 and 2.7 kg and ate 120 and 90 $g \cdot d^{-1}$, respectively. Monkeys that received the 24-mg zinc supplement had higher plasma zinc, lower plasma Cu, and somewhat increased plasma cholesterol. Plasma ceruloplasmin, hematocrit, and hemoglobin were not affected. Increased plasma cholesterol is a sign of Cu deficiency in rats and humans. In this experiment, zinc supplementation appeared to impair Cu status.

Adult cynomolgus monkeys weighing 4.2-4.8 kg were fed purified liquid diets containing Cu at about 0.4 $mg \cdot kg^{-1}$ of DM for 28 weeks (Milne et al., 1981). High concentrations of ascorbic acid are known to reduce Cu use in several species (Baker and Ammerman, 1995a), so the effect of ascorbic acid was evaluated by giving animals a supplement of 1 or 25 mg of ascorbic acid per kilogram of body weight. There was relatively little change in serum Cu or ceruloplasmin (a Cu-containing enzyme) concentrations, but there was a significant increase in serum cholesterol rising from 80 $mg \cdot dl^{-1}$ to 108 $mg \cdot dl^{-1}$. At the end of 28 weeks, approximately 2 mg of $Cu \cdot kg^{-1}$ of DM were added to the diet, furnishing a total Cu concentration of about 2.5 $mg \cdot kg^{-1}$ of dietary DM. After 4 weeks on this Cu-supplemented diet, serum cholesterol concentrations of animals receiving the higher amounts of ascorbic acid were elevated above those of animals receiving the lower amounts of ascorbic acid, suggesting that ascorbic acid may have interfered with Cu absorption.

Available data are not sufficient to establish a Cu requirement. Cu at 12-20 $mg \cdot kg^{-1}$ in commercial diets seems to be sufficient under most conditions (Knapka et al., 1995). However, it might not be sufficient for breeding colonies exposed to high concentrations of zinc from galvanized caging. Cu from $CuSO_4$ at about 2 $mg \cdot kg^{-1}$ of diet was sufficient to reverse an increase in cholesterol in adult cynomolgus monkeys (Milne et al., 1981). Cu at 15 $mg \cdot kg^{-1}$ of dietary DM should be sufficient to meet the dietary needs of animals not exposed to excessive dietary zinc.

Manganese

Manganese (Mn) is a constituent of several metalloenzymes, such as arginase, pyruvate carboxylase, glutamine synthetase, and Mn-superoxide dismutase. Such enzymes as oxidoreductases, lyases, ligases, hydrolases, kinases, decarboxylases, and transferases can be activated by Mn, but most of these can also be activated by other cations, particularly magnesium (Nielsen, 1999).

Manganous sulfate and manganous oxide are the most common supplemental forms of Mn used in animal feeds. Compared with manganous sulfate, the bioavailability of manganese oxide in chicks was 60-77%, and that of manganous carbonate was 32-36% (McDowell, 1992).

Mn deficiency has been demonstrated in a number of avian and mammalian species. Female rhesus *(Macaca mulatta)* monkeys fed a semisynthetic diet containing Mn at 0.5 $mg.kg^{-1}$ were mated and maintained on this low-Mn diet throughout their pregnancy. Their infants were

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continued on the same diet, and their behavior was compared with that of animals fed a diet that was similar but contained Mn at about 40 $mg \cdot kg^{-1}$. Mothers fed the deficient diet had normal pregnancies. The infants had normal birth weights and grew normally on the low-Mn diet. Behavioral development was evaluated with a series of tests. Infants fed the low-Mn diet had abnormally strong clasping and clinging responses, but their righting responses, which required release from clasping, were inadequate (Riopelle and Hubbard, 1977).

Signs of Mn deficiency other than the changes in behavioral development have not been described in nonhuman primates. Typical commercial diets, which appear to be adequate, contain Mn at 70-100 $mg \cdot kg^{-1}$ (Knapka et. al, 1995). Those concentrations are probably far in excess of the minimal requirement, which is 10 $mg \cdot kg^{-1}$ for rats and 2-20 $mg \cdot kg^{-1}$ for swine in various stages of their life cycle (National Research Council 1995, 1998). The level of Mn in the control diet used by Riopelle and Hubbard (1977) would provide about 44 $mg \cdot kg^{-1}$ of dietary DM and probably exceeds primate available Mn requirements, as well.

Zinc

Zinc (Zn) is the most abundant of intracellular trace elements and is involved in structural, catalytic, and regulatory roles. Loss of Zn from biomembranes, as a consequence of Zn deficiency, can result in increased susceptibility to oxidative damage, structural strains, and alterations in specific receptor sites and transport systems (King and Keen, 1999). Over 200 Zn enzymes with diverse functions have been found, and Zn is involved in the metabolism of carbohydrate, protein, lipids, and nucleic acids (DNA and RNA polymerase and thymidine kinase). Extracellular superoxide dismutase activity in primates is affected by dietary Zn intake (Olin et al, 1995a). Zn also serves as a structural part of several important cellular constituents, such as transcription factors. In so-called zinc-finger structures, Zn is involved in gene expression at a very fundamental level. Growth, reproduction (pregnancy outcome), bone formation, immune function, skin integrity, morbidity, appetite, cognitive function, and behavior have been shown to be impaired in Zn deficiency in nonhuman primates and in humans. Zn deficiency affects embryogenesis, resulting in malformations, stillbirths, abortions, and smaller than normal offspring (King and Keen, 1999). Although Zn deficiency affects organisms in many ways, some might be due to the effects of Zn deficiency on cytokine synthesis and metabolism, particularly Tumor Necrosis Factor-α (TNF-α) and interleukin-2. Cell cycle events and apoptosis (programmed cell death) are affected by Zn nutriture.

Zn is usually added to commercial diets as zinc sulfate, $ZnSO_4$; zinc oxide, ZnO; or zinc carbonate, $ZnCO_3$. The Zn in $ZnSO_4$ and $ZnCO_3$ has high biologic availability in livestock. In some earlier studies, Zn in ZnO was demonstrated to have high biologic availability, but more recent reports indicated a biologic availability of about 50% (McDowell, 1992; Baker and Ammerman, 1995b). A number of factors can affect Zn availability. Diets high in wheat bran lowered Zn concentrations in the serum and bone of male (but not female) baboons, despite a low phytate:Zn molar ratio and high Zn intake (Kriek et al., 1982). Dietary phytate, which can be present in significant amounts in oilseeds and cereal grains, markedly decreases the absorption of Zn in chicks, rats, and swine. High dietary calcium exacerbates the effect. The effect can be overcome by feeding higher concentrations of Zn (hence a high Zn requirement will be observed) or by the concurrent feeding of some, but not all, chelating agents (Baker and Ammerman, 1995b). Proprietary products containing Zn chelates, or other organic complexes containing Zn, are sometimes used in diets to ensure good absorption.

Diets based on soy protein have been used in studies of experimental Zn deficiency in primates because soy-protein sources usually contain enough phytate to inhibit Zn absorption (Lonnerdal et al., 1988). When phytate was removed or reduced in the soy-protein diet, Zn absorption by infant rhesus monkeys increased significantly (rising from 27% to 45%) (Lonnerdal et al., 1988, 1999), to a point similar to that of Zn absorption from milk-based formulas (46%). Zn absorption from monkey milk has been shown to be about 54% (Lonnerdal et al., 1988). Absorption of Zn from a formula based on casein hydrolysate was lower than that from a regular milk formula, but the presence of a soy-protein source reduced Zn absorption further (Rudloff and Lonnerdal, 1992).

It has been suggested that iron can interfere with the absorption of Zn (Solomons and Jacob, 1981). The interaction has been demonstrated in humans when high amounts of iron were given with Zn at a ratio of 25:1 in a water solution but not when iron and Zn were given in this ratio in a meal (Sandstrom et al., 1985). Studies in pregnant and lactating rhesus monkeys showed no negative effect of iron supplementation (iron at 4 $mg \cdot BW_{kg}^{-1} \cdot d^{-1}$) on Zn absorption when the diet contained Zn at 4 or 100 $mg \cdot kg^{-1}$ (Lonnerdal et al., 1990b). Similarly, when infant rhesus monkeys were given infant formulas with a high iron:Zn ratio (iron at 12 $mg \cdot L^{-1}$ and Zn at 1 $mg \cdot L^{-1}$), there was no difference in Zn absorption or retention as compared with those in infants fed formula with a lower iron:Zn ratio (1:1) (Polberger et al., 1996).

Rhesus monkeys (Sandstead et al., 1978) and bonnet monkeys (Swenerton and Hurley, 1980) have been used as animal models for human Zn deficiency. In both, the Zn-deficient diets contained Zn at less than 1 $mg \cdot kg^{-1}$. Signs included anorexia, apathy, weight loss, dermatitis, reproductive failure, and lowered plasma and tissue Zn

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concentrations. Oral supplementation with Zn rapidly reversed the signs of Zn deficiency, but Zn concentrations in hair remained low for some time (Swenerton and Hurley, 1980). Although the Zn-deficient diet was fed only during the third trimester of pregnancy, behavioral effects on the infants born to these mothers were noted: they played and explored less, associated more with their mothers, and were less active (Sandstead et al., 1978).

Most of the studies cited above used diets very low in Zn (less than 1 $mg \cdot kg^{-1}$) to induce Zn deficiency. In a series of studies on rhesus monkeys, moderate or marginal Zn deficiency was produced by feeding a purified diet with Zn at 2 or 4 $mg \cdot kg^{-1}$ of diet (air dry), respectively (Golub et al., 1982, 1984a,b,c, 1990a,b, 1992, 1994, 1995, 1996a,b; Baly et al., 1984; Leek et al., 1984; Haynes et al., 1985, 1987; Keen et al., 1989, 1993; Lonnerdal et al., 1990a,b). The marginal Zn deficiency resulted in changes in activity level, taste sensitivity, and immune function but not in the more severe signs of Zn deficiency, such as anorexia, alopecia, diarrhea, and dermatitis. The Zn requirement of nonpregnant female monkeys was not determined; but when a diet with Zn at 12 $mg \cdot kg^{-1}$ air-dry diet was fed, plasma Zn remained normal, whereas it decreased when the diet contained 8 $mg \cdot kg^{-1}$ or less (Golub et al., 1982).

When the diet containing Zn at 4 $mg \cdot kg^{-1}$ (air dry) was fed to pregnant females, the more severe signs of dermatitis, anorexia, and low plasma Zn were observed and suggested that the Zn requirement is higher during pregnancy. Stillbirths, abortions, and delivery complications were more frequent in the group fed the low-Zn diet. Frequent observations of reduced plasma vitamin A and iron-deficiency anemia (Golub et al., 1984b; Baly et al. 1984) indicated that impaired Zn status can affect the metabolism of other essential nutrients. Effects of the low-Zn diet were observed not only in pregnant females, but also in infants born to them, which had slower than normal growth, taste dysfunction, and reduced food intake (Golub et al, 1984b). Delayed skeletal maturation and defective bone mineralization were also observed in the infants (Leek et al., 1984). Monkeys fed the marginal-Zn diet appeared to increase Zn absorption homeostatically. Pregnant and lactating dams fed the low-Zn diet showed about 25% higher Zn absorption than control dams (Lonnerdal et al., 1990a). A similar increase in Zn absorption was found in infants born to dams fed the low-Zn diet; that suggests that the Zn status was also compromised in the offspring.

The Zn requirement of infant rhesus monkeys can be estimated from the study of long-term feeding with formulas that had different concentrations of Zn (Polberger et al., 1996). Although formula containing Zn at 1 $mg \cdot L^{-1}$ resulted in signs of Zn deficiency, infants consuming formula containing 4 $mg \cdot L^{-1}$ did not show any of the signs. A Zn intake of 1.6-2 $mg \cdot d^{-1}$ or 1-1.5 $mg \cdot BW_{kg}^{-1} \cdot d^{-1}$ appears to meet the Zn requirement of growing rhesus infants. Rhesus milk contains Zn at about 2-5 $mg \cdot L^{-1}$ during the first month of lactation and slightly lower concentrations (1-2 $mg \cdot L^{-1}$) after that (Lonnerdal et al., 1984). Thus, inasmuch as Zn bioavailability is high in monkey milk, lower Zn intakes than from formula are adequate for nursed infants.

The complexity of assessing Zn status contributes to difficulties in establishing Zn requirements. Plasma or serum Zn concentrations are often used to diagnose Zn deficiency, but substantial decreases in those concentrations often occur only in severe deficiency (King and Keen, 1999). The "normal" mean Zn concentration in cerebrospinal fluid of rhesus monkeys (*Macaca mulatta*) has been reported to be 1.0 $\mu g \cdot dl^{-1}$ (Hambleton et al., 1981). In many of the studies of marginal or moderate Zn deficiency discussed above, plasma or serum Zn concentrations were not markedly affected. Furthermore, the use of galvanized cages has been shown to increase plasma Zn (Stevens et al., 1977) and hair Zn (Marriott et al., 1996). Thus, "normal" plasma Zn concentrations cannot be used to rule out impaired Zn status. Measurement of concentrations of Zn and metallothionein in liver biopsies might be useful in assessment of long-term Zn deprivation (Keen et al., 1988). In a study with rhesus monkeys, infants fed formula with a somewhat lower than usual Zn concentration (1 vs 4 $mg \cdot L^{-1}$) had "normal" plasma Zn concentrations, but growth and neutrophil chemotaxis were significantly reduced, and a marked increase in Zn absorption indicated impaired Zn status (Polberger et al., 1996).

Zn deficiency has been produced in the squirrel monkey *(Saimiri sciureus)* (Macapinlac et al., 1967; Barney et al., 1967). The animals were fed a semipurified diet in which low-Zn casein was the protein source. Growth was retarded, the hair coat appeared unkempt, and some alopecia occurred. Hematologic measurements in deficient animals were unchanged. Blood albumin was moderately decreased. Zn in serum and hair was decreased in deficient animals. Thickening of the mucosa of the tongue, particularly over the anterior dorsal surface, occurred within 60 days. Parakeratosis of the tongue developed and appeared to be a unique characteristic of Zn deficiency in this species. The deficiency signs were prevented with Zn at 15 $mg \cdot kg^{-1}$ of air-dry diet.

The minimal dietary requirement of Zn for squirrel monkeys has not been determined, but Zn at 17 $mg \cdot kg^{-1}$ of dietary dry matter seems to be adequate for weanling animals in the absence of dietary phytate (Barney et al., 1967).

Zn deficiency also has been observed in the moustached tamarin (*Saguinus mystax)* (Chadwick et al., 1979). Animals were fed a commercial diet containing Zn at 150 $mg \cdot kg^{-1}$ of diet, according to the manufacturer, although this value was not confirmed by analysis. The diet was supplemented with apples and oranges. The marmosets developed alopecia on the tail, thinness of hair, open sores about the anus

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and tail, and were generally debilitated. The lesions were reversed by adding $ZnSO_4 \cdot 7H_2O$ to provide Zn at 40 $mg \cdot L^{-1}$ in drinking water. The alopecia returned when the animals were given Zn at 80 $mg \cdot L^{-1}$ of drinking water, and some hair regrowth occurred when Zn in the water was returned to 40 $mg \cdot L^{-1}$. The reason for the adverse effect of the higher concentration of Zn was not apparent.

Increased serum Zn has been found in Senegalese baboons (*Papio papio*) that were moderately sensitive to light-induced seizures. Chronic oral administration of the chelating agent, D-penicillamine, lowered serum Zn and protected against the seizures (Alley et al., 1981).

Iodine

Iodine (I) is a part of the thyroid hormones thyroxine (3,5,3′5′-tetraiodothyronine) and 3,5,3′-triiodothyronine (Stanbury, 1996). Thus, I plays a major role in the regulation of growth and of metabolic rate. Although it is found in generous amounts in oceans, much of the I originally present in soil has been leached from surface layers by glaciers, snow, and rain. Ocean winds carry I-bearing moisture to near-shore areas, but ancient interior soils and the plants growing on them are often I-deficient.

Potassium iodide, calcium iodate, ethylenediamine dihydriodide, and pentacalcium orthoperiodate are sources of I commonly added to animal diets to prevent deficiency. All four have high bioavailability. Calcium iodate, ethylenediamine dihydriodide, and pentacalcium orthoperiodate have greater physical stability (Miller and Ammerman, 1995).

Schultz et al. (1965) and Pickering (1968) reported on the uptake of radioiodine by the thyroid glands of pregnant rhesus monkeys *(Macaca mulatta)* and their fetuses. Fetal thyroids incorporated radioiodine more rapidly than maternal thyroids. Both maternal and fetal thyroids contained substantial I-containing thyroid hormones. Thyroidectomized infant rhesus monkeys exhibited nearly all the signs of cretinism seen in humans (Pickering and Fisher, 1953a, 1953b), but frank deficiency signs were not produced by feeding I-deficient diets. It is noteworthy that low protein concentrations (2%) in the diet of *Macaca nemestrina* resulted in thyroidal ultrastructural changes mimicking thyroid hypofunction induced by hypophysectomy or thyroxine administration (Worthington and Enwonwu, 1975). However, the thyroidal changes may be a consequence of tyrosine deficiency associated with low protein intake and have little relationship to the I supply.

Iodine deficiency has been produced in the common marmoset *(Callithrix jacchus)* by feeding a diet composed of natural ingredients selected for their low I content (Mano et al., 1985). The diet furnished I at about 0.36 $\mu g \cdot d^{-1}$. On the basis of DM intake of about 12-13 $g \cdot d^{-1}$, dietary I concentration was 0.03 $\mu g \cdot g^{-1}$ of DM. Body weights were maintained, and there were no clinical signs of ill health. However, mean plasma thyroxine concentration declined from an original value of 140.1 $nmol \cdot L^{-1}$ to 22.4 $nmol \cdot L^{-1}$, and mean plasma thyroid-stimulating hormone concentration increased from 1.8 $ng \cdot ml^{-1}$ to 9.0 $ng \cdot ml^{-1}$. Compared with newborn offspring of control marmosets receiving a potassium iodate supplement providing I at 7.9 $\mu g \cdot d^{-1}$ (0.65 $\mu g \cdot g^{-1}$ of dietary DM), the young of I-deficient females had heavier thyroid glands and lower thyroidal I concentrations. On histologic examination, their thyroid glands exhibited hypertrophy and hyperplasia; follicular colloid was absent.

The infants from first and second pregnancies were evaluated in further studies. Those of mothers fed the low-I diet had sparse hair coats but were not different from controls in body weight or skeletal development. The brain weights of deficient newborns from the second pregnancies were reduced, particularly those of the cerebellum, where brain-cell numbers were reduced. Brain-stem cell size was reduced in the cerebrum. Offspring from the second pregnancies were more severely affected than those from the first (Mano et al., 1987).

Young marmosets born of mothers fed an I-deficient diet in the studies of Mano et al. (1985) were fed a deficient or a normal diet (Goss et al., 1988). They were compared with animals born of mothers fed a normal diet and themselves fed a normal diet. Marmosets from I-deficient mothers and fed the deficient diet were smaller at birth and grew more slowly; whereas those fed the normal diet were smaller at birth but exhibited compensatory growth and were of nearly normal size by the age of 1 year. The I-deficient animals did not have a typical cretin face.

Specific quantitative requirements for I have not been determined. The studies with marmosets indicate that 0.03 $mg \cdot kg^{-1}$ of dietary DM is insufficient but that 0.65 $mg \cdot kg^{-1}$ is sufficient. Diets containing I at about 2.2 $mg \cdot kg^{-1}$ of dietary DM were previously deemed adequate for most growing and adult nonhuman primates (National Research Council, 1978), but this concentration appears not to have been judged a minimum requirement. Estimates of I requirements for other species reported in the National Research Council nutrient requirement series do not exceed 0.35 $mg \cdot kg^{-1}$ of dietary DM.

Selenium

Most of the selenium (Se) in biologic systems is in amino acid constituents of proteins. Proteins that contain Se in stoichiometric amounts are called selenoproteins; selenocysteine is the primary reactive structure in the animal selenoproteins that have been identified (Burk and Levander, 1999). A number of proteins contain Se in nonstoichiometric amounts and are called simply Se-containing proteins; this Se is often found in selenomethionine, and

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the proportion of Se in Se-containing proteins is usually related to the relative proportions of methionine and selenomethionine. Although higher plants appear not to need Se, Se enters the food chain through plants; Se exists primarily as selenomethionine and, to a lesser extent, as selenocysteine and other sulfur amino acid analogues. Selenium concentrations in plants depend on the plant species and available Se concentrations in soil, and vary widely from deficient to toxic for animals that consume them.

After absorption by animals, selenomethionine appears not to be recognized specifically as a Se compound and is metabolized in the methionine pool. When catabolized, the released Se enters regulated Se metabolism and can be incorporated into selenocysteine in selenoproteins, into Se-transport compounds of unidentified composition, or into methylated Se excretory metabolites. Selenocysteine and inorganic Se absorbed by animals also enter regulated Se metabolic pathways. Selenocysteine is degraded to selenide by selenocysteine β-lyase, whereas inorganic Se is reduced to selenide by glutathione. Selenide can enter anabolic pathways by conversion to selenophosphate or can be methylated and excreted (Burk and Levander, 1999).

Eleven selenoproteins have been identified in animals; the functions of several of them are still unknown, and apparently other selenoproteins exist. The four glutathione peroxidase selenoproteins that have been characterized use reducing equivalents from glutathione to catabolize hydroperoxides. Thus, they have been generally considered to protect cells from oxidative damage. However, their different locations and substrate specificities suggest that they can also be involved in metabolic regulation (Burk and Levander, 1999). Vitamin E functions in the protection of injury from hydroperoxides; consequently, there is an interaction between dietary needs for vitamin E and Se. Nevertheless, there is a dietary requirement for Se even if sufficient vitamin E is present (McDowell, 1992).

Selenium is involved in the metabolism of thyroid hormones, and combined deficiencies of iodine and Se are more severe than a deficiency of iodine alone (Levander and Burk, 1996). Iodothyronine deiodinases are selenoproteins that catalyze the deiodination of thyroxine, triiodothyronine, and reverse triiodothyronine and thus regulate the concentration of the active hormone triiodothyronine.

Thioredoxin reductase is an NADPH-dependent selenoprotein containing selenocysteine and regenerates ascorbic acid from dehydroascorbic acid in animals (May et al., 1997).

Selenoprotein P is an extracellular protein found in plasma and associated with endothelial cells. Its specific function has not been identified, but it accounts for about 45% of plasma Se in North American humans (Hill et al., 1996). Its concentration declines in Se deficiency, can be used for assessing Se status, and appears to be associated with oxidant defense.

Selenoprotein W has been found in muscle and a number of other tissues, and its concentration declines in Se deficiency (Vendeland et al., 1993). Its biochemical function is unknown, but the binding of one form to glutathione suggests that it can undergo redox changes.

Two selenophosphate synthetases that appear to be involved in Se homeostasis have been identified in animals (Guimaraes et al., 1996).

The Se in natural ingredients can be highly variable in quantity and in bioavailability (Henry and Ammerman, 1995; Levander and Burk, 1996). Se is usually added to commercial feeds in the form of sodium selenite.

Adult squirrel monkeys *(Saimiri sciureus)* appear to be more sensitive than rhesus monkeys to Se deficiency. Squirrel monkeys fed a semipurified torula-yeast diet with adequate vitamin E but without added Se showed weight loss, listlessness, alopecia, myopathy, and hepatic degeneration. The signs did not appear until the deficient diet was fed for 6-9 months. The signs were reversed by a single injection of 0.04 mg of Se from sodium selenite, and the animals were maintained by three injections of 0.04 mg at 2-week intervals followed by monthly injections. Untreated monkeys became moribund and died (Muth et al., 1971).

Pregnant rhesus *(Macaca mulatta)* monkeys were fed a semipurified diet containing Se at 0.03 or 0.2 $mg \cdot kg^{-1}$. No deficiency signs were seen in the mothers fed the Se-deficient diets for about 4 years. The young of the females fed the low-Se diets for about 2 years exhibited no deficiency signs. Although several animals fed the deficient diets died, no pathologic lesions characteristic of Se deficiency were seen. Hair analyses demonstrated that the animals fed the low-Se diet did indeed have low tissue concentrations. Plasma and erythrocyte glutathione peroxidase activities decreased in animals fed the diet low in Se and increased in animals fed the diet supplemented with Se. Cardiomyopathy, characteristic of Se deficiency, was found in a mother and infant fed a protein-deficient low-Se diet. That suggested that simultaneous deficiencies of protein and Se are required for signs of Se deficiency to be manifested (Butler et al., 1988).

Blood Se concentrations and glutathione peroxidase activities were compared in a number of species, including nonhuman primates (Butler et al., 1982; Beilsten and Whanger, 1983; Beilsten et al., 1984; Butler et al., 1988). A much greater portion of the Se was associated with glutathione peroxidase in erythrocytes of squirrel monkeys, rats, and sheep than of rhesus monkeys and humans.

The toxicity of L-selenomethionine was studied in 20 female *Macaca fascicularis* by administering various daily doses via a nasogastric tube (Cukierski et al., 1989). The researchers concluded that the maximal dose tolerated for 30 days was 150 $\mu g \cdot BW_{kg}^{-1} \cdot d^{-1}$ on the basis of mean body weight loss, hypothermia, dermatitis, xerosis, cheilitis, dis-

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turbances in menstruation, and the need for dietary intervention to prevent death at doses of 188 $\mu g \cdot BW_{kg}^{-1} \cdot d^{-1}$ or greater.

The effects of L-selenomethionine doses of 0, 25, 150, or 300 $\mu g \cdot BW_{kg}^{-1} \cdot d^{-1}$ via nasogastric intubation during organogenesis—gestation day [GD] 20-50— were studied in 40 pregnant *Macaca fascicularis* (Tarantal et al., 1991). Dose-dependent toxicity signs in the pregnant females increased with increasing duration of Se exposure and included anorexia, vomiting, and reduction in body weight. One growth-retarded fetus was recovered on GD 131 from a dam exposed to 25 $\mu g \cdot BW_{kg}^{-1} \cdot d^{-1}$. One infant exposed to 150 $\mu g \cdot BW_{kg}^{-1} \cdot d^{-1}$ prenatally exhibited a unilateral cortical cataract. One early embryonic death (on GD 35) and two fetal deaths (on GD 68 followed by maternal death on GD 123) occurred among dams exposed to 300 $\mu g \cdot BW_{kg}^{-1} \cdot d^{-1}$.

The Se requirement of squirrel monkeys appears to be about 0.11 $mg \cdot kg^{-1}$ of dietary DM, on the basis of the Se concentration adequate to cure deficiency signs (Muth et al, 1971). A quantitative requirement for Se for rhesus monkeys has not been established. The decrease in plasma glutathione peroxidase activity in rhesus monkeys fed a low-Se diet suggests a nutritional requirement, but it has been proposed that the higher levels of glutathione transferase (a non-Se glutathione peroxidase) in the tissues of this species accounts for its resistance to Se deficiency (Butler et al., 1988).

Cobalt

Cobalt (Co) is a component of vitamin B_{12} (cobalamin), a vitamin required by nonhuman primates. Vitamin B_{12} has been found only in foods of animal or microbial origin. Ruminant animals have a dietary requirement for Co, which is incorporated into vitamin B_{12} during bacterial synthesis in the rumen. A nutritional requirement for Co, independent of vitamin B_{12}, for nonhuman primates has not been demonstrated.

Presumably, herbivorous primates with adaptations of the stomach or hindgut that allow for microbial fermentation can synthesize vitamin B_{12} from Co. Vitamin B_{12} production has been observed in the gastrointestinal contents of baboons fed a vitamin B_{12}-deficient diet (Uphill et al., 1977), and the presumed synthesis of this vitamin by intestinal microorganisms was offered as a partial explanation of the observation that vitamin B_{12} deficiency was more severe in animals fed the antibiotic ampicillin than in controls. Cobalamin absorption has been studied in normal and gastrectomized baboons (Green et al., 1982). Primates practicing coprophagy can obtain B_{12} from their feces (Oxnard et al., 1989). In any case, there are no data to support a quantitative requirement for Co.

Excessive intakes of Co by humans have resulted in reduced thyroid activity, goiter, and cardiomyopathy (Barceloux, 1999).

Chromium

Chromium (Cr) appears to potentiate insulin and will reverse impaired glucose tolerance in a number of species, including humans (Stoecker, 1999). Cr presumably is involved in carbohydrate, lipid, protein, and nucleic acid metabolism, although until recently it has not been identified as a component or cofactor of any enzyme system. The oligopeptide chromodulin binds chromic ions in response to an insulin-mediated chromic ion flux, and this metal-saturated oligopeptide can bind to an insulin-stimulated insulin receptor, activating the receptor's tyrosine kinase activity. Thus, chromodulin might play a role in the autoamplification of insulin signaling (Vincent, 2000). A contrary proposal has been made that trivalent Cr (Cr^{+3}) can act clinically by interfering with iron absorption, decreasing the high iron stores that some have linked to diabetes and heart disease in humans and thus qualifying Cr as a pharmacologic agent rather than an essential element (Steams, 2000).

Cr^{+3} is the form usually used in animal nutrition. Hexavalent chromium (Cr^{+6}) should be avoided because of its higher toxicity (National Research Council, 1997). Concentrations of Cr in potable water, fruit juices, and soft drinks (Garcia et al., 1999) and in spices and aromatic herbs (Garcia et al., 2000) have been published. Chromic potassium sulfate and chromic chloride have served as sources of Cr in diets for animals, and Cr in yeast is quite bioavailable (National Research Council, 1995, 1997). Chromium picolinate is a commercial source of organic Cr but because of regulatory restraints can be added only to swine feed (American Feed Control Officials, 1997). In addition, evidence that it is absorbed and incorporated into cells in its original form suggests that the metabolism of chromium picolinate is different than of Cr occurring naturally in the diet. The picolinate ligands shift the redox potential of the chromic center in such a way that it can be reduced by biologic reducing agents, such as ascorbic acid and thiols. The resulting chromous complex can interact with oxygen catalytically, generating hydroxyl radicals, which have been shown in vitro to increase DNA cleavage substantially (Vincent, 2000). Thus, the long-term effects of chromium picolinate use need to be investigated.

Davidson et al. (1967) and Davidson and Blackwell (1968) reported a high prevalence of impaired glucose tolerance in young adult female squirrel monkeys maintained on a commercial diet. The animals weighed 600-800 g. The impaired tolerance was improved by supplementation with trivalent chromium acetate at 10 $mg \cdot kg^{-1}$ in drinking water if the water was maintained at a neutral

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pH. Supplementing with trivalent Cr in drinking water maintained at a mildly acidic pH was ineffective. Divalent Cr was not effective in improving glucose tolerance.

Martin et al. (1972) reported corneal opacities in eyes of adult female squirrel monkeys *(Saimiri sciureus)* weighing 600-800 g that were fed a semipurified diet containing Cr at 0.093 $mg \cdot kg^{-1}$ of DM and received drinking water with Cr at less than 0.01 $mg \cdot kg^{-1}$. Total intake of Cr was about 4 μg per animal per day. The mean daily food intake was 44 g. After 6 weeks on the deficient diet, eye lesions developed, starting as haziness of the cornea. The lesions developed into superficial maculae and progressed to deeper opacities with vascularization. The lesions were not reversible by Cr supplementation or the feeding of a commercial monkey diet for up to 9 months. Similar but milder lesions developed in squirrel monkeys fed the deficient diet for 2 weeks, then supplemented with trivalent chromium at 5 $mg \cdot kg^{-1}$ in the drinking water (total intake, about 400 μg per monkey per day). The results suggest that even a short-term dietary deficiency of Cr can lead to irreversible corneal lesions. Comparable lesions were not observed in animals maintained on diets similar in composition but higher in naturally occurring Cr or on a commercial monkey diet that furnished about 150 μg of Cr per day. Other than the eye lesions, the animals remained healthy over the 34-week period without any other signs of dietary deficiency.

Because of issues of biologic availability and the valence state of Cr (only trivalent and hexavalent chromium are biologically active), a quantitative requirement for Cr has not been established. The Cr content of the diet is thought to have little relationship to biologically active Cr, because of the diversity of dietary Cr forms (National Research Council, 1997). Chromium nutrition has not been studied in nonhuman primates other than squirrel monkeys.

Fluorine

Fluoride (F^-) reduces the incidence and severity of dental caries in humans (Phipps, 1996). The caries-preventive effect of F^- is attributed mainly to remineralization at the interface of teeth and oral fluids. F^- in saliva shifts the balance from demineralization, that leads to caries, to remineralization, presumably because of the F^--enhanced precipitation of calcium phosphates and formation of fluorhydroxyapatite (ten Cate, 1999). It is now considered a required element in human diets because of its cariostatic effect, when it is ingested, on pre-eruptive development of teeth. F^- in oral fluids also has a cariostatic effect on posteruptive teeth. The need for F^- in humans is most commonly met by addition to the drinking water at 1.0 $mg \cdot L^{-1}$, which is considered an optimal concentration (Institute of Medicine, 1997).

Natural ingredients used in manufactured diets for primates can contribute substantial amounts of F^-. Grains, oilseeds, and their byproducts frequently contain F^- at 1-2 $mg \cdot kg^{-1}$. Animal and fish byproducts containing bone can contribute to dietary F^-. F^- is a common contaminant in rock phosphate, the source of much of the feed-grade phosphate used as a phosphorus supplement. To qualify as feed-grade phosphate, it must be deflourinated to 1 part of F^- (or less) to 100 parts of phosphorus (AAFCO, 1997). Depending on the manufacturing process, the addition of 0.25% of phosphorus from dicalcium phosphate can contribute 20 $mg \cdot kg^{-1}$ or more F^- to the diet (McDowell, 1992). Thus, commercial diets for nonhuman primates, under some circumstances, can have substantially higher F^- concentrations than found in human diets.

F^- has been shown to have a cariostatic effect in monkeys. Cynomolgus monkeys *(Macaca fascicularis)* 11-13 months old were given drinking water containing F^- at 2 ppm for 5 years, beginning before eruption of their first permanent molars (Cohen and Bowan, 1966). The F^- concentration of the diet was thought to be low but was not measured. The diet was composed of an offering of bread, bananas, canned carrots, biscuits, peanut butter, boiled eggs, jam, complan, dates, marmie, and cheese (Cohen and Bowan, 1966). Animals receiving F^- had less caries than animals not receiving F^-. The F^- was more effective if teeth were being formed while exposed to F^- than if they were exposed after mineralization (Bowen, 1973). Those results are in contrast with the observations of Ockerse and de Jager (1957), who added F^- at 10 $mg \cdot kg^{-1}$ to the drinking water of African green monkeys (*Cercopithecus aethiops*) of unstated age that were fed a cariogenic diet; the added F^- had no effect on the incidence of caries.

An adequate F^- intake by men was recently estimated to be 4 $mg \cdot d^{-1}$ (Institute of Medicine, 1997). Assuming that average daily intake of food is 500 g of DM, that is equivalent to F^- at 8 $mg \cdot kg^{-1}$ of dietary DM. However, F^- needs of people of all ages seem to be best met by its inclusion in drinking water at 1.0-2.0 $mg \cdot L^{-1}$.

Some signs of mild fluorosis (mottling of the teeth) are seen when water contains F^- at 2 $mg \cdot L^{-1}$.

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7 Vitamins

FAT-SOLUBLE VITAMINS

Vitamin A and Carotenoids

The term *vitamin A* as used here applies to all derivatives of β-ionone (other than the provitamin A carotenoids) that have the biologic activity of all-*trans*-retinol. Vitamin A, also known as retinol, is found in foods of animal origin and in some microorganisms, either as the alcohol or as fatty acid esters, mostly palmitate and stearate (Baker, 1995; Ross, 1999). Vitamin A functions in vision as the metabolite 11-*cis*-retinal combined with proteins (opsins) to form the visual pigments rhodopsin (in rod cells) and iodopsin (in cone cells). When light strikes those pigments, 11-*cis*-retinal is converted to all-*trans*-retinal, triggering chemical events that lead to communication of neuronal cells with the visual cortex of the brain. Vitamin A also functions in cellular differentiation, embryologic development, spermatogenesis, cell-to-cell communication, and the immune response. The mechanisms of those functions have not been well elucidated, but retinoic acid appears to be a potent metabolite of vitamin A that may be involved in most of them, except for vision (Olson, 1996, 1999; Ross, 1999).

MEASURES OF BIOLOGIC ACTIVITY

The biologic activity of vitamin A can be expressed in international units (IU) or US Pharmacopeia (USP) units: 1 IU or 1 USP unit of vitamin A activity is equivalent to the activity provided by 0.3 μg of all-*trans*-retinol, 0.344 μg of all-*trans*-retinyl acetate, or 0.55 μg of all-*trans*-retinyl palmitate. Thus, 1 μg of all-*trans*-retinol provides 3.33 IU of vitamin A activity. Vitamin A activity also has been expressed in retinol equivalents (RE): 1 RE of vitamin A is equivalent to the activity provided by 1 μg of all-*trans*-retinol (Baker, 1995). An isomer of vitamin A found in freshwater fish, 3,4-didehydroretinol, has about 40% of the biologic activity of crystalline all-*trans*-retinol (Ross, 1999).

Most plants and some animal foods contain carotenoids. Over 600 have been identified, and about 50 have provitamin A activity. Of the provitamin A carotenoids, β-carotene, α-carotene, cryptoxanthin, β-zeacarotene, and the β-apocarotenals are of particular importance (Bauernfeind, 1981). Provitamin A carotenoids contribute to vitamin A nutriture after central cleavage to retinal, primarily in the gut mucosa. Conversion of dietary carotenoids to vitamin A has been demonstrated in rhesus monkeys (*Macaca mulatta*) (Krinsky et al., 1990), but the efficiency of the conversion has not been studied. On the basis of rat studies with synthetic crystalline β-carotene, 0.60 μg of all-*trans*-β-carotene is equivalent to 0.30 μg of all-*trans*-retinol. Later research with other species, including humans, showed that this quantitative relationship does not apply under natural conditions of carotenoid intake. Mixed carotenoids in a natural diet are used less efficiently than β-carotene, and crystalline β-carotene is more efficiently used than natural β-carotene in the various matrices in which it occurs in foods and feeds (Baker, 1995; Lee et al., 1999; Huang et al., 2000; van het Hof et al., 2000). It has been assumed that 6 μg of all-*trans*-β-carotene or 12 μg of other provitamin A carotenoids is equivalent to 1 μg (1 RE) of retinol in the human diet (National Research Council, 1989). Recently, it was proposed that this relationship be modified so that 12 μg of all-*trans*-β-carotene or 24 μg of other provitamin A carotenoids in the human diet would equal 1 retinol activity equivalent (RAE). One RAE would equal 1 μg of all-*trans*-retinol, as was the case for the previously used RE (Institute of Medicine, 2001). In the absence of more specific data, bioequivalence values similar to those used for humans can reasonably be used for provitamin A carotenoids in the diets of nonhuman primates. Thus, 1 μg of β-carotene in the nonhuman-primate diet would provide 0.555 IU of vitamin A activity, whereas 1 μg of other provitamin A carotenoids would provide 0.2775 IU.

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ABSORPTION AND CIRCULATION OF CAROTENOIDS

β-Carotene and other carotenoids appear to be absorbed by some animal species but not others. Individuals and species that do not circulate carotenoids in plasma, even though they are present in the diet, might convert dietary carotenoids to vitamin A in the intestine more efficiently than the ones that do circulate carotenoids (Olson, J.A., 1999). Although the efficiency of the conversion has not been specifically studied in nonhuman primates, serum or plasma concentrations of total carotenoids or of β-carotene, α-carotene, α-cryptoxanthin, β-cryptoxanthin, lutein plus zeaxanthin, or lycopene (both provitamin A and non-provitamin A compounds) have been measured in several species (de La Pena et al., 1972; Cornwell and Boots, 1981; Boots et al., 1983; Sabrah et al., 1990; Snodderly et al., 1990; Crissey et al., 1999; Slifka et al., 1999, 2000). Attempts were made in some studies to estimate carotenoid concentrations in the average diet, but individual primates were able to self-select preferred foods, so it was difficult to measure carotenoid intakes precisely.

Very low or nonmeasurable concentrations of serum carotenoids have been found in tamarins (*Saguinus oedipus*) and capuchins (*Cebus albifrons*), whereas high concentrations were found in serum of the sooty mangabey (*Cerocebus torquatus*) and the orangutan (*Pongo pygmaeus*). Rhesus (*Macaca mulatta*), cynomolgus (*Macaca fascicularis*), and squirrel (*Saimiri sciureus*) monkeys did not have significant concentrations of non-polar carotenoids, such as β-carotene, in their plasma, but appreciable concentrations of polar carotenoids, such as lutein and zeaxanthin, were found if they were in the diet (Krinsky et al., 1990; Snodderly et al., 1990). It is not clear whether the variability in plasma carotenoid concentration results from differences in carotenoid metabolism among primate species or from the presence of different dietary carotenoids or of different dietary carotenoid concentrations.

VITAMIN A AND CAROTENOIDS IN FEEDSTUFFS

Vitamin A and carotene concentrations in feedstuffs vary with origin—including species and growing conditions of plant feedstuffs, species and vitamin A and carotene intakes of animals used as food, and feedstuff processing and storage. To ensure an adequate vitamin A supply, primates in captivity are usually provided diets to which synthetic vitamin A has been added. Synthetic retinyl palmitate and retinyl acetate are the usual supplemental forms, and these are commonly microencapsulated with antioxidants to improve their stability. Nevertheless, if unaccounted for, heat, moisture, manufacturing procedures, and extended storage times can lead to lower than expected dietary vitamin A activity (Camire et al., 1990; Baker, 1995).

ABSORPTION, CIRCULATION, AND STORAGE OF VITAMIN A

Retinyl esters are hydrolyzed in the gut by pancreatic and intestinal brush-border ester hydrolases and the released retinol emulsified with bile salts and lipid. Retinol is absorbed rapidly by the intestinal villi, esterified primarily with palmitic and stearic acids in the mucosal cell, and transported to the liver as retinyl esters in the lipid core of chylomicra. The liver stores much of the retinol, mostly in ester form, and regulates its secretion into the plasma for transport to other tissues in association with retinol-binding protein (RBP) and a cotransport prealbumin, transthyretin (Olson, 1991, 1996; Ross, 1999). In humans, when vitamin A intake is adequate, 50-85% or more of body vitamin A is stored in the liver. Thus, liver levels of the vitamin are good indicators of vitamin A status.

Plasma retinol has proved useful in assessing vitamin A status in humans when plasma concentrations were very low (under 10 $\mu g \cdot dl^{-1}$) or very high (over 100 $\mu g \cdot dl^{-1}$). Very low concentrations were associated with depletion of vitamin A reserves, whereas very high concentrations were associated with vitamin A intakes exceeding need. When liver reserves (expressed as retinol) are adequate but not excessive (20-520 $\mu g \cdot g^{-1}$ of wet liver tissue), plasma vitamin A concentration tended to be homeostatically controlled at a point in each person that was largely independent of total body reserves (Olson, 1991). Although normally it is a small fraction (2-20%) of total plasma vitamin A, retinyl ester was highly concentrated relative to free retinol in humans with vitamin A intakes exceeding the storage capacity of the liver; this phenomenon might reflect conversion of excess vitamin A to a less toxic form (Lee and Nieman, 1993). A transient increase in plasma retinyl esters also occurs after consumption of a vitamin A-rich meal, so fasting blood samples should be used for status-assessment (Olson, 1996).

Plasma or serum vitamin A concentrations have been measured in captive rhesus monkeys (*Macaca mulatta*), cynomolgus monkeys (*Macaca fascicularis*), African green monkeys (*Cercopithecus aethiops*), capuchins (*Cebus* spp.), marmosets (*Callithrix jacchus*), tamarins (*Saguinus fuscicolis*), squirrel monkeys (*Saimiri sciureus*), owl monkeys (*Aotus trigatus*), spider monkeys (*Ateles geoffroyi*), colobus monkeys (*Colobus guereza*), sooty mangabeys (*Cercocebus torquatus*), Schmidt's monkeys (*Cercopithecus ascanius*), baboons (*Papio cynocephalus*), mandrills (*Papio sphinx*), chimpanzees (*Pan troglodytes*), orangutans (*Pongo pygmaeus*), and gorillas (*Gorilla gorrilla*) (O'Toole et al., 1974; Cornwell and Boots, 1981; Meydani et al., 1983; McGuire et al., 1989; Flurer and Schweigert, 1990; Rogers et al., 1993; Crissey et al., 1999). Circulating vitamin A concentrations varied between species and between studies. In one study, tamarins, squirrel monkeys, capuchins, and owl monkeys had plasma vitamin A concentrations that were

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about one-fourth those in rhesus, cynomolgus, and African green monkeys. The concentrations in the latter group were comparable with those in humans. Plasma retinol in gorillas appeared to be somewhat higher than in humans and that in baboons lower. However, there was considerable variability in observed values in both gorillas and baboons. Free-ranging black spider monkeys (*Ateles paniscus chamek*) in Bolivia had plasma retinol concentrations of 12-25 $\mu g \cdot dl^{-1}$, with a mean of 19.7 $\mu g \cdot dl^{-1}$ (Karesh et al., 1998). Captive spider monkeys (*Ateles geoffroyi*) had a mean serum retinol concentration of 17.5 $\mu g \cdot dl^{-1}$ and a mean serum retinyl palmitate concentration of 0.8 $\mu g \cdot dl^{-1}$. Calculated vitamin A activity (from retinol and carotenoids) in the captive diet was 14,000 $IU \cdot kg^{-1}$, on a dry-matter (DM) basis (Crissey et al., 1999).

Adequate dietary zinc is necessary for maintenance of normal plasma concentrations of vitamin A. When pregnant rhesus monkeys were rendered marginally deficient in zinc, plasma zinc was positively correlated with plasma vitamin A at 135 days of pregnancy and 2-3 months postpartum. There also was a positive correlation between plasma zinc and RBP concentrations. The ratio of RBP to vitamin A tended to be higher in zinc-deficient animals; this suggests that the relationship between zinc, vitamin A, and RBP is complex (Baly et al., 1984).

VITAMIN A DEFICIENCY

Signs of vitamin A deficiency have been described in rhesus and capuchin monkeys (Harden and Zilva, 1919; Saiki, 1929; Tilden and Miller, 1930; Turner and Loew, 1932; Grinker and Kandel, 1933; Hetler, 1934; Verder and Petran, 1937; Ramalingaswami et al., 1955; Rodger et al, 1961; Hayes, 1974b; O'Toole et al., 1974). The early studies were reviewed by Day (1944). The first manifestations of deficiency were weakness, diarrhea, loss of appetite, growth cessation, and an apparent increase in susceptibility to respiratory infection. Keratinization of the epithelial tissues also was observed. With a longer, chronic deficiency, pathologic changes in the eye became apparent; these changes were characterized by keratomalacia, xerophthalmia, night blindness, and eventual loss of day vision (Hetler, 1934: Verder and Petran, 1937; Ramalingaswami et al., 1955; Hayes, 1974b). In adult monkeys, the first sign of deficiency appeared after about a year of dietary vitamin A deficiency, by which time plasma vitamin A concentration had fallen from 26 $\mu g \cdot dl^{-1}$ to 10 $\mu g \cdot dl^{-1}$ or less in rhesus monkeys (O'Toole et al., 1974), and from 15-20 $\mu g \cdot dl^{-1}$ to less than 5 $\mu g \cdot dl^{-1}$ in capuchin monkeys (Hayes, 1974b). Two of four pregnancies carried to term by rhesus monkeys that were maintained on marginal intakes of vitamin A (400 IU twice a week after plasma vitamin A concentrations dropped below 10 $\mu g \cdot dl^{-1}$ on a vitamin A-deficient diet) produced infants with congenital xerophthalmia; a third infant developed xerophthalmia after receiving a vitamin A-deficient diet for 2 years.

VITAMIN A REQUIREMENTS

Despite relatively extensive studies of the deficiency syndrome, minimal requirements for vitamin A are not well established. It is apparent that 400 IU of vitamin A twice a week is insufficient for correction of vitamin A deficiency in adult female rhesus monkeys, although this amount will maintain plasma concentrations of about 10 $\mu g \cdot dl^{-1}$ (O'Toole et al., 1974). Control animals weighing 2-3 kg and receiving 175-700 IU of vitamin A per day appeared to be in satisfactory health (Tilden and Miller, 1930). Ramalingaswami et al. (1955) administered 1,500 IU of vitamin A twice a week to control animals that were receiving 100 g of air-dry diet per day. That dosage, which is roughly equal to 4,760 $IU \cdot kg^{-1}$ of dietary DM, was sufficient to prevent ocular lesions.

The transport of vitamin A in plasma and its metabolism by nonhuman primates that have been studied are similar to those in humans (Vahlquist, 1972; Muto et al., 1973; Burri et al., 1993), so it is reasonable to assume that the requirements of some nonhuman primates are comparable with those of humans. The estimated average requirement (EAR) to ensure adequate stores of vitamin A in adult male humans has been estimated to be 625 μg of all-*trans*-retinol per day (Institute of Medicine, 2001), roughly equivalent to 4,000 $IU \cdot kg^{-1}$ of dietary DM. The recommended daily allowance (RDA) for the human adult male is 900 μg of all-*trans*-retinol per day (Institute of Medicine, 2001), roughly equivalent to 6,000 $IU \cdot kg^{-1}$ of dietary DM. The RDA contains a safety factor so it should meet or exceed the needs of nonhuman primates. Commercial diets containing vitamin A activity at 20,000-30,000 $IU \cdot kg^{-1}$ appear to support normal growth, good health, and reproduction in nonhuman primates. Although there are few direct supporting data, vitamin A at 10,000 $IU \cdot kg^{-1}$ of dietary DM should be safe and adequate to meet the needs of primates. That is somewhat below the intake (12,000 $IU \cdot kg^{-1}$ of DM) used in purified diets for squirrel monkeys (Ausman et al., 1985).

Although effects of carotenoids (such as quenching singlet oxygen), beyond provitamin A activity, have been described in biologic systems, there are insufficient data to set minimal requirements for carotenoids.

HYPERVITAMINOSIS A

Signs of hypervitaminosis A have been described in young cynomolgus monkeys (*Macaca fascicularis*) weighing 1-1.8 kg and receiving single intramuscular injections of a water-miscible preparation containing retinyl acetate at 500,000 $IU \cdot ml^{-1}$, vitamin E at 50 $IU \cdot ml^{-1}$, and vitamin

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D_2 at 50,000 IU·ml^{-1} (Macapinlac and Olson, 1981). The injections provided the equivalent of retinol at 100-500 mg·kg^{-1} of body mass (bodyweight [BW]). Neither toxicity signs nor deaths were seen in monkeys given the equivalent of retinol at 100 mg·BW$_{kg}^{-1}$. The first signs of toxicity appeared within 3-35 minutes in those receiving the equivalent of retinol at 200-500 mg·BW$_{kg}^{-1}$. Most frequent were recurrent yawning, droopiness of the eyelids, and drowsiness, with transient and repeated closure of the eyes. Hyperextension of the neck, rapid jerky shaking of the head, hyperactivity, ataxia, and bouts of nausea and vomiting were seen in monkeys receiving 300-500 mg. Of those receiving the 200-mg dose, 67% died, whereas mortality was 100% in those receiving higher dosages, most dying in less than 3 days. The possibility that these effects were due in part to excesses of vitamins D and E was considered by the researchers but judged unlikely.

Subtoxic concentrations of retinyl esters at 17.0 ± 6.3 umol·μg^{-1} of liver were found in 3.5- to 28.2-year-old rhesus monkeys (*Macacca mulatta*) fed a widely used dry commercial diet with 40 IU vitamin A (label guarantee), as retinyl acetate, per gram. Histologic examination of the livers revealed Ito cell hypertrophy and hyperplasia, and it was suggested that preformed vitamin A concentrations in the diet were excessive (Penniston and Tanumihardjo, 2001).

Vitamin D

For the primate species that have been studied, vitamin D is not an essential component of the diet as long as they have adequate exposure to sunlight (Holick, 1994). But it appears to be essential in the tissues of most primates for maintenance of calcium and phosphorus homeostasis and for normal bone mineralization (Holick, 1996). In the absence of solar exposure, these primates must be exposed to sources of artificial light of appropriate wavelengths or must receive sufficient vitamin D in the diet. In this review we will try to put into perspective what is known about vitamin D in humans and to compare this information with what is known about its role in nonhuman primates and other vertebrates.

PHOTOBIOLOGY, METABOLISM, AND FUNCTION OF VITAMIN D

Vitamin D is a secosteroid (a split- or open-ringed steroid) that originates from a four-ringed steroid known as provitamin D, with double bonds at carbons 5 and 7. The 5,7-diene of the sterol has maximal ultraviolet (UV) radiation absorption at wavelengths of 265, 272, 281, and 295 nm and does not absorb radiation above 315 nm. Thus, when provitamin D_3 (7-dehydrocholesterol, the 5,7-diene counterpart of cholesterol) or provitamin D_2 (ergosterol, the 5,7-diene sterol found in fungi and plants) is exposed to solar UV radiation up to 315 nm, the 5,7-diene absorbs it and undergoes a transformation of the double bonds; the result is an opening of the B ring to yield previtamin D. Previtamin D exists in two conformers, the *cis, cis* and *cis, trans* forms. Although the *cis, trans* conformer is thermodynamically stable and therefore favored, only the *cis, cis* form ultimately can be converted to vitamin D. In nonbiologic systems (such as in organic solvents) at 37°C, it takes about 24 hours for 50% of previtamin D to be converted to vitamin D. However, in biologic systems, the previtamin D is sandwiched between fatty acids of the bilipid layer of the cell membrane. In that location, only the *cis, cis* conformer exists, and it is rapidly converted to vitamin D. This is evolutionarily important because cold-blooded vertebrates would have been unable to make vitamin D_3 in their skin efficiently at usual ambient temperatures in light of the slow conversion of previtamin D_3 to vitamin D_3.

During exposure to sunlight, 7-dehydrocholesterol in the epidermis and dermis of humans absorbs UV radiation between 290 and 315 nm, the shortest wavelengths that regularly penetrate the atmosphere and reach the earth's surface. After UV absorption, 7-dehydrocholesterol is converted to previtamin D_3 which undergoes an internal isomerization to form vitamin D_3. Vitamin D_3 is biologically inert and is exported out of the skin into the plasma, where it is bound to a vitamin D-binding transport protein. It can be stored in the fat for later use or—in most higher vertebrates, including amphibians, reptiles, birds, nonhuman primates, and humans—undergoes hydroxylation in the liver to form 25-hydroxyvitamin D_3, 25(OH)D_3 or calcidiol. This metabolite is the major circulating form used to assess vitamin D status in most terrestrial vertebrates.

When vitamin D is ingested, either as vitamin D_2 (ergocalciferol, or ercalciol) or vitamin D_3 (cholecalciferol, or calciol), it is incorporated into chylomicra, and about 80% in humans is absorbed into the lymphatic system and directed to the liver (Holick, 1999).

25(OH)D, although the major circulating form of vitamin D, is biologically inert at normal physiologic concentrations and undergoes 1α-hydroxylation in the kidney to form 1,25-dihydroxyvitamin D, 1,25(OH)$_2$D. 1,25(OH)$_2$D is considered the principal biologically functioning form of vitamin D, responsible for maintaining calcium and phosphorus homeostasis and normal bone metabolism. Specific nuclear receptors for 1,25(OH)$_2$$D_3$, known as vitamin D receptors (VDRs), have been identified in the tissues of rodents, birds, nonhuman primates, and humans. It is suspected that there are also nuclear vitamin D receptors in lower vertebrates, including amphibians and reptiles (Holick, 1996).

1,25(OH)$_2$D interacts with its target-tissue nuclear VDR and in birds, rodents, and humans combines with retinoic acid X receptor to form a heterodimeric complex. This

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heterodimeric complex then sits on vitamin D-responsive elements in the genomic DNA to alter transcriptional activity and modulate calcium metabolism (Holick, 1989; Darwish et al., 1993). In the small intestine, $1,25(OH)_2D$ enhances intestinal calcium transport along its entire length. However, the region of highest efficiency for vitamin D-mediated calcium transport is the duodenum. In bone, $1,25(OH)_2D$ interacts with osteoblasts to induce production of osteocalcin, osteonectin, osteopontin, and alkaline phosphatase (Lian et al., 1987; Darwish et al., 1993). It also stimulates the expression of the osteoclast differentiation factor in osteoblasts that, in turn, signals preosteoclasts to become mature (Holick, 1999). Thus, $1,25(OH)_2D_3$ indirectly increases the number of mature osteoclasts, which increase mobilization of calcium stores from the bone.

MEASURES OF VITAMIN D ACTIVITY

The World Health Organization has defined an international unit (IU) of vitamin D activity as that provided by 0.025 μg (65.0 pmol) of crystalline cholecalciferol (Norman, 1998). The US Pharmacopeia (USP; Rockville, MD) makes available a USP Reference Standard which provides 1 IU of vitamin D activity per 0.025 μg (or 40 $IU \cdot \mu g^{-1}$).

VITAMIN D DEFICIENCY

A deficiency of vitamin D in humans, rodents, birds, and nonhuman primates results in a decrease in intestinal calcium absorption. The decrease leads to a decline in plasma ionized calcium (detected by the calcium sensor in the parathyroid glands), which results in an increase in the production of parathyroid hormone (PTH) (Darwish et al., 1993). PTH has several effects on calcium and phosphorus metabolism. It interacts with osteoblasts to induce osteoclast differentiation factor, which stimulates preosteoclasts to become mature (Holick, 1999); this ultimately results in an increased number of osteoclasts and increased bone mineral mobilization. PTH enhances reabsorption of mobilized calcium in the distal renal convoluted tubules and increases loss of mobilized phosphate into the ultrafiltrate; this loss results in phosphaturia. PTH also stimulates the renal production of $1,25(OH)_2D$, which, in turn, enhances intestinal calcium absorption (Darwish et al., 1993).

Chronic vitamin D deficiency results in mineralization defects in the skeleton. During growth, before skeletal epiphyseal plates have closed, vitamin D deficiency can lead to marked epiphyseal plate hypertrophy, producing bulges at the ends of the long bones and at the costachondral junctions in the rib cage. In adults, after the epiphyseal plates have closed, vitamin D deficiency results in a more subtle defect known as osteomalacia. Although the osteoblasts function normally and lay down collagenous bone matrix, the deficiency of vitamin D results in an inadequate calcium x phosphate product, preventing normal mineralization of the soft osteoid and leading to an increased risk of bone fracture. Vitamin D deficiency and consequent secondary hyperparathyroidism also result in increased mobilization of precious calcium stores from the adult skeleton, thereby inducing and exacerbating osteoporosis. Chronic vitamin D deficiency with low calcium intake ultimately results in hypocalcemia; this can lead to severe spasms of skeletal muscle, with tetany, laryngospasms, and death.

There are numerous reports of rickets or osteomalacia in captive nonhuman primates (Vickers, 1968; Miller, 1973; Fiennes, 1974; Ullrey, 1986; Allen et al., 1995; Morrisey et al., 1995; Meehan et al., 1996). The syndrome has been called simian bone disease, woolly monkey disease, and cage paralysis. Signs of deficiency have been reported more frequently in young than in mature primates and in platyrrhines (New World monkeys) than in catarrhines (Old World monkeys and apes). Some have proposed that the difference is a result of higher vitamin D requirements in New World monkeys or a limited ability to use vitamin D_2 (Hunt et al., 1966). The suggestion by Freedman et al. (1976) that it is a failure to convert vitamin D_2 to vitamin D_3 is not consistent with known metabolic pathways (Norman and Collins, 1994; Holick, 1999)

Signs of vitamin D deficiency were seen in a nursing red howler (*Alouatta seniculus*) infant (Ullrey, 1986) and in three juvenile colobus monkeys (*Colobus guereza kikuyuensis*) (Morrisey et al., 1995) housed with their mothers in zoo exhibits without sunlight exposure or an artificial UVB source. The infants ate little solid food and depended heavily on mother's milk for their nutrient intake. Gradually, their activity declined, and they had difficulty in walking, climbing, and grasping their mothers. Physical examination revealed bone pain, bowed long bones, and limb joints that were lax and swollen. Changes visualized with radiography included cupping of the metaphyses, widening of the epiphyseal plates, and thinning of the cortices. Some bones exhibited fibrous osteodystrophy, and fractures were seen in the distal femoral epiphyses. Serum calcium, inorganic phosphorus, and alkaline phosphatase in a severely affected 10-month-old female colobus were 8.1 $mg \cdot dl^{-1}$, 2.7 $mg \cdot dl^{-1}$, and 1,293 $IU \cdot L^{-1}$, respectively. The serum 25(OH)D concentration was less than 10 $ng \cdot ml^{-1}$. A 2-month-old colobus monkey showed mild widening of epiphyseal plates radiographically and had increased serum alkaline phosphatase activity (2,268 $IU \cdot L^{-1}$) and low 25(OH)D concentration (10 $ng \cdot ml^{-1}$). After intramuscular injection of ergocalciferol and solar exposure, the radiographic appearance of the skeleton returned to normal, and serum 25(OH)D rose to 19 $ng \cdot ml^{-1}$. Although milk vitamin D concentrations were not measured, the authors proposed that nonhuman primate milk was low in vitamin

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D, as is human and cow's milk, and nursing infants that do not eat substantial amounts of other vitamin D-containing foods are at risk if not exposed to UVB. It is noteworthy that rickets has not been seen after installation of UVB-transparent skylights in the red howler and the colobus zoo exhibits.

DISCRIMINATION BETWEEN VITAMIN D_2 AND VITAMIN D_3

The major structural difference between vitamin D_2 and vitamin D_3 is that vitamin D_2, which originates from the fungal and plant sterol ergosterol, has a methyl group on carbon 24 and a double bond between carbons 22 and 23. In the 1930s, it was shown that chickens fed vitamin D_2 developed rickets (Holick, 1996), and ultimately vitamin D_3 was found about 10 times more effective than vitamin D_2 in preventing rickets in poultry (Hurwitz et al., 1967). For years, the biologic activities of the two vitamins were assumed equal in domestic mammals. However, studies showed that vitamin D_2 is also less active than vitamin D_3 in the pig, cow, and horse, but the difference is not as great as in the chicken. The vitamin D-binding and vitamin D-metabolite-binding transport proteins appear to vary among species (Edelstein, 1974; Hay and Watson, 1976a, 1976b, 1977), and Edelstein et al. (1973) speculated that the apparent dissimilarity between New World and Old World monkeys in the biologic activity of vitamins D_2 and D_3 (Hunt et al., 1967; Lehner et al., 1968) might be due to these differences. The mechanism of discrimination is not entirely understood, but Horst et al. (1988) published data suggesting that there is less absorption of vitamin D_2 from the gut and enhanced clearance of $25(OH)D_2$ and $1,25(OH)_2D_2$ from the blood than is the case for vitamin D_3 and its metabolites. Furthermore, there is some evidence that tissue vitamin D receptors do not recognize $1,25(OH)_2D_2$ as well as $1,25(OH)_2D_3$ (Holick, 1996).

There are about 100 species of New World monkeys (platyrrhines) and over 100 species of Old World monkeys and apes. Relatively few species in either group have been studied, and published research findings are inadequate to make generalizations about differences between them. Nevertheless, the evidence that vitamin D_2 is less active than vitamin D_3 in the New World species that have been studied is convincing. Well-controlled studies comparing the activities of the two vitamin forms in Old World species appear not to have been conducted.

Lehner et al. (1968) fed growing squirrel monkeys (*Saimiri sciureus*) no vitamin D or vitamin D_2 at 1,250, 2,500, 5,000, or 10,000 $IU \cdot kg^{-1}$ of diet. They grew poorly and exhibited rickets, regardless of treatment. In contrast, when squirrel monkeys were fed vitamin D_3 at 1,250, 2,500, 5,000 or 10,000 $IU \cdot kg^{-1}$ diet, all grew equally well, and no rickets were seen. Hunt et al. (1967) fed adult white-fronted capuchin monkeys (*Cebus albifrons*) purified diets containing 0.8% calcium, 0.46% phosphorus, vitamin A and D_2 at 12,500 and 2,000 $IU \cdot kg^{-1}$, respectively, for 2 years. The monkeys developed fibrous osteodystrophy, were thin and inactive, and had distorted limbs, kyphosis, and multiple fractures with no evidence of callus formation. When dietary vitamin D_2 was replaced by vitamin D_3 at 2,000 $IU \cdot kg^{-1}$ for 5 months, the appearance of the capuchin monkeys improved, and they became more active. Previous fractures became resistant to movement, and callus formation was evident radiographically. Hunt et al. (1967) also fed adult cotton-top tamarins (*Saguinus oedipus*), white-lipped tamarins (*Saguinus nigricollis*), and black-chested mustached tamarins (*Saguinus mystax*) a commercial primate diet containg vitamin D_2 at 2,200 $IU \cdot kg^{-1}$ for 8-12 months and observed deficiency signs that were similar to but less severe than those seen in the capuchins. Healing was initiated by feeding each animal 500 IU of vitamin D_3 per week. The researchers reported anecdotally that they had seen fibrous osteodystrophy in squirrel monkeys fed vitamin D_2 but not in squirrel monkeys or woolly monkeys (*Lagothrix* spp.) fed vitamin D_3 or exposed to sunlight. Although no information on dietary nutrient concentrations or husbandry was provided, they also stated that thousands of rhesus and other *Macaca* species (Old World monkeys) had been fed diets containing only vitamin D_2 without evidence of metabolic bone disease.

Vickers (1968) observed osteomalacia and rickets in capuchins fed a commercial primate diet containing vitamin D_2 and noted that injections of vitamin D (form unspecified) or vitamin D_3 at 2,200 $IU \cdot kg^{-1}$ diet would reverse the disease. Lehner et al. (1968) observed bone lesions in squirrel monkeys that could not be prevented by vitamin D_2 at 10,000 $IU \cdot kg^{-1}$ diet, but the lowest concentration of vitamin D_3 tested, 1,250 $IU \cdot kg^{-1}$ of diet, was effective.

METABOLIC RESISTANCE TO VITAMIN D_3 IN CALLITRICHIDS

In 1983, Shinki et al. reported blood concentrations of $25(OH)D_3$, $1,25(OH)_2D_3$, and $24,25(OH)_2D_3$ in seven adult (five males and two females) marmosets (*Callithrix jacchus*) that weighed about 300 g. They were fed a commercial diet ostensibly containing vitamin D_3 at 9,100 $IU \cdot kg^{-1}$ (not analyzed) and fruit. In addition, they were given 500 IU of vitamin D_3 orally twice a week. Housing was not described. Daily mean feed intake ($\pm$ SEM) was reported to be 20 $\pm$ 5 g, but there was no indication whether this was the intake of DM, whether fruit was included, or whether the mean was derived from daily food intake for the group or for individual animals. Serum calcium concentrations in these marmosets ranged from 7.9-9.9 $mg \cdot dl^{-1}$, and serum phosphorus ranged from 2.1-4.7 $mg \cdot dl^{-1}$. Circulating concentrations of $25(OH)D_3$ were 12.4-204.1 $ng \cdot ml^{-1}$, with a mean of 94.5 $ng \cdot ml^{-1}$, about 5 times that in six

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volunteer men from whom blood samples were taken. The mean $1,25(OH)_2D_3$ concentration of 418.8 pg·ml^{-1}, with a range of 196.1-642.4 pg·ml^{-1}, was about 10 times that in the volunteers. Two marmosets that had serum calcium concentrations of 8.8 and 9.9 mg·dl^{-1} with serum phosphorus concentrations of 2.1 mg·dl^{-1} and serum $25(OH)D_3$ concentrations of 16.5 and 12.4 ng·ml^{-1} had somewhat increased alkaline phosphatase values, were osteomalacic, and had bone fractures. Serum $24,25(OH)_2D_3$ concentrations ranged from less than 0.2 ng·ml^{-1} (in the marmosets with fractures) to 8.23 ng·ml^{-1}, but the mean, although numerically higher than the mean in the volunteers, did not differ significantly from it. It should be noted that a later report from the same research group (Yamaguchi et al., 1986) stated that marmosets were housed in pairs in cages and that the very low serum levels of $25(OH)D_3$ in osteomalacic marmosets were probably due to insufficient intake of food (and of vitamin D) because of interference in food selection by cagemates.

In the same study, six young adult female rhesus monkeys (*Macaca mulatta*) weighing 4-6 kg were fed a commercial diet containing vitamin D_3 at 2,400 IU·kg^{-1} of diet (not analyzed). The mean serum concentration of $25(OH)D_3$ (estimated by measuring column heights in Shinki et al. [1983], Figure 1) was 50 ng·ml^{-1} and of $1,25(OH)_2D_3$ was 96 pg·ml^{-1}. Those were not significantly different from the concentrations in the volunteers, who had a mean $25(OH)D_3$ concentration (estimated as above) of 17 ng·ml^{-1} and a mean $1,25(OH)_2D_3$ concentration of 44 pg·ml^{-1}. The mean $24,25(OH)_2D_3$ concentration in the serum of rhesus monkeys was essentially identical with that in the marmosets.

The finding of extremely high serum concentrations of $1,25(OH)_2D_3$ without hypercalcemia in common marmosets was duplicated in emperor tamarins (*Saguinus imperator*) by Adams et al. (1984).

Another study of the common marmoset (*Callithrix jacchus*) as an animal model for vitamin D-dependent rickets, type II, was published by Suda et al. (1986). (Apparently this study was republished by Yamaguchi et al. [1986] with slightly different marmoset data.) Seventeen adult marmosets weighing about 300 g were fed a diet containing vitamin D_3 at 1,480 IU·kg^{-1} and were given an additional 1,000 IU of vitamin D_3 orally twice a week. On the basis of a mean daily intake of 20 g of diet, vitamin D_3 intakes were estimated to be 110 IU·BW_{100g}^{-1}·day^{-1}. Five rhesus monkeys (*Macaca mulatta*) weighing about 5 kg were fed a diet containing vitamin D_3 at 2,400 IU·kg^{-1}. On the basis of a daily diet intake of about 100 g, vitamin D_3 intake was estimated to be 5 IU·BW_{100g}^{-1}·day^{-1}. Two of the 17 marmosets were found to have bone fractures and radiographic evidence consistent with osteomalacic changes in their bones despite the high vitamin D intake, whereas none of the five rhesus monkeys showed any signs of osteomalacia. The mean ($\pm$ SEM) serum $25(OH)D_3$ concentration in the rhesus monkeys was 50 $\pm$ 4 ng·ml^{-1}; in the 15 marmosets showing no osteomalacia, it was 478 $\pm$ 108 ng·ml^{-1}. The serum level of $1,25(OH)_2D_3$ in the rhesus monkeys was 95 $\pm$ 17 pg·ml^{-1}; in the marmosets, it was 491 $\pm$ 93 pg·ml^{-1}. The two osteomalacic marmosets had serum calcium concentrations of 8.8 and 9.9 mg·dl^{-1} and serum inorganic phosphorus concentrations of 2.2 mg·dl^{-1} compared with means of 8.4 $\pm$ 0.2 and 4.5 $\pm$ 0.2 mg·dl^{-1}, respectively, in the normal marmosets. Serum $25(OH)D_3$ and $1,25(OH)_2D_3$ concentrations in the osteomalacic marmosets were 17 and 12 ng·ml^{-1} and 642 and 524 pg·ml^{-1}, respectively. Two rhesus monkeys were given vitamin D_3 at 900 IU·BW_{100g}^{-1}·day^{-1} for 1 month; it resulted in serum $25(OH)D_3$ concentrations of 1,352 and 1,651 ng·ml^{-1} and serum $1,25(OH)_2D_3$ concentrations of 73 and 74 pg·ml^{-1}. *In vitro* studies with kidney homogenates and intestinal cytosols led these researchers to conclude that 1α-hydroxylase activity is higher in the kidney of the marmoset and 24-hydroxylase activity is higher in the kidney of the rhesus monkey. In addition, there appeared to be fewer $1,25(OH)_2D_3$ receptors and lower activity of the receptor-binding complex in the intestine of the marmoset than in that of the rhesus monkey (see also Takahashi et al., 1985). Whether the differing dietary history of the tissues used in the *in vitro* tests might have influenced the results was not explored.

To put the above observations on vitamin D metabolite concentrations in the serum of captive primates in perspective, it should be noted that 18 free-ranging, wild cotton-top tamarins (*Saguinus oedipus*) in Colombia had serum 25(OH)D concentrations of 25.5-120 ng·ml^{-1} with a mean of 76.4 ng·ml^{-1} (Power et al., 1997). Serum 25(OH)D concentrations in six normal captive cotton-top tamarins consuming diets containing vitamin D_3 at 2,500 IU·kg^{-1} of dry matter were 48-236 ng·ml^{-1} with a mean of 143.5 ng·ml^{-1}. Serum 25(OH)D concentrations in 24 captive cotton-top tamarins consuming diets containing vitamin D_3 at 26,000 IU·kg^{-1} of dry matter were 11-560 ng·ml^{-1}; two were 11 and 12 ng·ml^{-1}, five ranged from 46 to 60 ng·ml^{-1}, three were between 126 and 176 ng·ml^{-1}, and the remaining 14 were over 224 ng·ml^{-1}. None of the tamarins exhibited bone disease (Ullrey et al., 1999). Analyses of $1,25(OH)_2D$ and $24,25(OH)_2D$ were not performed in the studies of either Power et al. (1997) or Ullrey et al. (1999).

Liberman et al. (1985), using soluble extracts of Epstein-Barr virus-transformed B lymphocytes, found that extracts from a single common marmoset (*Callithrix jacchus*) had a lower binding affinity for $1,25(OH)_2D_3$ (K_d, 2.2 nM) than did extracts from three normal humans (K_d, 0.27 nM). $1,25(OH)_2D_3$ binding capacity for extracts from the marmoset lymphocytes also were lower (6.9 fmol·mg^{-1} of protein) than those from human lymphocytes (15.4 fmol·mg^{-1} of protein). Soluble extracts from herpesvirus papio-trans-

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formed B lymphocytes from a stump-tailed macaque (*Macaca arctoides*) had a $1,25(OH)_2D_3$ binding affinity of 0.40 nM and a $1,25(OH)_2D_3$ binding capacity of 14 fmol·mg^{-1} of protein. The researchers speculated that a defective receptor for $1,25(OH)_2D_3$ could account for target-tissue resistance to this hormone in the common marmoset, but they acknowledged that the type of defect (binding affinity versus capacity) appeared to vary with the cell system analyzed. For example, Chandler et al. (1984) found that LLC-MK2 cells isolated from renal tissue of rhesus monkeys (*M. mulatta*) had a $1,25(OH)_2D_3$ binding affinity lower by a factor of 30 than LLC-MK2 renal cells from humans.

Gacad and Adams (1992) studied the specificity of steroid binding in B95-8 B-lymphoblastoid cell lines established by Epstein-Barr virus transformation of peripheral blood mononuclear cells from the common marmoset (*Callithrix jacchus*). The binding of $1,25(OH)_2D_3$ and $25(OH)D_3$ in extracts of the lymphoblastoid cells was studied in the presence and absence of potentially competitive ligands, including $1,25(OH)_2D_3$, $25(OH)D_3$, 17β-estradiol, testosterone, and progesterone. Compared with extracts containing the authentic nuclear $1,25(OH)_2D_3$ receptor, extracts of B95-8 cells bound 180% more $1,25(OH)_2D_3$ and 12 times more $25(OH)D_3$ by weight. The rank order of steroid binding by this intracellular competitive binding component was $25(OH)D_3 > 1,25(OH)_2D_3 \geq$ estradiol = progesterone = testosterone. The investigators suggested that the higher concentrations of $25(OH)D_3$ in the serum of some New World primates result from the relative lack of $25(OH)D_3$-24-hydroxylase activity and are necessary to ensure that there is adequate substrate for maintenance of the increased $1,25(OH)_2D_3$ concentrations that these primates require. Furthermore, they speculated that the elevated $1,25(OH)_2D_3$ concentrations represented an evolutionary adaptation to ancestral diets that included hypercalcemic plants similar to *Solanum glaucophyllum*, containing high concentrations of $1,25(OH)_2D_3$ glycosides. One means of avoiding life-threatening hypercalcemia would be for the authentic nuclear $1,25(OH)_2D_3$ receptor to coexpress or overexpress an intracellular steroid-binding protein that would intercept such glycosides. Alternatively, the intracellular binding protein might have evolved to protect against non-vitamin D steroid-like compounds. Because the nocturnal *Aotus trivirgatus* also expresses this protein, but at a much lower level, these workers suggested that the vitamin D so readily supplied via cutaneous photosynthesis during daytime in an equatorial environment also might have contributed to the development of vitamin D-resistant primate phenotypes.

ANIMALS NOT EXPOSED TO NATURAL SUNLIGHT OR UNABLE TO MAKE VITAMIN D IN THEIR SKIN

Diverse terrestrial vertebrate species are never exposed to sunlight, these including some species of bats and some rodents. The rodent species *Rattus rattus* has 7-dehydrocholesterol in the skin, providing the substrate required for cutaneous photosynthesis of vitamin D; considering this rat's nocturnal behavior, it is uncertain whether vitamin D requirements are met mostly by photosynthesis or by the diet. Intense skin pigmentation and minimal exposure to sunlight might put some species at substantial risk for vitamin D deficiency. Some nonhuman primate species are nocturnal, and solar UVB exposure is slight. It has not been established how such species obtain their vitamin D supply or, in some cases, whether they require vitamin D.

Naked mole rats spend their entire lives underground and are never exposed to sunlight. Furthermore, vitamin D has not been found in the roots and other foods that they eat (Skinner et al., 1991). There is evidence that naked mole rats have extremely low circulating concentrations of 25(OH)D and $1,25(OH)_2D$ (Buffenstein et al., 1993). Little is known about parathyroid function in these animals, but it appears that their intestine is able to transport calcium adequately in the absence of vitamin D (Pitcher et al., 1992).

A remarkable observation is that cats have extremely low concentrations of 7-dehydrocholesterol in their skin for which Morris (1999) provide convincing evidence of an ineffectiveness in photosynthesizing vitamin D. As a result, vitamin D must be present in their diet to maintain circulating concentrations of 25(OH)D and $1,25(OH)_2D$ in the physiologic ranges needed to satisfy requirements for normal calcium homeostasis and bone metabolism. However, cats are carnivorous, in contrast with most primate species; because tissues of carnivore prey usually contain sufficient vitamin D, there presumably would be little need for cutaneous vitamin D photosynthesis. Whether any nonhuman primate species resembles cats in that regard has not been established.

VITAMIN D REQUIREMENTS

Presumably, if nonhuman primates have little or no exposure to UVB radiation, either from the sun or from artificial sources, they require vitamin D in their diet. Few studies have been conducted to define requirements quantitatively. Lehner et al. (1968) made it clear that the form of vitamin D used in setting the requirement is important when they found that vitamin D_3 at 1,250 IU·kg^{-1} of diet (the lowest concentration studied) was adequate for growing squirrel monkeys (*Saimiri sciureus*) but that vitamin D_2 at 10,000 IU·kg^{-1} was not. Because the difference in biologic activity between vitamins D_2 and D_3 has been observed in so many species, estimates of vitamin D requirements will be given here only in terms of vitamin D_3.

In a study of vitamin E deficiency, Ausman and Hayes (1974) fed a purified diet for 2 years that furnished vitamin D_3 at 1,000 IU·kg^{-1} to juvenile crab-eating macaques

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(*Macaca fascicularis*) and capuchins (*Cebus albifrons*, *apella*), Old World and New World monkeys, respectively. Growth was normal, and no bone lesions were observed in any of the monkeys.

Hunt et al. (1967) induced fibrous osteodystrophy in adult white-fronted capuchins (*Cebus albifrons*) by feeding a purified diet containing vitamin D_2 at 2,000 IU·kg^{-1} for 2 years. When vitamin D_3 at 2,000 IU·kg^{-1} (lowest concentration studied) replaced the vitamin D_2 for 5 months, callus formation began and the fractures were stabilized. The previous National Research Council (1978) recommendation for nonhuman primates was vitamin D_3 at 2,000 IU·kg^{-1} of diet (presumably 90% DM), and Flurer and Zucker (1987) reported that this concentration supported serum 25(OH)D concentrations of 30-300 nmol·L^{-1} (12-120 ng·ml^{-1}) in saddle-back tamarins (*Saguinus fuscicollis*) and was sufficient to meet their needs.

To establish baseline serum 25(OH)D concentrations for assessing vitamin D status of captive callitrichids, Power et al. (1997) collected blood samples from 18 wild, free-ranging cotton-top tamarins (*Saguinus oedipus*) in Colombia. They found serum 25(OH)D concentrations of 25.5-120 ng·ml^{-1} with a mean of 76.4 ng·ml^{-1}. Assuming that cotton-top tamarins that have serum 25(OH)D concentrations in or near that range are adequately nourished with respect to vitamin D, the minimal dietary concentration of vitamin D_3 supporting such concentrations in captive cotton-top tamarins with no UVB exposure could be used as an estimate of the minimal dietary requirement. Ullrey et al. (1999) found that a diet containing vitamin D_3 at 2,500 IU·kg^{-1} of DM, fed to six captive cotton-top tamarins with no UVB exposure for 2 years, supported growth, reproduction, and serum 25(OH)D concentrations of 48-236 ng·ml^{-1} with a mean of 143.5 ng·ml^{-1}, with no evidence of pathologic changes. Lower dietary concentrations of vitamin D_3 were not tested.

The growth of common marmosets (*Callithrix jacchus*) fed purified diets was studied by Tardiff et al. (1998). Power et al. (1999) then tested the ability of adult marmosets on these diets (males and nulliparous and pregnant or lactating multiparous females) to distinguish between water and calcium lactate solutions. According to Power (2000, personal communication), those and related studies involved feeding the purified diets to marmosets for 5 years. The initial dietary vitamin D_3 concentration was 3,000 IU·kg^{-1}, and it was used for about 2½ years. Because of concern about suspected vitamin D deficiency in some animals, the dietary vitamin D_3 was increased to 9,000 IU·kg^{-1}, although there was no evidence of pathologic changes in most of the marmosets at the lower concentration. No other dietary vitamin D_3 concentrations were tested, and no explanation for the variation in response has been provided.

Barnard and Knapka (1993) discussed callitrichid nutrition and summarized much of the research related to callitrichid nutrient requirements and dietary husbandry. They noted that when commercial primate diets were "supplemented" with fruit, preferences for fruit often reduced the intake of more nutritious food and resulted in nutrient imbalances and deficiencies. Ultimately, a highly palatable pelleted diet was formulated that, when fed alone, maintained normal weight in adult *Saguinus mystax* (Barnard et al., 1988). It was designated the NIH 48 Open Formula Pelleted Diet, and Barnard and Knapka (1993) presented details of its composition. The vitamin premix supplied vitamin D_3 at 2,145 IU·kg^{-1} of diet. The diet contained 10.3% moisture, so the premix added vitamin D_3 at about 2,400 IU·kg^{-1} of dietary DM. Information on vitamin D supplied by the other ingredients was not provided, but on the basis of published analyses, amounts of vitamin D supplied by ingredients other than the vitamin premix would be negligible.

Because few studies were designed to define vitamin D requirements and there are disparate findings, it is not possible to identify a minimal dietary requirement with certainty. For the species that have been studied, it appears that in the absence of solar or artificial UVB exposure, dietary vitamin D_3 concentrations of 1,000-3,000 IU·kg^{-1} DM meet the needs of most. However, considering our present degree of uncertainty about minimal requirements and safe upper limits of vitamin D_3 in the diet, it might be prudent to provide some exposure to natural or artificial UVB radiation. That requires either unimpeded exposure to solar radiation, careful selection of UVB-transparent plastics for windows or skylights, or use of artificial light sources that emit substantial UVB energy at appropriate wavelengths. Ullrey and Bernard (1999) have published information on UVB-transmitting plastics and UVB-emitting artificial lights.

HYPERVITAMINOSIS D

Daily oral doses of 50,000-100,000 IU of Vitamin D_3 produced hypervitaminosis D in squirrel monkeys and white-fronted capuchins, whereas similar amounts of vitamin D_2 did not (Hunt et al., 1969). The syndrome in squirrel monkeys included hypercalcemia, hyperphosphatemia, uremia, and death in 20-35 days, with no substantial metastatic calcification and minimal nephrocalcinosis. The capuchins died in 52-89 days and exhibited widespread metastatic calcification, including mineralization in the kidneys, aorta, lungs, myocardium, stomach, and various tissue arteries and arterioles. Bone lesions were not seen in either species.

Daily oral doses of 50,000-200,000 IU of vitamin D_2 produced hypercalcemia in rhesus monkeys, but no soft-tissue calcification or deaths (Hunt et al., 1972). However, comparable oral doses of vitamin D_3 produced marked

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hypercalcemia, death in 16-160 days, and evidence of nephrocalcinosis at necropsy.

Regular consumption of diets containing vitamin D_3 at 6,000-8,200 IU·kg^{-1} by several New World and Old World primate species has resulted in increased serum 25(OH)D concentrations and speculation about whether such dietary concentrations might be excessive. When rhesus monkeys were fed a commercial primate diet containing vitamin D_3 at 6,600 IU·kg^{-1}, serum concentrations of calcium, inorganic phosphorus, and parathormone were normal, but the mean (± SD) serum 25(OH)D concentration was 188 ± 94 ng·ml^{-1} and was considered high (Arnaud et al., 1985).

Free-ranging rhesus monkeys maintained on Cayo Santiago by the Caribbean Primate Research Center (CPRC) in Puerto Rico were fed a commercial high-protein monkey diet containing vitamin D_3 at 8,200 IU·kg^{-1} to complement wild foods (Vieth et al., 1987). However, monkey density was very high, and the commercial diet made up most of the food consumed (Ullrey, personal observation). Serum from 48 monkeys (six samples from each sex in each of four age classes) that were transferred from Cayo Santiago to the CPRC Sabana Seca Field Station was analyzed for 25(OH)D and 1,25$(OH)_2$D. Group means for 25(OH)D were 143-230 ng·ml^{-1} and were considered high. Serum concentrations of 1,25$(OH)_2$D were variable (group means, 59-247 pg·ml^{-1}) but were also considered high, and the authors suggested that, if the higher concentrations of this metabolite were sustained in individual monkeys, subtle changes in calcium and phosphorus metabolism might partially explain the calcium pyrophosphate dihydrate crystal deposition arthropathy that was a problem in the colony.

Marx et al. (1989) studied the differences between four species of nonhuman primates in response to vitamin D_2 and vitamin D_3, including a comparison of serum 25(OH)D concentrations. Consumption of a commercial primate diet containing vitamin D_3 at 6,000-6,600 IU·kg^{-1} resulted in mean 25(OH)D values of 96, 144, 88, and 148 ng·ml^{-1} in the serum of crab-eating macaques, rhesus macaques, night monkeys, and squirrel monkeys, respectively. After transfer to a diet containing vitamin D_3 at 1,500 IU·kg^{-1} for 5 months, serum 25(OH)D concentrations were 44, 68, 56, and 60 ng·ml^{-1}. There was no hypercalcemia, parathormone suppression, or azotemia in primates fed the commercial diet, which would be suggestive of hypervitaminosis D; but the lack of biochemical and histologic evidence of vitamin D deficiency in monkeys fed diets containing vitamin D_3 at 1,500 IU·kg^{-1} suggested to the researchers that the commercial diet with vitamin D_3 at 6,000-6,600 IU·kg^{-1} was providing more of the vitamin than was needed.

Gray et al. (1982) offered brown lemurs (*Lemur fulvus*) a commercial primate diet containing vitamin D_3 at 6,600 IU·kg^{-1} plus fresh fruit and a "supplement" containing oats, soy flour, eggs, wheat germ, evaporated milk, sugar, and bananas. Calcium concentrations in the serum from 20 lemurs were 9.6-12.6 mg·dl^{-1}. Serum 25(OH)D_3 concentrations were 3.4-94.8 ng·ml^{-1}, and serum 1,25$(OH)_2D_3$ concentrations were less than 4 to 220 pg·ml^{-1}. Because the lemurs could make a variety of food choices, it was not possible to relate composition of the diet consumed directly to animals whose biochemical measures appeared to be outside a normal range. Nevertheless, the researchers suggested that some lemurs were hypercalcemic and might have had increased 25(OH)D_3 or 1,25$(OH)_2D_3$ because of episodic intoxication by vitamin D from the commercial diet. Some animals had low 25(OH)D_3 or 1,25$(OH)_2D_3$ concentrations, so it is also possible that some lemurs consumed a diet that was low in vitamin D_3, although no clinical signs of deficiency were reported.

In some circumstances, hypervitaminosis D might be less of a threat to nonhuman primates than to other species that are housed with them. Pacas (*Cuniculus paca*) and agoutis (*Dasyprocta aguti*) housed in mixed-species exhibits at three zoos died with extensive soft-tissue mineralization, including mineralization of the kidneys, leading to renal failure (Kenny et al., 1993). New World primates shared the exhibits, and zoo personnel reported that dropped primate diets, containing vitamin D_3 at 7,000 to 22,000 IU·kg^{-1}, were consumed by the affected animals. Analyses of blood from four moribund pacas revealed reduced packed red-cell volume and increases in serum calcium, inorganic phosphorus, urea nitrogen, and creatinine. Histologic examination of affected paca tissues confirmed extensive mineralization of the kidneys, heart, major blood vessels, stomach, intestinal tract, liver, spleen, and skeletal muscle. Serum vitamin D metabolites were not analyzed, but a provisional diagnosis of vitamin D toxicity was made.

Vitamin E

CHEMISTRY AND MEASURES OF ACTIVITY

Vitamin E is a collective term for compounds that were thought to have the biologic activity of α-tocopherol (Traber, 1999). Eight are found in nature. Four are tocols (tocopherols) with a saturated side chain and variable placement and numbers of methyl groups on the chromanol ring; they are designated α- (methyls on carbons 5, 7, and 8), β- (methyls on carbons 5 and 8), γ- (methyls on carbons 7 and 8), and δ- (methyl on carbon 8) tocopherols. Four are tocotrienols with an unsaturated side chain and comparable placement and numbers of methyl groups on the chromanol ring; they are designated α-, β-, γ-, and δ-tocotrienols. Those eight compounds are synthesized by higher plants and are found principally as free alcohols in lipid-containing fractions of green leaves and seeds. They differ in vitamin E potency based on the rat fetal-resorption assay (Bunyan et al., 1961); because α-tocopherol has been assigned the

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highest relative potency, it is common to assay only for this isomer rather than to perform the more difficult separation and measurement of all eight natural compounds.

The principal commercially available forms of vitamin E are acetate and hydrogen succinate esters of *RRR*-α-tocopherol (formerly *d*-α-tocopherol) and of all-*rac*-α-tocopherol (formerly *d,l*-α-tocopherol). *RRR*-α-tocopherol is usually concentrated from natural sources, but it can be synthesized. All-*rac*-α-tocopherol is a condensation product of trimethylhydroquinone and racemic isophytol; the process results in a totally synthetic mixture of four 2*R*-stereoisomers (*RRR*-, *RSR*-, *RRS*-, and *RSS*-α-tocopherol) and four 2*S*-stereoisomers (*SRR*-, *SSR*-, *SRS*-, and *SSS*-α-tocopherol). It is sometimes confused with 2-*ambo*-α-tocopherol (also labeled *d,l*-α-tocopherol), a partially synthetic condensation product of trimethylhydroquinone and natural phytol that, as the acetate, served as the vitamin E standard for the international unit (IU) until its distribution was discontinued in 1956 (WHO, 1963). The confusion was of concern to Ames (1979) who claimed that the two synthetic forms differed in their relative potency, on the basis of retrospective examination of fetal-resorption bioassays over the previous 21 years. However, Weiser and Vecchi (1981) concluded from more recent research that the previously established biopotency ratios of 1:1 for all-*rac*-α-tocopheryl acetate to 2-*ambo*-α-tocopheryl acetate and 1.36:1 for *RRR*-α-tocopheryl acetate to 2-*ambo*-α-tocopheryl acetate were still valid. The US Pharmacopeia and National Formulary (1985) accepted those relationships, although relative plasma concentrations in humans after oral administration of *RRR*-α-tocopheryl acetate and all-*rac*-α-tocopheryl acetate suggested that *RRR*-α-tocopheryl acetate can have 2-3 times the bioavailability of the synthetic form per unit of weight (Acuff et al., 1994; Kiyose et al., 1995, 1997). Nevertheless, use of the traditionally defined IU persists: 1 IU = 1 USP unit = 1 mg of all-*rac*-α-tocopheryl acetate = 0.74 mg *RRR*-α-tocopheryl acetate = 0.67 mg *RRR*-α-tocopherol.

Alternatively, α-tocopherol equivalents (α-TEs) have been used to characterize vitamin E activity in human and animal diets; 1 α-TE was defined as the activity of 1 mg of *RRR*-α-tocopherol. Other natural compounds that once were thought to provide substantial vitamin E activity are β-tocopherol, γ-tocopherol, α-tocotrienol, and β-tocotrienol. When present and assayed, their contributions to dietary α-TEs were estimated by multiplying their concentrations in milligrams by 0.5, 0.1, 0.3, and 0.05, respectively (National Research Council, 1989). However, these other naturally occurring forms of vitamin E appear not to contribute toward meeting the vitamin E requirements of humans because, although absorbed, they are not converted to α-tocopherol and are recognized poorly by the α-tocopherol transfer protein in the liver. Because the 2*S*-stereoisomers of synthetic α-tocopherol are not maintained in human plasma or tissues, the relative vitamin E activity of 1 mg of all-*rac*-α-tocopherol has been set at 50% that of 1 mg of *RRR*-α-tocopherol (Institute of Medicine, 2000). Whether these quantitative relationships apply to nonhuman primates has not been established.

ABSORPTION, METABOLISM, AND EXCRETION

Absorption of tocopherols from the small intestine depends upon bile and pancreatic secretions, as involved in the typical processes of fat digestion (Traber, 1999). Pancreatic esterases are required for release of free fatty acids from dietary triglycerides and for hydrolytic cleavage of tocopheryl esters. Bile acids, monoglycerides, and free fatty acids form mixed micelles in the gut, in which the tocopherols dissolve. Chylomicrons—incorporating triglycerides, free and esterified cholesterol, phospholipids, and apolipoproteins—are synthesized in intestinal mucosal cells. Tocopherols enter the mucosal cells by an unknown mechanism and are incorporated into the chylomicrons, which are secreted into the mesenteric lymphatics and later enter the blood.

Although the efficiency of vitamin E absorption is relatively low in humans (about 15-45%) (Blomstrand and Forsgren, 1968), there appears to be no discrimination against different forms of vitamin E in the gut. During later chylomicron catabolism in the circulation, some of the absorbed forms of vitamin E are transferred to plasma lipoproteins, but much appears to remain with the chylomicron remnants taken up by the liver parenchyma. During catabolism of chylomicron remnants in the liver, *RRR*-α-tocopherol can be preferentially transferred (compared with other isomers) by α-tocopherol transfer protein in the hepatocytic cytosol to very-low-density lipoproteins (VLDLs) (Hosomi et al., 1997). VLDLs are later secreted by the liver into the plasma. In the circulation, VLDL-bound tocopherols are transferred nonspecifically to various plasma lipoproteins. Traber et al. (1990) demonstrated the preferential association of *RRR*-α-tocopherol with VLDLs in the livers of cynomolgus monkeys by feeding various deuterated tocopherols and finding that *RRR*-α-tocopherol was about 80% of the VLDL-bound tocopherol in hepatic perfusate. After secretion of VLDLs into plasma, lipolysis by lipoprotein lipase and hepatic tryglyceride lipase results in transfer and preferential enrichment of plasma lipoproteins with *RRR*-α-tocopherol. That is consistent with observations that *RRR*-α-tocopherol is the primary form of vitamin E circulating in plasma in the species that have been studied.

Tocopherols circulate in the body as components of several plasma lipoproteins, and no specific vitamin E-transport protein has been identified in the plasma. In the plasma of African green monkeys (Carr et al., 1993), the molar ratio of α-tocopherol to high-density lipoprotein

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(HDL) was greater than that of α-tocopherol to low-density lipoprotein (LDL), or to VLDL and LDL combined, and α-tocopherol was associated with the protein component of the HDL particle. However, vitamin E is readily transferred to other lipoproteins in a process catalyzed by phospholipid transfer protein in human plasma. HDLs can play an important role in delivering vitamin E to circulating blood cells. LDLs appear to be important in supplying vitamin E to peripheral tissues, where it is rapidly exchanged with cell membranes.

Vitamin E turnover rates vary among tissues. Erythrocytes, liver, and spleen are in rapid equilibrium with the plasma α-tocopherol pool. The heart, muscle, and spinal cord have slower turnover rates and the brain is slowest of all.

More than 90% of the human body α-tocopherol pool has been found in adipose tissue, and over 90% of that is in fat droplets, not in cell membranes (Traber and Kayden, 1987). The turnover rate of this pool is quite low, and the relative bioavailability of α-tocopherol in human adipose tissue compared with that in other tissues is controversial (Traber, 1999).

The primary oxidation product of α-tocopherol is α-tocopheryl quinone, which, after reduction to the hydroquinone, can be conjugated to yield a glucuronate. The glucuronate can be excreted in the bile or can be degraded to α-tocopheronic acid in the kidneys and excreted in urine (Drevon, 1991), with possible further oxidation to dimers, trimers, or other adducts (Kamal-Eldin and Appleqvist, 1996). Vitamin E isomers that are not preferentially used, such as γ-tocopherol and some of the isomers in synthetic racemic mixtures, are probably excreted in bile.

BIOLOGIC FUNCTIONS

Vitamin E functions as a chain-breaking antioxidant in biologic membranes. It is a potent peroxyl-radical scavenger that prevents free-radical damage to polyunsaturated fatty acids (PUFAs) in membrane phospholipids and plasma lipoproteins. Lipid hydroperoxides, oxidized to peroxyl radicals ($ROO^{\cdot}$), react much faster with vitamin E in its reduced state (vit E-OH) than with PUFAs to form the corresponding hydroperoxide (ROOH) and a tocopheroxyl radical (vit $E\text{-}O^{\cdot}$). The tocopheroxyl radical formed in the cell membrane emerges from the lipid bilayer into the aqueous medium, where hydrogen donors, such as vitamin C or glutathione, react with the tocopheroxyl radical to return it to its reduced state (vit E-OH). Thus, the antioxidant function of oxidized vitamin E can be restored if aqueous antioxidants are present in sufficient amounts (Halpner et al., 1998a, 1998b).

The relative order of peroxyl radical scavenging reactivity of α-, β-, γ-, and δ-tocopherol (100, 60, 25, and 27, respectively) is similar to their relative biologic activities (1.5, 0.75, 0.15, and 0.05 $IU \cdot mg^{-1}$, respectively) as determined by the rat fetal-resorption assay. However, the biologic activities of vitamin E isomers appear not to reside exclusively in their ability to function as antioxidants. For example, α-tocotrienol has antioxidant activity that is at least equivalent to that of α-tocopherol but has only about one-third of its ability to prevent fetal resorption. It has been suggested that α-tocopherol's activity is associated with unique structural features that interact preferentially with stereospecific cellular ligands, such as the hepatic protein α-TTP. Some forms of vitamin E modulate the activity of enzymes (such as suppression of arachidonic acid metabolism via inhibition of phospholipase A_2 by α-tocopherol), and γ-tocotrienol enhances degradation of an enzyme (3-hydroxy-3-methyl glutaryl coenzyme A reductase) that regulates rates of cholesterol biosynthesis (Traber, 1999).

VITAMIN E DEFICIENCY

Vitamin E status depends not only on vitamin E forms and concentrations in the diet, but also on dietary concentrations of PUFA, nutritional history, concentrations of other antioxidants, and the presence of xenobiotics and some clinical abnormalities, such as malabsorption (Machlin, 1991). Indeed, vitamin E deficiency was observed in *Saguinus labiatus* and *Callithrix jacchus* (Baskin et al., 1983; Chalmers et al., 1983) in association with malabsorption, but Gutteridge et al. (1986) found no increase in vitamin E deficiency among marmosets with wasting syndrome.

Mason and Telford (1947) were among the first to observe signs of vitamin E deficiency in monkeys (*Macaca mulatta*) fed diets containing 4% lard and 0.57% cod liver oil. After 5 months, the animals developed muscular dystrophy and brownish intracellular pigmentation in several organs and tissues, including striated and smooth muscle. During the late 1950s and into the late 1960s, several investigators conducted studies of vitamin E deficiency in rhesus monkeys. A profound deficiency state—characterized by anemia, muscular dystrophy, and increased urinary excretion of creatine and allantoin—was reported after 167-391 days (Dinning and Day, 1957; Marvin et al., 1960; Porter et al., 1962; Fitch et al., 1980; Fitch and Dinning, 1963). Fitch et al. (1965) showed that the anemia was cured by α-tocopherol in doses approximating $0.378\ mg \cdot BW_{kg}^{-1} \cdot d^{-1}$. Remissions of shorter duration could also be achieved by coenzyme Q_{10} and hexohydrocoenzyme Q_4, although their potencies with respect to curing the anemia were markedly lower (Dinning et al., 1962; Farley et al., 1967). It was demonstrated that the anemia was due both to ineffective erythropoiesis, because of defective α-aminolevulinic acid synthesis (Porter and Fitch, 1966), and to hemolysis and shortened red-cell life span as measured by chromium-51 labeling (Fitch 1968a,b). The ineffective

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erythropoiesis was characterized by the presence of multinucleated red-cell precursors in both bone marrow and peripheral-blood smears (Porter and Fitch, 1966; Ausman and Hayes, 1974; Fitch et al., 1980). The hemolytic anemia occurred nearly at the end stage and was initially normocytic and then macrocytic, with insufficient reticulocytosis to ameliorate the anemia. Severe anemia was characterized by segmented erythrocytes in the blood and evidence of localized folate deficiency in bone marrow (Ausman and Hayes, 1974). In addition to those observations, Morris et al. (1966) reported defective cholesterol metabolism in vitamin E-deficient monkeys—a finding that was later supported by Mickel et al. (1975).

The initial experimental diets used by the above investigators were rich in animal-based saturated fat but contained small amounts of plant or fish oils to provide essential fatty acids. Bieri and Evarts (1972) showed that *RRR*-α-tocopherol at 5 $mg \cdot kg^{-1}$ of diet was insufficient to return plasma α-tocopherol concentrations to normal in monkeys experimentally depleted for periods of 20-60 days, whereas 10 $mg \cdot kg^{-1}$ of diet re-established baseline plasma α-tocopherol concentrations of 12-14 $mg \cdot L^{-1}$. They calculated that the α-tocopherol requirement was 0.72 $mg \cdot g^{-1}$ of linoleic acid in the diet.

Fitch and Dinning (1963) showed in the rhesus monkey and Horwitt et al. (1972) in humans that the vitamin E requirement depends on concentrations of PUFAs in the diet. In a series of long-term experiments, both cebus monkeys (*Cebus albifrons*) and cynomolgus monkeys (*Macaca fascicularis*) were fed experimental diets containing 22% by weight of either coconut oil or stripped safflower oil (Ausman and Hayes, 1974; Hayes, 1974a,b; Mickel et al., 1975). Neither species fed the diet that was nearly devoid of PUFAs developed signs of vitamin E deficiency within a 2-year period. In contrast, cebus monkeys fed the diet containing stripped safflower oil developed classic signs of vitamin E deficiency within 12 months (lethargy, weakness, muscular dystrophy, hemolytic anemia, jaundice, splenomegaly, hemosiderosis, and lipofuscin and ceroid pigments in various organs), as well as evidence of peroxidation of retinal lipids in the macula of the eye (Hayes 1974b). Cynomolgus monkeys developed the same signs after 24 months. That moderate to large amounts of PUFAs will hasten the development of vitamin E deficiency also has been observed in common marmosets (McIntosh et al., 1987; Ghebremeskel et al., 1991), African green monkeys (Parks et al., 1987, 1990), and cynomolgus monkeys (Kaasgaard et al., 1992; Thomas et al., 1994; Thomas and Rudel, 1996). Finally, in a series of experiments examining immune function in cynomolgus monkeys fed marine- and plant-derived n-3 fatty acids it was possible to ensure adequate vitamin E status by adjusting dietary tocopherol content in relation to fatty acids, according to the formula of Muggli (1989). Thus, vitamin E requirements of nonhuman primates appear to vary (in part) in relation to dietary concentrations of 18:2 and 18:3 fatty acids.

VITAMIN E REQUIREMENTS

The dependent variables used most often to assess vitamin E status or to define vitamin E requirements are plasma α-tocopherol concentrations, followed by the presence or absence of clinical signs of deficiency. α-Tocopherol concentrations in the plasma of apparently normal nonhuman primates have been reported to be 5-10 $mg \cdot L^{-1}$ in chimpanzees and orangutans (Ghebremeskel and Williams, 1988; Crissey et al., 1999), 10-11.6 $mg \cdot L^{-1}$ in gorillas (McGuire et al., 1989; Crissey et al., 1999), 5-8 $mg \cdot L^{-1}$ in baboons (de La Pena et al., 1972; Slifka et al., 2000), 9-10.6 $mg \cdot L^{-1}$ in mandrills (Slifka, 1994; Crissey et al., 1999), 12-16 $mg \cdot L^{-1}$ in rhesus monkeys (Nelson et al., 1981), 5-10.5 $mg \cdot L^{-1}$ in common marmosets (Charnock et al., 1992; Flurer and Zucker, 1989; Ghebremeskel et al., 1990), and 5 $mg \cdot L^{-1}$ in *Saguinus fuscicollis* (Flurer and Zucker, 1989). Six free-ranging black spider monkeys (*Ateles paniscus chamek*) had a mean plasma α-tocopherol concentration of 3.7 $mg \cdot L^{-1}$, with a range of 2.3-4.8 $mg \cdot L^{-1}$ (Karesh et al., 1998). Animals made experimentally deficient or exhibiting frank malabsorption or other illnesses that potentially affect vitamin E status had plasma α-tocopherol concentrations ranging from undetectable to 1 $mg \cdot L^{-1}$ (Ausman and Hayes, 1974; Fitch et al., 1980; Baskin et al., 1983; Chalmers et al., 1983; McIntosh et al., 1987; McGuire et al., 1989). In studies in which plasma concentrations of both α- and γ-tocopherol were determined, γ-tocopherol concentrations were generally no more than 10% of α-tocopherol concentrations (Slifka, 1994, 2000; Crissey et al., 1999)

Aside from prevention of the classical signs of deficiency, vitamin E has been used as a supplement to help prevent a variety of chronic diseases. Marmosets given neurotoxin to induce Parkinson's disease appeared to derive no benefit from the intramuscular injection of α-tocopherol at 1,000 $mg \cdot BW_{kg}^{-1}$ (Perry et al., 1987), although such an injection proved beneficial in mice (Perry et al., 1985). Verlangieri and Bush (1992) were able to show that 79 mg of *d*-α-tocopherol per day was beneficial in prevention and reversal of aortic stenosis in long-term atherogenic studies in the cynomolgus monkey. In a series of investigations of the rhesus monkey as a model of age-related macular degeneration (ARM) in humans (Crabtree et al., 1996a, 1996b, 1997), vitamin E concentrations in the peripheral neural retina correlated with concentrations of retinal protein, plasma α-tocopherol, and dietary vitamin E. The lowest concentration of vitamin E found in the retina of rhesus monkeys was in the foveal crest, which is where ARM begins in humans.

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More recently, immune function has been used as a dependent variable to help to determine proper vitamin E nutriture. In a rat model, Bendich et al. (1986) showed that vitamin E concentrations required for optimal T- and B-lymphocyte responses to mitogens were greater than 50 $mg \cdot kg^{-1}$ of diet, whereas 7.5 $mg \cdot kg^{-1}$ and 15 $mg \cdot kg^{-1}$ of diet were sufficient for normal rates of growth and prevention of red-cell hemolysis, respectively. In a randomized, double-blind, placebo-controlled intervention study in healthy elderly human subjects fed a placebo or vitamin E at 60, 200 or 800 $mg \cdot d^{-1}$ for 235 days, Meydani et al. (1997) were able to demonstrate that at least 200 $mg \cdot d^{-1}$ were needed to enhance in vivo indexes of T-cell-mediated function. That dosage is about 10-12 times higher than the 15-19 $mg \cdot d^{-1}$ currently recommended for adult humans (Institute of Medicine, 2000). A careful examination of the immune response, as reflected in a dose-response experiment with vitamin E, has not been conducted in nonhuman primates.

A number of studies have provided evidence that vitamin E metabolism or requirements might vary among species. The New World monkey *Cebus albifrons* appeared to develop vitamin E deficiency twice as fast as an Old World species *Macaca fascicularis* when the two species were fed identical diets (Ausman and Hayes, 1974). The cause of the greater sensitivity of the cebus monkey than the cynomolgus monkey to vitamin E deficiency in this study was not established. Ghebremeskel et al. (1990) observed that common marmosets exhibit higher erythrocyte hemolysis and lower plasma α-tocopherol:cholesterol ratios compared to humans at equivalent plasma α-tocopherol concentrations of 10 $mg \cdot L^{-1}$. Some karyotypes of owl monkeys (*Aotus trivirgatus*) developed a hemolytic anemia and cardiomyopathy that were ameliorated with intramuscular vitamin E and selenium injections (Sehgal et al., 1980; Beland et al., 1981; Meydani et al., 1983). Further investigations into the mechanism of this apparent vitamin E-deficiency anemia indicated that susceptible *Aotus* had no change in activity of the glutathione peroxidase system (Brady et al., 1982; Meydani et al., 1982). However, they did have decreased concentrations of PUFAs and increased cholesterol concentrations in their erythrocytes, leading to a markedly increased free-cholesterol:phospholipid ratio in red-cell membranes (Walsh et al., 1982). That presumably made the erythrocytes more susceptible to hemolysis. Susceptible *Aotus* monkeys suffered from chronic enteritis and inflammatory bowel disease (Meydani, 1983), which might have led to decreased absorption of PUFA, vitamin E, and cholesterol and later abnormal cholesterol metabolism and decreased cholesterol esterification (Mickel et al., 1975). The anemia observed in some *Aotus* might also be secondary to genetically determined dietary allergies and an associated malabsorption.

Table 7-1 is a summary of individual studies in which nonhuman primates were fed one or more diets in an attempt to assess vitamin E requirements. Studies in which only a deficiency was produced without an estimation of requirements are omitted. Vitamin E requirements are reported or calculated as α-tocopherol both in $mg \cdot kg^{-1}$ dietary DM and in $mg \cdot BW_{kg}^{-1} \cdot d^{-1}$.

For the Old World macaques and African green monkeys fed diets that did not contain large amounts of n-3 fatty acids (fish oils), minimal dietary requirements were variously estimated to be 3.2, 5-10, 12, less than 50, less than 60, or 87 $mg \cdot kg^{-1}$ of DM. Dinning and Day (1957) showed that 333 $mg \cdot kg^{-1}$ of dietary DM was more than enough to cure vitamin E-deficiency anemia. In the short term, with one exception, α-tocopherol at 50 $mg \cdot kg^{-1}$ dietary DM appears to be a reasonable estimate of the requirement on the basis of published data. In relation to body weight, the vitamin E requirement appears to be about 3.0 $mg \cdot BW_{kg}^{-1} \cdot d^{-1}$.

The New World monkeys that have been studied include *Cebus albifrons* and *Callithrix jacchus*. The minimal dietary requirements of the former were estimated to be about 3.0 $mg \cdot kg^{-1}$ of DM and of the latter 4-48 $mg \cdot kg^{-1}$ of DM. When fish oils were included in the diet, vitamin E requirements appeared to be greater than 95 $mg \cdot kg^{-1}$ of DM but certainly less than the one dose of 1,600 $mg \cdot kg^{-1}$ of DM that was used. In relation to body mass, *Cebus albifrons* appeared to require α-tocopherol at least at 0.165 $mg \cdot BW_{kg}^{-1} \cdot d^{-1}$, and *Callithrix jacchus* at 0.4-4.7 $mg \cdot BW_{kg}^{-1} \cdot d^{-1}$. When fish oils were added to the diet, the estimate increased to something less than 14 $mg \cdot BW_{kg}^{-1} \cdot d^{-1}$.

All the above estimates should be used with caution because of uncertainty about the relative biologic activity per unit of weight of all-*rac*-α-tocopherol vs *RRR*-α-tocopherol and because the forms of tocopherol used in some of the published studies were not identified. In addition, many observations in other animals have shown that vitamin E requirements for support of optimal immune function are higher than for prevention of clinical signs of deficiency.

Vitamin K

Vitamin K is the collective name for compounds with a 2-methyl-1,4-napthoquinone nucleus and a lipophilic side chain (attached at carbon 3) that have antihemorrhagic activity. The principal active compound in higher plants is phytylmenaquinone (phylloquinone, or vitamin K_1) with a 20-carbon phytyl side chain. Prenylmenaquinones (menaquinones, or vitamin K_2) are compounds with polyisoprenyl side chains of varied length, generically designated menaquinone-*n* (MK-*n*). Those produced by bacteria have side chains with seven to 13 unsaturated isoprenyl units and are designated menaquinone-7 to menaquinone-13 (MK-7 to MK-13). The synthetic provitamin menadione (formerly known as vitamin K_3) has no side chain but can be alkylated

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TABLE 7-1 Survey of Data Used to Estimate Vitamin E Requirement

Species	Age and Body Weight	Daily DM Consumption	Type of Diet	Nutrient Levels Studied	Criteria Used to Estimate Requirement	Estimated Requirement		Reference
						$mg \cdot kg^{-1}$ of dietary DM	mg (or IU)·$BW_{kg}^{-1} \cdot d^{-1}$	
Macaca mulatta	Young 2 kg	Assumed 30 $g \cdot BW_{kg}^{-1} \cdot d^{-1}$	Purified	0 (+ suppl) or 20 $mg \cdot d^{-1}$	Dose needed for anemia remission, number days of remissions	<10 mg·0.03 kg^{-1} = <333 mg of α-tocopherol	<10 mg of α-tocopherol	Dinning and Day, 1957
Macaca mulatta	Immature 1.5-2.5 kg	Assumed 30 $g \cdot BW_{kg}^{-1} \cdot d^{-1}$	Purified	0 (+ suppl) or 34 $mg \cdot d^{-1}$	Dose needed to keep urinary creatine:creatinine ratio below 1	2.6 mg·0.03 kg^{-1} = 87 mg of *d,l*-α-tocopherol	2.6 of mg *d,l*-α-tocopherol	Fitch and Dinning, 1963
Macaca mulatta	Young 1.3-1.8 kg	Assumed 30 $g \cdot BW_{kg}^{-1} \cdot d^{-1}$	Purified	0 (+ suppl) or 34 $mg \cdot d^{-1}$	Dose needed for anemia remission, number days of remission	0.378 mg·0.03 kg^{-1} = 12.6 mg of *l*-α-tocopherol	0.378 ± 0.108 mg of *l*-α-tocopherol	Fitch et al., 1965
Macaca mulatta	4.5 and 4.0 kg	170 g (ME at 3.48 $kcal \cdot g^{-1}$ of DM)	Purified	0, 5, and 10 $mg \cdot kg^{-1}$ of diet	Plasma vitamin E concentrations	>5 mg and <10 mg of *d*-α-tocopherol	>0.4 mg <0.75 mg of *d*-α-tocopherol	Bieri and Evarts, 1972
Cebus albifrons	14 mos 1.4-1.8 kg	86 g (ME at 185 $kcal \cdot BW_{kg}^{-1}$)	Purified	Trace vs 100 $mg \cdot kg^{-1}$ of diet	Dose needed for anemia remission, number days of remission	3.0 mg of α-tocopherol	0.165 ± 0.02 mg of α-tocopherol	Ausman and Hayes, 1974
Macaca fascicularis	14 mos 2.2 kg	67 g (ME at 105 $kcal \cdot BW_{kg}^{-1}$)	Purified	Trace vs 100 $mg \cdot kg^{-1}$ of diet	Curing anemia	3.2 mg	0.10 mg	Ausman and Hayes, 1974
Callithrix jacchus	80-90% mature 306-344 g	Assumed 32 g	Purified	4 or 48 $mg \cdot kg^{-1}$ of diet	Plasma α-tocopherol concentrations, ability to reduce peroxidative hemolysis	>4 mg to <48 mg of *d*-α-tocopherol	Calc: (>4 mg) (0.032 g of diet) = 0.128 mg·0.325 kg^{-1} = >0.4 mg; (<48 mg) (0.032 g) = 1.536 mg·0.325 kg^{-1} = <4.7 mg	McIntosh, 1987
Callithrix jacchus	400 ± 20 g	31 g	Purified (+ fish oils)	2.94 mg per monkey	Plasma concentrations and erythrocyte hemolysis	>95 mg	<7.4 mg	Ghebremeskel et al., 1990
Callithrix jacchus	Adult 392 g	31 and 33 g	Purified (+ fish oils)	2.94 mg and 52.7 mg per monkey	Hydrogen peroxide-induced hemolysis—64% (high) vs 2% (normal)	>95 mg <1,600 mg	>7.4 mg <134 mg	Ghebremeskel et al., 1991
Callithrix jacchus	Young, 9-12 mos 295-330 g	Assumed 32 g	Purified	130 $IU \cdot kg^{-1}$ of diet	Plasma tocopherol concentrations	<130 IU of α-tocopherol	Calc: (130 IU)(0.032 kg of diet) = 4.16 IU·0.33 kg^{-1} = <12.6 IU	Charnock et al., 1992
Macaca fascicularis	N.A.	Assumed 30 $g \cdot BW_{kg}^{-1} \cdot d^{-1}$	Purified	60 or 270 $mg \cdot kg^{-1}$ of diet	Liver α-tocopherol, lipofuscin pigments, enzymes, and TBRS	<60 mg >270 mg if ω-3 fatty acids present	N.A.	Kaasgaard et al., 1992[a]
Cercopithecus aethiops	Adult	30 $g \cdot BW_{kg}^{-1} \cdot d^{-1}$ (ME at 90 $kcal \cdot BW_{kg}^{-1} \cdot d^{-1}$)	Purified	Vitamin E at 30-50 $mg \cdot kg^{-1}$ of diet	Plasma concentrations	<50 mg	N.A.	Carr et al., 1993[a]

[a] Report did not identify minimal vitamin E requirements, but data provide an upper boundary of need based on criteria used.

in the liver of rats and chicks to form menaquinone-4 (MK-4) (Olson, R.E., 1999).

Vitamin K is the cofactor for γ-glutamyl carboxylase, a microsomal enzyme responsible for the posttranslational carboxylation of glutamyl residues (producing γ-carboxyglutamic acid, Gla) in seven coagulation proenzymes (clotting factors II, VII, IX, and X and proteins C, S, and Z) and in intracellular protein Gas 6 (growth-arrest-specific factor, homologous to protein S), matrix Gla protein, and bone Gla protein (osteocalcin) (Hauschka et al., 1989; Liu et al., 1996; Ferland, 1998).

It is now apparent that vitamin K is important not only in blood coagulation but also in bone metabolism. Matrix Gla protein is found in the organic matrix of bone, dentin,

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and cartilage but does not bind with hydroxyapatite. Osteocalcin appears to be derived from osteoblasts, is one of the most abundant noncollagenous proteins in bone, and binds to hydroxyapatite. Synthesis of those two proteins in cultured osteosarcoma cells was regulated by 1,25-dihydroxyvitamin D_3, and there is evidence that matrix Gla protein inhibits growth-plate mineralization, whereas osteocalcin can stimulate bone remodeling and mobilization of bone calcium (Olson, 1999).

Metta and Gopalan (1963) attempted to produce a vitamin K deficiency in *Macaca mulatta* by feeding a vitamin K-deficient diet (vitamin K [expressed as menadione] at 0.06 $\mu g \cdot g^{-1}$ of diet) and by administering antibiotics to limit intestinal production of vitamin K by bacteria. No alterations in clotting were observed, so it was assumed that this amount of dietary vitamin K was adequate. Hill et al. (1964) conducted similar experiments, but clotting times increased over a 270-d period. Administration of vitamin K [as the tetrasodium salt of 2-methyl-1,4-napthohydroquinone diphosphate] at 0.1 $\mu g \cdot BW_{kg}^{-1} \cdot d^{-1}$ was sufficient to normalize clotting times. Two decades later, Suttie (1985), on the basis of data in Griminger (1971), reported that *M. mulatta* required vitamin K (form not specified) at 2 $\mu g \cdot BW_{kg}^{-1} \cdot d^{-1}$; this was equivalent to vitamin K at 0.06 $mg \cdot kg^{-1}$ of diet. That dietary concentration may be compared with about 3 and 12 $mg \cdot kg^{-1}$ found in two commercial monkey diets (Lab Diet® and Harlan®, respectively). The vitamin K concentrations in the two commercial diets seem more than adequate.

Because vitamin K deficiency produced by medical use of warfarin has sometimes been associated with negative effects on bone mass, Binkley et al. (2000) assessed the skeletal status of healthy adult (7-18 years) rhesus macaques during long-term warfarin administration. Bone mass of the total body, lumbar spine, and distal and central radius was determined by dual energy X-ray absorptiometry (DEXA) at baseline and after 6, 12, and 18 months. At these times, serum total and bone-specific alkaline phosphatase concentrations, total and percent unbound osteocalcin concentrations, and urinary calcium:creatinine ratios also were measured. Warfarin administration produced an elevation in serum undercarboxylated osteocalcin but did not alter markers of skeletal turnover or calcium excretion, nor was bone mineral density altered at any measured site. The authors concluded that long-term warfarin administration did not have adverse skeletal consequences in healthy primates with high intakes of vitamin K, calcium, and vitamin D.

Infant humans are more likely to develop vitamin K deficiency than are adults, and this possibility should be considered in infant nonhuman primates. The special sensitivity of the young is associated with poor placental transfer of lipids, limited ability of the liver of the newborn to synthesize prothrombin, low concentrations of vitamin K in breast milk, and sterility of the infant gut at birth, which limits microbial synthesis of menaquinones.

Setting a minimal dietary requirement for vitamin K is difficult because of uncertainty about the quantity and availability of the menaquinones produced by intestinal bacteria. Intestinally active antibiotics can severely limit gut synthesis of menaquinones and increase the importance of vitamin K in the diet. Clotting times, as a means of assessing vitamin K status, are neither particularly precise nor sensitive. Vitamin K deficiency differentially affects the degree of γ-carboxylation of each of its dependent proteins, and there are changes in carboxylation long before changes in clotting time become clinically apparent (Hodges et al., 1993; Sokoll et al., 1997). The presence of des-γ-carboxyprothrombin in the plasma has been used as an early and sensitive indicator of vitamin K deficiency in humans. In healthy people, plasma concentrations should be zero. In people with vitamin K deficiency or liver disease, des-γ-carboxyprothrombin values can reach 30% of total prothrombin levels.

Forms of vitamin K commonly incorporated into nonhuman-primate diets include the water-soluble derivatives menadione dimethylpyrimidinol bisulfite (MPB), menadione sodium bisulfite (MSB), and menadione sodium bisulfite complex (MSBC). Vitamins K_1 and K_2 and menadione also have been used, but they are fat-soluble, so it is difficult to distribute them uniformly in dry feeds. The vitamin K activities of the three water-soluble forms are related to their molecular proportions of menadione, which are 46%, 52%, and 33% for MPB, MSB, and MSBC, respectively. Moisture, alkalinity, and contact with trace minerals and choline chloride can impair their stability. Coelho (1991) reported that MPB and MSBC can lose up to 80% of their activity after 3 months in vitamin-trace mineral premixes containing choline. However, when choline was not included in the premixes, declines in vitamin K activity were much smaller. Microencapsulation of vitamin K compounds also has improved their stability.

WATER-SOLUBLE VITAMINS

Thiamin

Thiamin, as the coenzyme thiamin pyrophosphate, functions in oxidative decarboxylation of α-ketoacids. The vitamin is critical for decarboxylation of pyruvate in preparation for its entry into the tricarboxylic acid cycle. The coenzyme also is involved in the decarboxylation of α-ketoglutarate and the α-ketoacids resulting from metabolism of branched-chain amino acids. And it functions in transketolase reactions and may play a role in neurotransmission and nerve conduction (Rindi, 1996; Tanphaichitr, 1999).

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Thiamin is added to diets as the salt of chloride-hydrochloride (usually called thiamin hydrochloride) or as the mononitrate. Those forms are stable under dry and acidic conditions, but thiamin is destroyed under alkaline conditions, especially when accompanied by heat. It also is destroyed by X-rays, γ-rays, UV irradiation, and sulfites (Rindi, 1996; Tanphaichitr, 1999).

Thiamin status can be influenced by its bioavailability in food, the presence of antithiamin factors, and dietary concentrations of folate and protein (Tanphaichitr, 1999). Thiaminase I (found in several microorganisms and certain plants, raw fresh-water fish, shellfish, and marine fish) and thiaminase II (found in several microorganisms) are thermolabile antithiamin factors that destroy the vitamin activity of thiamin during food storage or preparation, prior to ingestion or during food passage through the gastrointestinal tract. Thermostable antithiamin factors have been found in plants and a few animal tissues. Those in plants are related to *ortho-* and *para*-polyphenolic compounds, such as caffeic acid, chlorogenic acid, and tannic acid. In the presence of oxygen, active quinones are generated that interact with thiamin to produce thiamin disulfide and other less active or inactive compounds. Ascorbic acid and other reducing agents tend to inhibit this process. The bioavailability of thiamin in foods also may be reduced by divalent cations, such as Ca^{2+} and Mg^{2+}, which tend to augment the precipitation of thiamin by tannins. Ascorbic acid, tartaric acid, and citric acid will inhibit this precipitation, apparently by sequestering these cations. Subjects with a folate or protein deficiency exhibit a reduction in thiamin absorption that can be reversed by folate and protein supplementation.

Thiamin deficiency has been produced in rhesus monkeys *(Macaca mulatta)* by Lebond and Chaulin-Serviniere (1942), Waisman and McCall (1944), Rinehart et al. (1948,1949a), Blank et al. (1975), Witt and Goldman-Rakic (1983a), and Cogan et al. (1985). Deficiency signs include weight loss, anorexia, apathy, weakness, ophthalmoplegia, loss of reflexes, paralysis, incoordination, convulsions, cardiac failure, and death. Thiamin-deficient animals also exhibit behavioral abnormalities and memory loss (Witt and Goldman-Rakic, 1983b).

Observations of pathologic conditions have focused on the myocardium and the nervous system. Focal necrosis of myocardial fibers is a relatively constant finding and has been associated with electrocardiographic abnormalities. Degeneration of the fibers in the myocardial conduction system also has been seen (Waisman and McCall, 1944; Rinehart and Greenberg, 1949a). Both peripheral nerve (Lebond and Chaulin-Serviniere, 1942) and central nervous system degeneration similar to Wernick's encephalopathy (Rinehart et al., 1949; Blank et al., 1975; Witt and Goldman-Rakic, 1983a, 1983b) have been described in rhesus monkeys. Wernick's encephalopathy is a disease often associated with chronic alcoholism in humans.

Waisman and McCall (1944) found that rhesus monkeys weighing about 3 kg and consuming 100-200 g of food per day required thiamin at 15 $\mu g \cdot BW_{kg}^{-1} \cdot d^{-1}$ to prevent deficiency signs and support maintenance. Optimal growth was obtained at 25-30 $\mu g \cdot BW_{kg}^{-1} \cdot d^{-1}$, whereas borderline deficiency signs appeared in animals receiving less than 10 $\mu g \cdot BW_{kg}^{-1} \cdot d^{-1}$.

Rinehart et al. (1948) described an anemia associated with reduced erythropoiesis in thiamin deficiency. They estimated the thiamin requirement by observing the time necessary to replete thiamin-deficient rhesus monkeys weighing 1.7-5.0 kg after administration of a single small thiamin dose separate from food. The researchers concluded that the thiamin requirement was about 15.5 $\mu g \cdot BW_{kg}^{-1} \cdot d^{-1}$.

Thiamin-deficient rhesus monkeys have reduced blood transketolase activity (Mesulam et al., 1977), an accepted end point for assessing thiamin status (Rindi, 1996). However, measurements of transketolase activity have not been applied to studies of the quantitative thiamin requirement.

The quantitative requirement for thiamin has not been studied in nonhuman primates other than rhesus monkeys. However, the thiamin requirement of nonhuman primates is estimated to be 1.1 $mg \cdot kg^{-1}$ of dietary DM, primarily on the basis of the report of Waisman and McCall (1944). That estimate was based on the use of purified diets, and the biologic availability of thiamin in natural ingredients and the destruction of thiamin during feed processing or storage were not taken into account. These studies are summarized in Table 7-2.

Riboflavin

Riboflavin is a precursor of the coenzymes flavine adenine mononucleotide (FMN) and flavine adenine dinucleotide (FAD). Those coenzymes and their associated enzymes catalyze oxidation-reduction reactions and are important in the metabolism of carbohydrates, fats, and proteins. The enzymes function in the transfer of electrons in oxidation-reduction reactions (Rivlin, 1996). A riboflavin coenzyme also plays a role in the conversion of pyridoxine to pyridoxamine phosphate, which acts as a coenzyme in the conversion of tryptophan to niacin. Thus, riboflavin may be involved indirectly in the biosynthesis of niacin from tryptophan (Cooperman and Lopez, 1991; McCormack, 1999).

Riboflavin is added to animal feeds in the form of the crystalline vitamin. The biologic availability to humans of riboflavin in natural foods is estimated to be about 95% (Institute of Medicine, 1998).

Riboflavin deficiency has been induced and studied in rhesus monkeys (*Macaca mulatta)* by Day et al. (1935),

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TABLE 7-2 Estimates of Thiamin Requirement

Species	Age	Body Weight	Daily Air-Dry Diet Consumption	Type of Diet	Thiamin Levels Studied	Criteria	Estimated Requirement	Reference
Macaca mulatta	Not specified	3 kg	100-200 g	Purified	10-100 $\mu g \cdot d^{-1}$	No deficiency signs, maintained weight	15 $\mu g \cdot BW_{kg}^{-1} \cdot d^{-1}$ for maintenance	Waisman and McCall, 1944
Macaca mulatta	Not specified	3 kg	100-200 g	Purified	10-100 $\mu g \cdot d^{-1}$	Growth	25-30 $\mu g \cdot BW_{kg}^{-1} \cdot d^{-1}$	Waisman and McCall, 1944
Macaca mulatta	Not specified	1.7-5.0 kg		Purified	Not specified	Dose divided by time to replete deficient monkeys	15.5 $\mu g \cdot BW_{kg}^{-1} \cdot d^{-1}$ for maintenance	Rinehart et al., 1948

Waisman (1944), Cooperman et al. (1945), and Greenberg and Moon (1963). The signs of deficiency in rhesus monkeys include growth failure, "freckled" dermatitis, incoordination, faulty grasping reflexes, impaired vision, scanty hair coat, reduced red-cell count, anemia, leukopenia, fatty liver, blindness, and eventual death. The dermatitis begins as small, dry, red spots about the face and progresses to dark scabs over the entire body. The severe anorexia seen in thiamin deficiency has not been observed.

There are two reports on the riboflavin requirement of macaques. The riboflavin concentration required to cure deficiency signs and allow excretion in the urine of animals weighing 3-4 kg was 25-30 $\mu g \cdot BW_{kg}^{-1} \cdot d^{-1}$ (total intake, 90 μg) (Cooperman et al., 1945). In another investigation, the requirement of monkeys weighing 3 to 4 kg was estimated to be 41 $\mu g \cdot BW_{kg}^{-1} \cdot d^{-1}$; this estimate was based on the difference in urinary excretion of riboflavin between animals receiving sufficient riboflavin and those fed a deficient diet for 5 weeks (Greenberg, 1970).

Mann et al. (1952) and Mann (1968) described riboflavin deficiency in capuchin monkeys (*Cebus albifrons*). Weight loss, dermatitis, alopecia, ataxia, and sudden death were the reported signs. Severe anemia did not develop in capuchin monkeys, although seen consistently in rhesus monkeys. The concentration of plasma riboflavin was considered a good indicator of riboflavin status. A riboflavin intake of 50-55 $\mu g \cdot BW_{kg}^{-1} \cdot d^{-1}$ was required to restore maximal growth rate in deficient animals. That represented a daily supplement of 30-40 μg of riboflavin in a basal diet furnishing 10-15 $\mu g \cdot BW_{kg}^{-1} \cdot d^{-1}$ (Mann et al., 1952). Although the weights of the animals were not specified, monkeys used in similar studies in the same report, but not involved in the requirement study, weighed 0.9-1.4 kg and consumed 40-60 g of diet per day.

Foy et al. (1964, 1972) and Foy and Kondi (1984) described riboflavin deficiency in the baboon (*Papio anubis)* as characterized by weight loss, apathy, severe dermatitis, anemia, gingivitis, diarrhea, and adrenal cortical hemorrhage. The dermatitis progressed to nodular lesions that formed mud-pack-like masses on the face, arms, legs, and feet. The lesions extended into the lower third of the esophagus (Foy and Kondi, 1984). An increased concentration of xanthurenic acid, but not of anthranilic acid (both are metabolites of tryptophan), was found in the urine of riboflavin-deficient baboons by Foy et al. (1964). Increased anthranilic acid but unchanged concentrations of xanthurenic acid in the urine were reported by Verjee (1971). No explanation for the different findings was offered. An erythroid aphasia characterized by a fall in marrow erythroid activity leading to reduced hemoglobin, packed-cell volume, and total blood volume was reported in baboons made riboflavin-deficient. A reversal of the albumin:globulin ratio also was observed (Foy et al., 1964, 1968; Foy and Kondi, 1968).

The signs of riboflavin deficiency in the baboon were reversed with a therapeutic dose of about 10-50 mg of riboflavin per animal per day for 3-7 days (Foy and Kondi, 1968). No attempt was made to see whether the same effect could be achieved with smaller doses.

There are insufficient data to show whether different species of primates have similar or different riboflavin requirements. The estimated riboflavin requirement of nonhuman primates has been set at 1.7 $mg \cdot kg^{-1}$ of dietary DM. That requirement is based on studies with purified diets fed to rhesus and capuchin monkeys, summarized in Table 7-3.

Pantothenic Acid

Pantothenic acid is a part of coenzyme A, which is involved in metabolic acetylation reactions. Coenzyme A serves as a cofactor in the tricarboxylic acid cycle, in fatty-acid synthesis and degradation, and in the formation of acetylcholine in nervous tissue (Plesofsky-Vig, 1996, 1999). Biologic availability of pantothenic acid in the average American human diet is estimated to be about 50% (Tarr et al., 1981; Institute of Medicine, 1998). The supplemental form usually added to diets is D-calcium pantothenate, equivalent in activity to 85% pantothenic acid.

McCall et al. (1946) reported that pantothenic acid deficiency in rhesus monkeys *(Macaca mulatta)* resulted in lack of growth, anemia, loss of hair, and ataxia. Only partial

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TABLE 7-3 Estimates of Riboflavin Requirement

Species	Age	Body Weight	Daily Air-Dry Diet Consumption	Type of Diet	Riboflavin Levels Studied	Criteria	Estimated Requirement	Reference
Macaca mulatta	Not specified	3.3 kg	100 g	Purified	40-90 $\mu g \cdot d^{-1}$	Reverse deficiency signs, allow riboflavin excretion in urine	90 $\mu g \cdot d^{-1}$ or 25-30 $\mu g \cdot BW_{kg}^{-1} \cdot d^{-1}$	Cooperman et al., 1945
Macaca mulatta	Not specified	3.0-4.0 kg	Not specified	Not specified, probably purified	0 and 1.0 $mg \cdot d^{-1}$	Difference in urinary riboflavin excretion between animals receiving sufficient and no riboflavin	41 $\mu g \cdot BW_{kg}^{-1} \cdot d^{-1}$	Greenberg, 1970
Cebus albifrons	Young adult	Not specified; probably 900-1,400 g	40-60 g	Purified	20-70 $\mu g \cdot d^{-1}$	Weight gain of deficient animals	50-55 $\mu g \cdot d^{-1}$ or 30-40 $\mu g \cdot BW_{kg}^{-1} \cdot d^{-1}$	Mann et al., 1952

improvement was noted with oral administration of D-calcium pantothenate at 1-3 $mg \cdot BW_{kg}^{-1} \cdot d^{-1}$. Complete recovery was noted when supplements of both calcium pantothenate and liver powder were included in the diet, so a simultaneous deficiency of nutrients other than pantothenic acid is likely to have occurred. Greenberg (1970), citing unpublished studies, reported a dramatic response to 3 mg of calcium pantothenate per animal per day. Those are the only studies describing pantothenic acid deficiency in nonhuman primates.

Semipurified diets with calcium pantothenate at about 22-23 $mg \cdot kg^{-1}$ DM (equivalent to pantothenic acid at 19-20 $mg \cdot kg^{-1}$ DM) have been fed to rhesus monkeys (Kark et al., 1974) and to squirrel monkeys (Rasmussen et al., 1979) without signs of deficiency. These latter studies do not provide the basis for estimating minimum pantothenic acid requirements, and the concentrations used exceed the minimum pantothenic acid requirements reported for other species in the National Research Council nutrient requirement series.

Niacin

Niacin (also known as nicotinic acid) is a component of the coenzymes nicotinamide adenine dinucleotide (NAD) and nicotinamide adenine dinucleotide phosphate (NADP), which play a part in metabolic oxidation-reduction and dehydrogenase reactions, serving as electron receptors or hydrogen donors (Jacob and Swenside, 1996; Cervantes-Laurean et al., 1999). Although niacin is widely distributed in natural foodstuffs, it is bound and largely unavailable in grains, such as wheat and corn (Jacob and Swenside, 1996). Niacin supplements are commonly added to diets as nicotinic acid or nicotinamide.

Estimating the niacin requirement is complicated by the ability of many mammals to synthesize niacin from a dietary excess of the amino acid tryptophan. That ability has been identified in some primate species (Tappan et al., 1952; Banerjee and Basak, 1957). Thus, to some extent the niacin requirement is related to the tryptophan supply in the diet. Deficiencies of a number of other nutrients—including vitamin B_6, riboflavin, iron, and copper—can inhibit the conversion of tryptophan to niacin (van Eys, 1991).

Niacin deficiency has been studied in rhesus monkeys *(Macaca mulatta)* by Tappan et al. (1952), Belavady et al. (1968), and Belavady and Rao (1973). The deficiency syndrome was characterized by weight loss, alopecia, anemia, skin hyperpigmentation, anorexia, chronic gastritis, and diarrhea. Declines in serum albumin and blood pyridine nucleotide concentrations and development of chronic atrophic gastritis and atrophic necrotizing enterocolitis were also observed.

Tappan et al. (1952) reported that deficiency signs in rhesus monkeys weighing 1.4-3.2 kg and fed purified diets containing 7% protein from casein were ameliorated by weekly administration of 10-35 mg of niacin (equivalent to about 0.7-1.8 $mg \cdot BW_{kg}^{-1} \cdot d^{-1}$) or 1-4 g of D,L-tryptophan. A weekly dose of 5 mg of niacin was not adequate to reverse deficiency signs, and 30-35 mg of niacin per week was more effective than 10 mg. Intermediate dosages were not tested. Belavady et al. (1968) reported that niacin deficiency in rhesus monkeys was reversed by giving animals 25 mg of niacin per day in the first week and 10 mg per day for 3 more weeks; lower dosages were not tested. The animals weighed 6.0-11.0 kg. Belavaday and Rao (1973) induced niacin deficiency by supplementing the diet of rhesus monkeys with 1.5 g of leucine (a niacin antagonist) per day. That resulted in reduced synthesis of nicotinamide

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nucleotides in erythrocytes, weight loss, and alopecia, which were reversed by injection of 40 mg of niacin.

Data are insufficient to estimate niacin requirements of nonhuman primates with confidence. It is probable that the dietary niacin requirement of rhesus monkeys with minimal synthesis from tryptophan is 16-56 $mg \cdot kg^{-1}$ of DM.

Vitamin B_6

Vitamin B_6 occurs as pyridoxine, pyridoxal, and pyridoxamine. These compounds function metabolically as the coenzymes pyridoxal phosphate and pyridoxamine phosphate. The vitamin B_6 coenzymes are important cofactors in amino acid metabolism and in glycogen and lipid metabolism. Vitamin B_6 coenzymes also can be involved in the synthesis of niacin from tryptophan (Leklem, 1996, 1999). The bioavailability of vitamin B_6 in a mixed human diet is about 75% (Tarr et al., 1981). That in foods used for laboratory animals has been reported to be as low as 40-60% under some conditions (Baker, 1995). Supplemental vitamin B_6 is usually added to feeds as pyridoxine hydrochloride, with a vitamin B_6 potency of 92%.

Vitamin B_6 deficiency has been produced in rhesus monkeys *(Macaca mulatta)* by a number of investigators, beginning with McCall et al. (1946), who described the resulting syndrome as consisting of weight loss, hypochromic anemia, and ataxia. Clinical improvement was noted in 2 weeks after provision of 1 mg of pyridoxine per day to 1.5- to 2-kg monkeys. Others have confirmed those clinical signs and modified the description of the deficiency to include widespread arteriosclerosis, leukopenia, anemia, liver cirrhosis, decreased plasma albumin, and increased plasma globulin, dental caries, and neural degeneration of the cerebral cortex (Rinehart and Greenberg, 1949a, 1951, 1956; Greenberg et al., 1952; Poppen et al., 1952; Mushett and Emerson, 1956; Victor and Adams, 1956; Greenberg et al., 1958; Greenberg, 1964; Wizgird et al., 1965). Arteriosclerosis involving many tissues and organs, anemia, leukopenia, alopecia, and dermatitis are the most frequently reported signs.

The interrelationship between essential fatty acids and vitamin B_6 has been investigated because it was thought that vitamin B_6 might be required for the conversion of linoleic acid to arachidonic acid. In turn, a deficiency of arachidonic acid might be responsible for atherosclerosis in primates. The vascular lesions of animals with a combined deficiency of essential fatty acids and vitamin B_6 were no more severe than those seen in animals with simple vitamin B_6 deficiency. The fatty acid patterns in plasma and erythrocytes of control and vitamin B_6-deficient animals were similar and unlike those of animals deficient in essential fatty acids. The conclusion was that no metabolic interrelationship exists between the two nutrients (Greenberg and Moon, 1959, 1961; Greenberg 1964), although the role of vitamin B_6 in lipid metabolism remains controversial (Leklem, 1999).

Arteriosclerosis develops in vitamin B_6-deficient cynomolgus monkeys *(Macaca fascicularis)* and rhesus monkeys (Kuzuya. 1993). At least partial regression of the lesions occurs upon refeeding vitamin B_6 (Yamada et al., 1965).

Vitamin B_6 requirements were investigated in several studies, which are summarized in Table 7-4.

Rinehart and Greenberg (1956) tested graded levels of pyridoxine hydrochloride and measured growth of rhesus monkeys weighing 1.3-3.0 kg. They concluded that the requirement was 62 $\mu g \cdot BW_{kg}^{-1} \cdot d^{-1}$ for optimal growth. But Emerson et al. (1960) fed pyridoxine hydrochloride at 50-2,000 $\mu g \cdot d^{-1}$ to rhesus monkeys weighing 4.1 kg. Ataxia and alopecia persisted in animals receiving 500 $\mu g \cdot d^{-1}$ or less, and higher dosages were required to alleviate deficiency signs. A dosage of 1.0-2.0 $mg \cdot d^{-1}$ (244-488 $\mu g \cdot BW_{kg}^{-1} \cdot d^{-1}$) was required for optimal growth. Specific reasons for the difference in observed requirements reported by these investigators are not apparent, but the low requirement reported by Rinehart and Greenberg (1956) was observed in animals fed diets that were lower in protein than those fed by Emerson et al. (1960). In a number of studies of vitamin B_6 deficiency, administration of 3.5 mg of vitamin B_6 two times per week or 1.0 $mg \cdot d^{-1}$ has been sufficient to prevent signs of deficiency (Rinehart and Greenberg, 1949b, 1956; Poppen et al., 1952; Victor and Adams, 1956; Wizgard et al., 1965).

Mann (1968) described a vitamin B_6 deficiency in capuchin monkeys (*Cebus albifrons*) that consisted of weight loss, profound hypochromic microcytic anemia, hair loss, dermatitis (especially about the hands and toes), and, rarely, convulsions. The livers were mildly fatty, but no cirrhosis was observed. In contrast with vitamin B_6 deficiency in rhesus monkeys, cardiovascular changes and arteriosclerosis were not observed. A minimal therapeutic dose of vitamin B_6 at 50-100 $\mu g \cdot BW_{kg}^{-1} \cdot d^{-1}$ was required to promote optimal weight gain. Although it was not summarized in tabular form, inspection of a graph of hematocrit vs pyridoxine dose suggests that a level of about 175-200 $\mu g \cdot BW_{kg}^{-1} \cdot d^{-1}$ was required for an optimal hematocrit response (Mann, 1969).

Vitamin B_6 deficiency also has been produced in male baboons *(Papio anubis)* weighing 7-15 kg. The deficient animals became apathetic and anorexic and had occasional bloody diarrhea for a day or two. Some animals' genitalia remained juvenile. Nervous tremors were sometimes observed. The baboons died after 6-8 months unless they were given pyridoxine parenterally. Some animals were kept on intermittent pyridoxine administration to sustain a concentration of serum pyridoxine known to be compatible with life. After 2 or more years of chronic deprivation, fatty degeneration of the liver was seen with hyperplastic nodules similar to premalignant or neoplastic lesions,

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TABLE 7-4 Estimates of Vitamin B_6 Requirement

Species	Age	Body Weight	Daily Air-Dry Diet Consumption	Type of Diet	Vitamin B_6 Levels Studied	Criteria	Estimated Requirement	Reference
Macaca mulatta	Immature	1.3-3.0 kg	Not specified	Purified	50-1,000 $\mu g \cdot d^{-1}$	Growth of depleted animals	62 $\mu g \cdot BW_{kg}^{-1} \cdot d^{-1}$	Rinehart and Greenberg, 1956
Macaca mulatta	Not specified	4.1 kg	60-170 g	Purified fat 2-20%	Pyridoxine HCl at 0.5-2.0 $mg \cdot d^{-1}$	Growth of depleted animals	1.0-2.0 $mg \cdot d^{-1}$ or 0.24-0.49 $mg \cdot BW_{kg}^{-1} \cdot d^{-1}$ 1.0 $mg \cdot d^{-1}$ required to prevent all deficiency signs; 2.0 $mg \cdot d^{-1}$ supported faster growth	Emerson et al., 1960
Cebus albifrons	Not specified	900-1,500 g	Not Specified	Purified	0-1,100 $\mu g \cdot BW_{kg}^{-1} \cdot d^{-1}$	Weight gain and hematocrit recovery in depleted animals	50-100 $\mu g \cdot BW_{kg}^{-1} \cdot d^{-1}$ for growth; 175-200 $\mu g \cdot BW_{kg}^{-1} \cdot d^{-1}$ for optimum hematocrit	Mann, 1968
Papio hamadryas	Adolescent males	7-15 kg	Probably 190-378 g	Purified	1.11 $mg \cdot d^{-1}$	Control animals exhibit no deficiency signs.		Foy et al., 1974

although the baboons had received no carcinogenic substance. Serum vitamin B_6 concentrations dropped from 200-350 $ng \cdot ml^{-1}$ to 5-10 $ng \cdot ml^{-1}$ (Foy et al., 1970; Foy et al., 1974). The urine of pyridoxine-deficient baboons had increased concentrations of the tryptophan metabolites xanthurenic acid, kynurenine, and 3-hydroxykynurenine (Foy et al., 1974; Verjee, 1971).

Control baboons in the investigations of Foy et al. (1974) received a daily oral supplement of 1.0 mg of pyridoxine hydrochloride and an additional 0.11 mg from ingredients in the diet. That dosage level was equivalent to 74-158 $\mu g \cdot BW_{kg}^{-1} \cdot d^{-1}$, or about 3.1 $mg \cdot kg^{-1}$ of dietary DM, and apparently exceeded the requirement.

A syndrome similar to vitamin B_6 deficiency has been observed after chronic administration of isoniazid, a drug used for prevention of and treatment for tuberculosis. Although evidence of an induced B_6 deficiency was equivocal, urinary vitamin B_6 was increased when the drug was administered to humans (Levy et al., 1967). Manning and Clarkson (1971) did not observe a decrease in vitamin B_6 concentrations in the serum of rhesus monkeys receiving isoniazid when fed a diet containing vitamin B_6 at 21 $mg \cdot kg^{-1}$. That is a high dietary intake of vitamin B_6 and suggests that supplemental vitamin B_6 should be considered for primates receiving this drug even though the pathogenesis of the syndrome induced by isoniazid is not understood.

The dietary vitamin B_6 requirement has been estimated to be 4.4 $mg \cdot kg^{-1}$ of DM. The preponderance of evidence suggests that that level is adequate to meet the needs of rhesus and capuchin monkeys. However, if the details of the study by Emerson et al. (1960) were correctly reported, the dietary requirement under some conditions could be as high as 9.6 $mg \cdot kg^{-1}$ of DM.

Biotin

Biotin serves as a cofactor in carboxylation and decarboxylation reactions. It is concerned with introduction of bicarbonate, as a carbonyl group, into metabolic steps involved in gluconeogenesis, fatty acid synthesis, and amino acid metabolism (Mock, 1996, 1999). Substantial amounts of biotin can be synthesized by the microbial flora in the intestinal tract. Signs of biotin deficiency have been produced experimentally by feeding raw egg white. Raw egg white contains the protein avidin, which binds biotin and prevents its absorption (Bonjour, 1991). Biotin is widely distributed in natural feedstuffs. However, the biologic availability of biotin in wheat, wheat byproducts, barley, and oats is low (Frigg, 1976; Anderson et al., 1978).

Biotin deficiency has been produced in rhesus monkeys *(Macaca mulatta)* by feeding deficient diets and by feeding deficient diets containing raw egg white. A more severe deficiency is produced by feeding sulfa drugs (sulfguanidine or sulfasuxidine) to prevent production of biotin by the intestinal microflora (Lease et al., 1937; Waisman and Elvehjem, 1943; Waisman et al., 1945). Animals fed a biotin-deficient purified diet, without egg white or sulfa drugs, showed a gradual loss of fur color followed by loss of fur. These deficiency signs could be reversed or prevented by the daily administration of 20 μg of biotin. Rhesus monkeys receiving 12 μg of biotin daily did not show deficiency signs, whereas those receiving 1.7-9.0 μg per day showed

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mild signs after an extended time. The monkeys in the study were consuming 200 g of air-dry food per day, so a biotin requirement of 60 $\mu g \cdot kg^{-1}$ of air-dry diet (2.4 $\mu g \cdot BW_{kg}^{-1} \cdot d^{-1}$) was suggested. When a biotin deficiency was produced in animals fed egg white or sulfa drugs, acute dermatitis developed around the hands, face, and feet and was accompanied by watering of the eyes, loss of fur color, and loss of weight (Lease et al., 1937; Waisman et al., 1945). Complete blood profiles of animals receiving sulfa drugs revealed no changes in hemoglobin concentration, red-cell or white-cell numbers, or differential white-cell count. Biotin at 20 $\mu g \cdot d^{-1}$ reversed deficiency signs in animals receiving either egg white or sulfa drugs (Waisman et al., 1945).

On the basis of the data of Waisman, biologically available biotin at 110 $\mu g \cdot kg^{-1}$ of dietary DM is adequate to prevent deficiency in animals fed egg white or receiving sulfa drugs. That requirement estimate assumes little or no synthesis of the vitamin by intestinal microflora and no biologic availability of biotin in natural feed ingredients.

Folacin

Folacin is the term used to refer to a family of pteroylglutamates or folates. *Folic acid*, which is sometimes used as an alternative name for folacin, is a pteroylmonoglutamate. In the older primate literature, folic acid is referred to as vitamin M. Folic acid is part of a coenzyme involved in receiving or donating one-carbon fragments in metabolic reactions, in much the same way that pantothenic acid is involved in metabolism of two-carbon acetyl fragments. Folic acid is involved in the metabolism of nucleotides, essential components of DNA and RNA. Folic acid coenzymes also are involved in the synthesis of serine from glycine and the synthesis of methionine from homocystine (Selhub and Rosenberg, 1996; Herbert, 1999).

Folacin in natural ingredients exists as polyglutamate conjugates. Before absorption by humans, folic acid must be released from the polyglutamate by hydrolysis to the monoglutamate form via intestinal conjugases (Selhub and Rosenberg, 1996). Humans have two intestinal conjugases, one on the brush border of intestinal cells and the other an intracellular soluble enzyme. Rhesus monkeys *(Macaca mulatta)* fed a nonpurified diet containing synthetic folic acid did not have a conjugase on the intestinal-cell brush border (Wang et al., 1985). Other species of monkeys appear not to have been studied in this respect. The lack of a brush-border conjugase in rhesus monkeys might be related to the predominant form of folic acid in the diet. However, complete biologic availability of polyglutamate forms to nonhuman primates in natural dietary ingredients cannot be assumed. Folic acid is the supplemental folacin form usually added to feeds.

Dietary factors can affect folic acid availability. Gyr et al. (1974) reported a decrease in folic acid absorption in patas monkeys (*Erythrocebus patas*) fed a protein-deficient diet (0% protein). Ethanol also has been shown to inhibit folic acid absorption (Blocker and Thenen, 1987). In humans, the bioavailability of synthetic folic acid consumed with food is estimated to be 85%, whereas the bioavailability of folic acid in natural foods is estimated to be 50%. Folic acid in natural foods is concluded to be about 60% as available as synthetic folic acid ($50/85 \times 100 = 59\%$) (Institute of Medicine, 1998).

Folic acid deficiency has been studied in macaques, marmosets, squirrel monkeys, and capuchin monkeys. The most consistent deficiency signs in all species were leukopenia and megaloblastic anemia. The anemia was characterized by lowered hemoglobin and red-cell counts and higher mean corpuscular volumes (Blocker and Thenen, 1987).

Langston et al. (1938) first demonstrated the need for folic acid (then designated vitamin M) in the rhesus *(Macaca mulatta)* monkey. The deficiency signs in rhesus monkeys were weight loss, anorexia, diarrhea, leukopenia, thrombocytopenia, and megaloblastic anemia (Waisman and Elvehjem, 1943; Cooperman et al., 1946). Folic acid-deficient female rhesus monkeys also had abnormalities of their reproductive system characterized by atresic and cystic ovarian follicles with loss of granulosa cells. Proliferation of the granulosa cells appeared to be associated with interruption of DNA synthesis. The normal cyclic changes in the vaginal and cervical epithelium were impaired, and multiple abnormal cells were seen (Mohanty and Das, 1982). Folic acid deficiency in cynomolgus monkeys (*Macaca fascicularis)* was similar to that in rhesus monkeys, with megaloblastic anemia and weight loss predominant. Folic acid-depleted animals also had lower concentrations of folic acid in red-cells, plasma, and liver. Urinary excretion of formiminoglutamic acid was increased (Blocker and Thenen, 1987).

Folic acid deficiency in the squirrel monkey (*Saimiri sciureus*) resulted in weight loss, alopecia, scaly dermatitis, and megaloblastic anemia with profound intramedullary hemolysis in the bone marrow. Deficient animals had reduced plasma and red-cell folic acid and increased urinary formiminoglutamic acid (Rasmussen et al., 1979). The folic acid status of pregnant squirrel monkeys fed a commercial stock diet with and without a folic acid supplement was evaluated (Rasmussen, 1979; Rasmussen et al., 1980). Females supplemented with folic acid had greater maternal weight gain during pregnancy, and infants from supplemented females had higher birth weights. Higher red-cell folic acid concentrations and somewhat lower mean cell volumes were also seen in supplemented animals. Those results indicated that the stock diet, presumably adequate

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in folic acid for reproduction in other monkey species, was not optimal for reproduction in the squirrel monkey.

Capuchin monkeys (*Cebus albifrons*) exhibited deficiency signs similar to those of squirrel monkeys (Rasmussen et al., 1980; Thenen et al., 1991), including megaloblastic anemia, leukopenia, increased polymorphonuclear leukocyte lobe counts, and increased urinary formiminoglutamic acid. A wide variability in the severity of deficiency signs in dams and suckling neonates fed folic acid-deficient diets has been reported (Gillet et al., 1987); megaloblastic anemia was the sign most consistently present. Pregnant animals fed folic acid sufficient to support reproduction, but apparently below the requirement, had lowered blood and liver folate concentrations, increased urinary formiminoglutamic acid excretion, and reduced milk folate (Blocker et al., 1989).

Folic acid deficiency in marmosets (*Callithrix jacchus*) produced the usual deficiency signs (weight loss, alopecia, diarrhea, megaloblastic anemia, leukopenia, and granulocytopenia) and lesions of the oral mucosa, described as bilateral angular cheilosis, in about half the deficient animals (Dreizen and Levy, 1969). The stomatitis seemed to be a result of interference with maturation of the epithelial cells and later ulceration and secondary infection (Dreizen et al., 1970). The folic acid deficiency was prevented by supplementing the test diet with 0.1 mg of folic acid per day for animals consuming 30 g of diet per day.

Signs of folic acid deficiency in the baboon *(Papio cynocephalus)* were similar to those seen in other primate species, including weight loss, anorexia, gingivitis, diarrhea, severe leukopenia and thrombocytopenia, and sometimes macrocytic anemia. The animals lost weight before becoming anorexic. Abnormalities in the white cells appeared well before the development of anemia (Siddons et al., 1974a).

The proposed association between low folate status, hyperhomocyst(e)inemia, and vascular dysfunction has led to research with nonhuman primate models. A diet-induced hyperhomocyst(e)inemia in cynomolgus monkeys resulted in decreased blood flow to the leg when platelets were activated by intraarterial infusion of collagen (Lentz et al., 1996). Supplementation of atherosclerotic cynomolgus monkeys with 5 mg folic acid, 400 μg vitamin B_{12}, and 20 mg vitamin B_6 daily reduced plasma homocyst(e)ine concentrations but plasma cholesterol remained elevated, and normal vascular function was not restored (Lentz et al., 1997).

Folic acid requirements have been studied in a number of primate species, but the conclusions have not been consistent, because different measures were used as end points in assessing folic acid status. Findings from these studies are summarized in Table 7-5. The minimal folic acid requirement for growing rhesus monkeys has been estimated to be 30-60 $\mu g \cdot BW_{kg}^{-1} \cdot d^{-1}$ (Cooperman et al., 1946; Day and Trotter, 1947, 1948). The requirement for squirrel monkeys for weight maintenance, based on regression analysis, was estimated to be 28 $\mu g \cdot BW_{kg}^{-1} \cdot d^{-1}$. That was furnished by folic acid at about 0.3 $mg \cdot kg^{-1}$ of air-dry diet. However, the data suggest that 0.55 $mg \cdot kg^{-1}$ of air-dry diet was needed to ensure maximal growth. To maintain normal hematologic measures and cytologic features in bone marrow, the requirement was more than 75 $\mu g \cdot BW_{kg}^{-1} \cdot d^{-1}$, which was furnished by folic acid at 0.84 $mg \cdot kg^{-1}$ of air-dry diet (Rasmussen et al., 1979). A higher dietary concentration was required to support reproduction in squirrel monkeys. Rasmussen et al. (1979) and Rasmussen (1980) reported that a stock diet containing folic acid at 1.4 $mg \cdot kg^{-1}$ of air-dry diet did not support optimal reproduction and was improved by supplementation with crystalline folic acid; this concentration was equivalent to folic acid at 3.0 $mg \cdot kg^{-1}$ of air-dry diet. Biologic availability of folic acid in natural ingredients is poorly understood, so these authors suggested a total folic acid requirement of 450 $\mu g \cdot BW_{kg}^{-1} \cdot d^{-1}$, on the basis of 25% availability of food forms. Capuchin monkeys appear to have a folic acid requirement for growth and normal hematologic status of 45-75 $\mu g \cdot BW_{kg}^{-1} \cdot d^{-1}$; this requirement is similar to that of squirrel monkeys and could be met by providing folic acid at 0.84 $mg \cdot kg^{-1}$ of air-dry diet (Rasmussen et al., 1980).

The folic acid requirement of rhesus monkeys has been estimated to be 1.5 $mg \cdot kg^{-1}$ of dietary DM, on the basis of the data discussed above. The folic acid requirement of squirrel monkeys and capuchin monkeys is estimated to be 1.5 $mg \cdot kg^{-1}$ of dietary DM for growth and 3.3 $mg \cdot kg^{-1}$ dietary DM for reproduction. Data are insufficient for setting quantitative requirements of other species. The above requirement estimates take no account of the reduced biologic availability of folic acid in natural diets (Institute of Medicine, 1998). If all dietary folic acid is from natural ingredients, it is suggested that the requirements be increased to 2.55 and 5.61 $mg \cdot kg^{-1}$ dietary DM for growth and reproduction, respectively.

Vitamin B_{12}

Vitamin B_{12}, also known as cobalamin, contains cobalt. The two active cofactor forms are adenosylcobalamin and methylcobalamin. The two mammalian enzymes for which vitamin B_{12} is a coenzyme are methylmalonyl-CoA mutase and methionine synthase. The vitamin is part of a metabolic enzyme system that removes the methyl group from folacin, regenerating that vitamin. Vitamin B_{12} also is involved in the formation of methionine from homocysteine and in nucleic acid metabolism. It is found only in animal products and microorganisms. Vegetables and grains contain no vitamin B_{12} (Herbert, 1996; Weir and Scott, 1999). Microorganisms in the rumen synthesize vitamin B_{12} if the cobalt supply is adequate. Thus, ruminants have a nutritional requirement for cobalt but not for vitamin B_{12} itself. It is

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TABLE 7-5 Estimates of Folacin Requirement

Species	Age	Body Weight	Daily Air-Dry Diet Consumption	Type of Diet	Folacin Concentrations Studied	Criteria	Estimated Requirement	Reference
Macaca mulatta	Young, immature	2-3 kg	About 88 g for 2.0 to 2.5 kg monkeys	Casein, rice, wheat, mineral mix, vitamin mix	30-150 $\mu g \cdot d^{-1}$	Prevent anemia and leukopenia	60-100 $\mu g \cdot d^{-1}$	Day and Totter, 1947
Macaca mulatta	Young, immature	2.1-2.9 kg	About 88 g	Casein, rice, wheat, mineral mix, vitamin mix	N/A	Additional unpublished data indicated 100 μg daily dose required. Basal diet furnished 19 $\mu g \cdot d^{-1}$ (Day and Totter, 1947).	119 $\mu g \cdot d^{-1}$	Day and Totter, 1948
Saimiri sciureus	12-38 months	440-710 g	Not specified	Purified	0-0.84 $mg \cdot kg^{-1}$ air-dry diet.	Growth and normal hematologic status	75 $\mu g \cdot BW_{kg}^{-1} \cdot d^{-1}$ furnished by 0.84 $mg \cdot kg^{-1}$ of air-dry diet. Liver folic acid concentrations low compared with other colony animals.	Rasmussen et al., 1979
Saimiri sciureus	Breeding adults	665 g	Not specified	Natural ingredients	1.43 $mg \cdot kg^{-1}$ air-dry diet compared with supplementation with 80 $\mu g \cdot d^{-1}$ 5 $days \cdot week^{-1}$	Hematologic status, folate status, maternal weight gain during pregnancy, infant birth weight	3.0 $mg \cdot kg^{-1}$ of air dry matter	Rasmussen et al., 1980, Rasmusen, 1979
Cebus albifrons	3 years	1,570-2,170 g		Purified	0-1.05 $mg \cdot kg^{-1}$ of air-dry diet	Growth and normal hematologic status	45-75 $\mu g \cdot kg^{-1}$	Rasmussen et al., 1992

not known how nonhuman primates, consuming only plant material, obtain this vitamin, but it is possible that vitamin B_{12} is synthesized by microorganisms in the gastrointestinal tract (Uphill et al., 1977). Primates that practice coprophagy may obtain vitamin B_{12} from ingested feces (Oxnard, 1989). Little is known about the biologic availability of vitamin B_{12} in natural food ingredients (Baker, 1995). Supplemental vitamin B_{12} is usually added to animal feeds as cyanocobalamin.

The signs of vitamin B_{12} deficiency in humans are megaloblastic anemia and progressive demyelination and neuropathy (Herbert, 1996). A frank deficiency of vitamin B_{12} was produced under controlled conditions in rhesus monkeys *(Macaca mulatta)* by feeding a purified diet containing soy protein rather than casein to avoid potential contamination by vitamin B_{12} in the latter. During the first 12-18 months, serum concentrations of B_{12} dropped to 5-10% of initial values. Liver vitamin B_{12} concentrations were less than 5% of those in supplemented animals. Methlymalonic acid concentrations in the urine, a biochemical indicator of deficiency, increased in deficient animals but not in supplemented controls. In spite of the apparent depletion of vitamin B_{12} stores, no other manifestations of deficiency were seen (Kark et al., 1974). The studies were then extended. Monkeys fed the deficient diet for a total of 33-45 months exhibited additional deficiency signs, including visual impairment that gradually progressed to blindness, spastic paralysis of the hind limbs and tail, general weakness, apathy, and death. At necropsy, degeneration of nervous tissue was evident, with eventual destruction of the myelin sheath and loss of axons (Agamanolis et al., 1976, 1978; Chester et al., 1980). The degeneration of central nervous tissue was similar to "subacute combined degeneration," one of the clinical diseases seen in human vitamin B_{12} deficiency. Even in the most severe cases of vitamin B_{12} deficiency, no signs of anemia or any other blood disorders were observed.

Chronic deficiency of vitamin B_{12} in nonhuman primates under somewhat less controlled conditions has also been described. Blood concentrations of vitamin B_{12} in newly

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captured rhesus monkeys (*Macaca mulatta*), patas monkeys (*Erythrocebus patas*), baboons (*Papio anubis*), and owl monkeys (*Aotus trivirgatus*) decreased over time in captivity. During captivity, the primates were fed a vegetarian stock diet consisting of potatoes, bread, carrots, root vegetables, and green vegetables supplemented with ascorbic acid and halibut liver oil (Oxnard, 1964). A condition called "cage paralysis" in captive monkeys is similar to "subacute degeneration" of the spinal cord in humans and might be due to vitamin B_{12} deficiency. Animals with cage paralysis had lowered serum vitamin B_{12} concentrations, degeneration of the spinal cord, and patchy demyelination of peripheral nerves (Oxnard and Smith, 1966; Torres et al., 1971). Visual impairment with histologic changes in the visual pathway also were described (Hind, 1970).

Manifestations of vitamin B_{12} deficiency seem to be similar in rhesus and patas monkeys (Oxnard et al., 1970; Torres et al., 1971; Hind, 1970). In controlled deficiency studies in baboons *(Papio cynocephalus)*, serum and liver vitamin B_{12} decreased to very low concentrations, and urinary excretion of methylmalonic acid increased after a loading dose of valine. Growth of the deficient animals decreased in the second year. No frank deficiency signs were seen, perhaps because the study was only 24 months long (Siddons, 1974b; Verjee et al., 1975). Siddons and Jacob (1975) found that vitamin B_{12} concentrations in baboon tissues were highest in the liver, followed by the pituitary, kidney, heart, spleen, and pancreas. The main site of vitamin B_{12} absorption appeared to be the distal half of the small intestine. Satisfactory body stores were maintained by dietary intakes of 1 to 2 μg per day. Because gastric intrinsic factor is considered important for absorption of vitamin B_{12}, cobalamin absorption was measured in normal baboons and after total gastrectomy (Green et al., 1982). Cobalamin absorption was diminished but not completely abolished by gastrectomy. Provision of intrinsic factor enhanced absorption of orally administered cyanocobalamin, but physiologically significant amounts of cobalamin were still absorbed in its absence. Evidence also was obtained that the form of cobalamin excreted in the bile was more readily absorbed than oral cyanocobalamin, or bile itself may have enhanced cobalamin absorption. The absorption of cobalamin in bile was enhanced further by provision of gastric intrinsic factor, and these studies suggest that the enterohepatic circulation of cobalamin may be an important vitamin B_{12} conservation measure.

Kark et al. (1974) injected 20 μg of vitamin B_{12} every 14 days into control animals that weighed about 4.4 kg at the beginning of the study but eventually weighed about 10 kg. All measures of vitamin B_{12} status were normal. Siddon (1974b), working with baboons fed purified diets, supplemented control animals with vitamin B_{12} at 1 $\mu g \cdot d^{-1}$ for 9 months and 2 $\mu g \cdot d^{-1}$ for the next 15 months. The 2-μg dosage promoted a slightly higher body weight gain and a more satisfactory serum vitamin B_{12} concentration. The baboons weighed about 7.5 kg at the beginning of the study and about 12.3 kg at the beginning of the second year. Wilson and Pitney (1955) found that rhesus monkeys required more than 2 μg but less than 10 μg daily to maintain serum concentrations of vitamin B_{12}. The weights of the animals were not given.

The requirement of nonhuman primates for vitamin B_{12} has been estimated to be 11 $\mu g \cdot kg^{-1}$ of dietary DM; this is adequate to prevent deficiency signs and should provide a reasonably normal serum concentration.

Vitamin C

Vitamin C, also known as ascorbic acid or ascorbate, is required as a cofactor in numerous enzymatic reactions. Some of them concern the hydroxylation of proline or lysine, steps in the formation of collagen. Other metabolic reactions involving ascorbic acid are carnitine biosynthesis, catecholamine synthesis, peptide amidation, and tyrosine metabolism (Levine et al., 1996; Jacob, 1999). Vitamin C enhances the absorption of nonheme iron and decreases copper absorption (Moser and Bendich, 1991). It is added to primate diets in the form of ascorbic acid or L-ascorbyl-2-polyphosphate. L-ascorbyl-2-polyphosphate is a form of ascorbic acid that is less susceptible to oxidation and yet is biologically available to nonhuman primates. Presumably, the phosphate ester is hydrolyzed by intestinal phosphatase before absorption (Machlin et al., 1979). Another form, L-ascorbyl-2-sulfate, although resistant to oxidation and used in fish diets, has no vitamin C activity in primates (Machlin et al., 1976; Kotze and Menne, 1978).

Many mammals have the ability to synthesize ascorbic acid from glucose, but most primates, including humans, lack gulonolactone oxidase, the enzyme required for ascorbic acid synthesis. Many, perhaps most, prosimians possess this enzyme and presumably do not require a dietary source of vitamin C. Fifteen species of prosimians—including sifakas (*Propithecus verreauxi*), pottos (*Perodicticus potto*), and a number of species of lemurs, bushbabies, and lorises—have substantial liver concentrations of gulonolactone oxidase; these species might be able to synthesize ascorbic acid (Elliot et al., 1966; Nakajima et al., 1969; Pollock and Mullen, 1987). However, the enzyme is not found in the liver of western tarsiers (*Tarsius bancanus*), so perhaps prosimians are not all alike in their ability to synthesize this vitamin (Pullock and Mullin, 1987). Confirmatory studies in which diets devoid of vitamin C have been fed to prosimians for extended periods have not been conducted. The ability to synthesize vitamin C is clearly lacking in all other higher primates that have been studied to date.

Effects of vitamin C deficiency in the macaque species include weakness, lethargy, anorexia, weight loss, and mus-

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cle and joint pain. As the deficiency progresses, other signs appear, including gingival hemorrhage, loose teeth, subperiosteal hemorrhage, normocytic anemia, reduced serum iron concentrations, leukopenia, joint soreness, epiphyseal fractures with loss of bone substance, and exophthalmos (Tomlinson, 1942; Shaw et al., 1945; Greenberg and Rinehart, 1954; Banerjee and Bal, 1959a, 1959b; Ratterree et al., 1990; Eisele et al., 1992; Line et al., 1992). The signs of vitamin C deficiency are collectively called "scurvy," and deficient animals are called "scorbutic." Scorbutic rhesus monkeys excrete increased amounts of *p*-hydroxyphenyl compounds and keto acids in the urine when given test loads of tyrosine or phenylalanine, indicating abnormalities in tyrosine metabolism (Salmon and May, 1950; Rohatgi et al., 1958). Scorbutic animals have increased blood concentrations of glycoproteins and mucoproteins (Bandyopadhyay and Banerjee, 1964). Blood concentrations of nonprotein nitrogen and creatinine also are increased, and urine contains increased concentrations of nonprotein nitrogen and creatine (Rohatgi et al., 1958).

Gingival bleeding and fibrous gingival hyperplasia were reported in African green monkeys (*Cercopithecus aethiops*) deficient in vitamin C (De Klerk et al., 1973). Hydroxyproline concentrations were decreased in the gingiva, and synthesis of hydroxproline almost stopped in deficient animals; that suggests the lesions were caused by an inability to synthesize normal collagen (Ostergaard and Loe, 1975).

Squirrel monkeys (*Saimiri sciureus*) fed a vitamin C-deficient diet developed a characteristic subperiosteal hematoma, which progressed to a large swelling over the parietal area of the head (a cephalhematoma). In animals that were given ascorbic acid and recovered, the skull calcified, and this resulted in cranial hyperostosis. Cephalhematomas seem to be the primary diagnostic feature of vitamin C deficiency in squirrel monkeys (Lehner et al., 1968; Blackwell et al., 1974; Demary et al., 1978; Kessler et al., 1980).

Cephalhematomas are also seen in vitamin C deficiency in capuchin monkeys (*Cebus apella*) (Borda et al., 1996). However, capuchin monkeys also can exhibit all the traditional signs of scurvy, including weakness, joint tenderness, and extensive hemorrhages of the head, arms, and legs. Oral lesions develop, including necrosis of the gums, destruction of alveolar bone, and sloughing of the teeth (Shaw, 1949).

The common marmoset (*Callithrix jacchus*) has been shown to require a dietary source of vitamin C. Spontaneous physical mobility was decreased in deficient animals, and feed intake was reduced. Mean red-cell volume, packed red-cell volume, and red-cell counts decreased by about 10% overall, but hemoglobin concentration increased slightly. Vitamin C-deficient marmosets were generally free of clinical signs for 10 weeks, then suddenly became seriously ill, and many died within a few days despite therapeutic treatment with ascorbic acid. The disease was prevented by dietary vitamin C (Flurer et al., 1987). Extensive hemorrhages and loss of density about the periodontal ligament were seen, but the type of gingivitis seen in the rhesus monkey was not a prominent feature in the common marmoset (Driezen et al., 1969).

The white-lipped tamarin (*Saguinus fuscicollis*) and the common marmoset (*Callithrix jacchus*) appear to differ in their metabolism of vitamin C. When fed a diet ostensibly containing ascorbic acid at 2,000 $mg \cdot kg^{-1}$, the serum ascorbate concentration of the tamarins was about one-fifth that of the common marmosets (Flurer and Zucker, 1987). Stress appeared to increase the rate of ascorbic acid metabolism in both marmosets and tamarins, and there is some evidence that the difference in blood ascorbate concentrations was due to differences in susceptibility to stress between the two species (Flurer et al., 1990). It should be noted that the concentration of ascorbic acid in the diet at the time of feeding was not determined, and the stated concentration of 2,000 $mg \cdot kg^{-1}$ was based on the amount of vitamin C added before pelleting (Flurer and Schweigert, 1990).

There are wide ranges in the estimated ascorbic acid requirements of nonhuman primates. Table 7-6 summarizes the studies in which requirements were estimated. Day (1944) estimated that rhesus monkeys weighing less than 4 kg required 2.0 mg or less per day to prevent signs of scurvy; this estimate was based on calculation of vitamin C intakes from a number of published studies and was based primarily on the amount of orange juice required to prevent scurvy. Solv'ena et al. (1966) reported that a dose of 4 mg of vitamin C per animal per day protected monkeys weighing up to 4.3 kg from scurvy, but it did not prevent a drop in vitamin C concentrations in leukocytes and whole blood. Blood ascorbate is thought to reflect recent intake of ascorbic acid, whereas leukocyte ascorbate is a measure of the body's reserve (Moser and Bendich, 1991; Turnbull et al., 1980). Machlin et al. (1976) administered vitamin C at 5 $mg \cdot BW_{kg}^{-1} \cdot d^{-1}$ to rhesus monkeys and observed a slow decline of blood ascorbate from 1.3 $mg \cdot dl^{-1}$ to 0.3-0.4 $mg \cdot dl^{-1}$. Increasing the ascorbic acid intake to 10 $mg \cdot BW_{kg}^{-1} \cdot d^{-1}$ stopped the decline and prevented all signs of scurvy. Blood ascorbate levels fell to 0.3-0.4 $mg \cdot dl^{-1}$ in animals fed a natural diet furnishing ascorbic acid at less than 1.0 $mg \cdot BW_{kg}^{-1} \cdot d^{-1}$, to render them deficient, but deficiency signs were mild and appeared only sporadically. More persistent signs were observed only when the animals were placed on a more deficient liquid purified diet. Working with cynomolgus monkeys, Tillotson and O'Connor (1980) found that adult and young monkeys required ascorbic acid at 3 and 6 $mg \cdot BW_{kg}^{-1} \cdot d^{-1}$, respectively, to sustain blood concentrations of vitamin C. At that intake, leukocyte ascorbate concentrations, a measure of total body ascorbate, were minimal, indicating that the tissues were

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TABLE 7-6 Estimates of Ascorbic Acid Requirement

Species	Age	Body Weight	Daily Air-Dry Diet Consumption	Type of Diet	Ascorbic Acid Concentrations Studied	Criteria	Estimated Requirement	Reference
Macaca mulatta	Not specified	2.0-4.0 kg	Not specified	Not specified	0.25-3.0 $mg \cdot d^{-1}$	Protection from scurvy	$\leq 2\ mg \cdot d^{-1}$	Day, 1944; calculated from data of Harden and Zilva, 1920; Greenberg et al., 1936; Langston et al., 1938; Fraser, 1942
Macaca mulatta	Not specified	Up to 4.3 kg	Not specified	Not specified	4 $mg \cdot d^{-1}$ for 2 months	Protected against scurvy; leukocyte and whole-blood ascorbic acid decreased		Solov'eve et al., 1966
Macaca mulatta	Not specified	10 kg deficient animal	Purified diet	Not specified	50, 100 and 250 $mg \cdot d^{-1}$	Clinical scurvy, weight, and plasma ascorbate	50 $mg \cdot d^{-1}$ cured clinical scurvy; 250 $mg \cdot d^{-1}$ required for normal plasma ascorbate	Bucci et al., 1975; Baker et al., 1975
Macaca mulatta	Young	3.5-8.0 kg	Not specified	Auto-claved natural diet, purified liquid diet	0, 5, and 10 $mg \cdot BW_{kg}^{-1} \cdot d^{-1}$	Prevent blood ascorbic acid decrease	10 $mg \cdot BW_{kg}^{-1} \cdot d^{-1}$; blood ascorbate decreased with 5 $mg \cdot BW_{kg}^{-1} \cdot d^{-1}$, but this level prevented deficiency signs	Machlin et al., 1976
Macaca fascicularis	Young (2½-3 yr) and adult (at least 7 yr)	3.8-3.9 kg and 4.2-6.9 kg	Not specified	Liquid purified diet	0-6 $mg \cdot BW_{kg}^{-1} \cdot d^{-1}$ of young, 0-3 $mg \cdot BW_{kg}^{-1} \cdot d^{-1}$ of adult	Plasma and whole blood ascorbic acid	6 $mg \cdot BW_{kg}^{-1} \cdot d^{-1}$ in young, 3 $mg \cdot BW_{kg}^{-1} \cdot d^{-1}$ in adult	Tillotson and O'Connor, 1980
Macaca fascicularis	4-5 yr.	3.0 kg deficient animals	90-110 g	Purified diet	130 $mg \cdot kg^{-1}$ of diet followed by three daily injections of 50 mg of ascorbate	Periodontal health, weight loss, whole-blood ascorbate	130 $mg \cdot kg^{-1}$ of diet prevented deficiency signs; injections needed to reverse weight loss; whole-blood ascorbate remained low	Alvares et al., 1981
Cercopithecus aethiops	Not specified	1.5-6.8 kg	Not specified	Not specified, but diet included apples and bananas	10, 20, and 30 $mg \cdot d^{-1}$ plus 7-30 mg of ascorbic acid from fruit	Serum ascorbate	27-50 $mg \cdot d^{-1}$; includes ascorbic acid from fruit	DeKlerk et al., 1973
Callithrix jacchus	3-5 yr	400 g	16 g	Natural ingredient diet	250, 500, 2,000, and 4,000 $mg \cdot kg^{-1}$ of diet	Serum ascorbic acid above kidney threshold	500 $mg \cdot kg^{-1}$ of diet or 20 $mg \cdot BW_{kg}^{-1} \cdot d^{-1}$ (2,000 $mg \cdot kg^{-1}$ diet produced near saturation of serum with ascorbate)	Flurer et al., 1987

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not saturated. Bucci et al. (1975) and Baker et al. (1975) studied the amounts of ascorbic acid required by 10-kg monkeys to reverse the deficiency; 50 $mg \cdot d^{-1}$ (equivalent to 5 $mg \cdot BW_{kg}^{-1} \cdot d^{-1}$) were sufficient to reverse the deficiency signs, but plasma ascorbate concentrations remained low. Plasma ascorbate concentrations were increased by ascorbic acid at 250 $mg \cdot d^{-1}$ (equivalent to 25 $mg \cdot BW_{kg}^{-1} \cdot d^{-1}$). The above data suggest that the ascorbic acid requirement for macaques is about 1.0 $mg \cdot BW_{kg}^{-1} \cdot d^{-1}$ to prevent deficiency signs and between 5 and 10 $mg \cdot BW_{kg}^{-1} \cdot d^{-1}$ to maintain blood concentrations of ascorbic acid.

Alveres et al. (1981) studied the effect of subclinical ascorbate deficiency on periodontal health. They fed a recovery diet containing ascorbic acid at 130 $mg \cdot kg^{-1}$ to cynomolgus monkeys previously fed an ascorbate-free diet for 9 weeks. During the first 3 weeks of the recovery phase, the animals continued to lose weight and were given injections of 50 mg of ascorbic acid per day for 3 days. The animals then began to gain weight, and they weighed nearly the same as the control animals by the end of the study. After 16 weeks, the animals exhibited no clinical signs of ascorbic acid deficiency, but whole-blood ascorbate remained low compared with that in control animals fed a diet containing 2,000 $mg \cdot kg^{-1}$. The results suggested that ascorbic acid at 130 $mg \cdot kg^{-1}$ of diet was required to prevent deficiency signs but might have been insufficient to build body stores. Neither spontaneous gingivitis nor periodontitis was evident, but animals fed ascorbic acid at 130 $mg \cdot kg^{-1}$ of diet were more susceptible to experimentally induced plaque-associated periodontitis.

DeKlerk et al. (1973) found that fruit, estimated to furnish 7-30 mg of ascorbic acid per day, was not sufficient to prevent vitamin C deficiency or to maintain a satisfactory serum concentration of vitamin C in African green monkeys weighing 1.5-6.8 kg. However, animals receiving fruit and 20 mg of ascorbic acid per day were able to maintain satisfactory serum concentrations, and deficiency signs were alleviated. When stress was introduced, serum ascorbate decreased; this suggested that stressed animals have an increased vitamin C requirement.

It has been suggested that some callitrichids have higher requirements for vitamin C than some other primate species. On the basis of the concentration of ascorbic acid needed to maintain blood ascorbate above the kidney threshold, Flurer et al. (1987) concluded that the common marmoset required ascorbic acid at 20 $mg \cdot BW_{kg}^{-1} \cdot d^{-1}$ or a dietary level of 500 $mg \cdot kg^{-1}$. That concentration ensured that a small amount of ascorbic acid was excreted in the urine. Serum ascorbic acid concentrations were much higher in marmosets fed 2,000 $mg \cdot kg^{-1}$ of diet.

A dietary level of ascorbic acid at 55-110 $mg \cdot kg^{-1}$ of DM has appeared to prevent signs of deficiency in all species except possibly some marmosets and tamarins. A concentration of 275 $mg \cdot kg^{-1}$ of dietary DM might be required to maintain "normal" blood concentrations of ascorbic acid in captive primates, although few blood ascorbate concentrations in free-ranging primates have been reported. Some tamarins and marmosets appear to have higher requirements. Stressed animals have lower blood ascorbic acid concentrations than unstressed animals. That has been observed in rhesus monkeys (Baker et al., 1975), African green monkeys (DeKlerk et al., 1973), and tamarins (Flurer et al., 1990). It is conceivable that stressed animals need more vitamin C. As much dietary ascorbic acid as 560 $mg \cdot kg^{-1}$ of DM may be required for small amounts of urinary ascorbate excretion.

It should be noted that few dietary studies with nonhuman primates used a stable form of vitamin C, such as L-ascorbyl-2-polyphosphate. Because of the susceptibility of crystalline ascorbic acid to oxidation, the amounts of vitamin C actually consumed in studies of vitamin C requirements might have been less than expected. As a consequence, estimated vitamin C requirements might be exaggerated. There is no question that crystalline ascorbic acid can be lost from the diet during preparation, storage, or feeding. With respect to the latter, ascorbic acid loss also occurs as a consequence of soaking the feed to render it more palatable.

Few analyses of natural foods consumed by nonhuman primates have been conducted, and it is not rational to conclude that dietary vitamin C requirements greatly exceed the amounts available in the wild. However, a wild fruit (*Terminalia ferdinandiana*) was found in Australia that was said to have fifty times the vitamin C content of oranges (Brand et al., 1982). Whether this finding has relevance to the vitamin C needs of nonhuman primates has not been established.

One of the metabolites of excess dietary ascorbic acid is oxalic acid. Baboons fed a diet containing ascorbic acid at 25 $g \cdot kg^{-1}$ for 20 months had no histologic evidence of oxalate crystals in soft tissues or visible oxalate calculi in the kidneys or bladder (Du Bruyn et al., 1977). It appears that in the baboon, at least, high dietary concentrations of ascorbic acid are not pathogenic.

Choline

Choline is essential for the normal function of all cells and ensures the structural integrity and signaling functions of cell membranes (Zeisel, 1999). It directly affects neurotransmission via acetylcholine and is a major source of labile methyl groups for the synthesis of metabolites via transmethylation. In this latter role, the metabolism of choline, methionine, and methylfolate is closely interrelated. Most choline in the body is found in phospholipids, such as phosphotidylcholine and sphingomyelin. Because an endogenous pathway for synthesis of choline has been identified, choline has not been considered an essential

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nutrient for humans. However, signs of choline deficiency have been described when dietary choline concentrations are low and supplies of other methyl donors, such as methionine, are inadequate. Choline usually is added to the diet as choline chloride or choline bitartrate. Choline chloride is quite hydrophilic and often is added as a liquid containing 70% choline (Chan, 1991).

Many factors influence the choline requirement. Rats fed low-protein diets or diets containing suboptimal amounts of methionine require choline supplementation, whereas rats fed diets containing 0.8% methionine show no requirement for choline (National Research Council, 1995a).

The evidence of choline need in normal primate diets is not clear. Wilgram et al. (1958) fed a diet devoid of choline to both rhesus monkeys *(Macaca mulatta)* and capuchin monkeys (*Cebus* spp.) (four animals of each species) for over a year. The diet contained about 0.16% methionine and 18% fat. Although the protein concentration of the diet was unspecified, it appeared to be 13-14%. When the diet was supplemented with 0.3% choline chloride, weight gains were greater, and one female had a baby and successfully nursed it. After a year, liver biopsies were taken by laparotomy. Liver lipid concentrations were 12-22% in unsupplemented animals and 6-9% in animals that were choline-supplemented. Liver phospholipids were lower and liver cholesterol was higher in unsupplemented animals. Histologic examination of the livers from animals fed the choline-free diet revealed lipid droplets throughout the liver, but no cirrhosis. The livers of the choline-supplemented animals were normal.

The production of fatty livers in rhesus monkeys fed a choline-free diet was confirmed, and one death from liver disease was described by Cueto et al. (1967). Patek et al. (1975) also observed cirrhosis of the liver in a rhesus monkey fed a low-protein, low-choline diet.

Studies with a low-choline diet were extended; diets were modified to contain less protein and 2% cholesterol (Wilgram, 1959; Gaisford and Zuidema, 1965; Ruebner et al., 1969; Rutherford et al., 1969). The diet was said to contain 5% protein, but the formulation indicates about 9% protein. In any event, it produced liver cirrhosis in capuchin and rhesus monkeys. It was suggested that the increased dietary cholesterol might have made the animals more susceptible to liver cirrhosis (Patek et al., 1975). Whether supplemental choline would prevent or reverse the cirrhosis seen with the low-choline, high-cholesterol diet was not tested.

In an attempt to produce choline deficiency in baboons (*Papio doguera*), a high-fat, low-protein diet that had been shown to produce severe choline deficiency in rats was fed (Hoffbauer and Zaki, 1965). The baboons developed mildly fatty livers after 2 months, but the degree of fat accumulation remained unchanged after 5 months. A control diet with added choline was not fed. The lesions were reversed when the animals were returned to a normal diet. The results suggest that the requirement of the adult baboon for choline, if there is one, is substantially lower than that of the rat. It should be noted that Lieber et al. (1994) were able to prevent fatty liver and fibrosis caused by ethanol ingestion when the diet of baboons was supplemented with phosphatidylcholine.

No studies have clearly established a dietary choline requirement for nonhuman primates independent of other dietary modifications. It does seem clear that a fatty liver, and occasionally cirrhosis, will result from feeding a low-protein, methionine-deficient, low-choline diet. The effect of supplemental methionine has not been investigated, but the fatty liver observed after feeding such a diet can be prevented by supplementation with 0.3% choline chloride (furnishing about 0.23% choline) (Wilgram et al., 1958). Kark et al. (1974) fed a semipurified diet containing 0.1% choline chloride (about 0.075% choline) without producing deficiency signs.

Carnitine

Carnitine is a required vitamin for some insects, but it is not generally recognized as an essential nutrient for mammals. Metabolically, carnitine functions in the transport of fatty acids into the mitochondria (Borum, 1991). There is no evidence that nonhuman primates require carnitine. Carnitine is found only in animal products, so presumably the control diets fed by Kark et al. (1974) and Agamanolis et al. (1976) to rhesus monkeys (*Macaca mulatta*) for 45 months contained no carnitine. The animals showed no signs of a deficiency disease, so it seems unlikely that there is a substantial carnitine requirement.

Inositol

Inositol has occasionally been considered a vitamin, primarily on the basis of early work that suggested it was a required nutrient for mice. Later research has shown that conventionally reared mice do not require dietary inositol although gnotobiotic or antibiotic-treated mice possibly do (National Research Council, 1995b).

An inositol requirement has not been demonstrated in nonhuman primates, but there has been no attempt to do so. It is not recognized as a required nutrient for humans (Cody, 1991). In obese, insulin-resistant rhesus monkeys (*Macaca mulatta*), dietary myo-inositol in pharmacologic doses ($1.65\ g \cdot BW_{kg}^{-1} \cdot d^{-1}$) produced a mild decrease in postprandial plasma glucose concentrations without increasing postprandial insulin concentrations (Ortemyer, 1996). However, that relatively small effect of such a large dose cannot be regarded as demonstrating a nutrional requirement.

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If there is an undemonstrated dietary requirement, it is likely that inositol is present in sufficient concentrations in diets formulated from natural ingredients. Inositol is usually not added to commercial diets, but myo-inositol has been added to semipurified diets at 0.1% (Kark et al., 1974; Ausman et al., 1985).

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8 Water

Water, sometimes overlooked as an essential nutrient, is critical for the health and well-being of all primates. It serves as a medium within which the chemical reactions of the body take place (Harris and Van Horn, 1992), and "life without water is impossible" (Widdowson, 1987). However, water is more than a passive solvent within which inorganic elements, gases, and organic compounds are dissolved or suspended. Water is involved in hydrolytic processes; transport of hormones, nutrients, and metabolites; lubrication of joints; transmission of light in the eyes and sound in the ears; and excretion of waste (Robinson, 1957). Water also gives form to the body and provides protective cushioning for the nervous system (Askew, 1996).

Water's role in thermoregulation is particularly vital. Water absorbs heat at the point of generation with little temperature rise and dissipates it throughout the fluid compartments of the body. Thus, damage to enzymes and structural proteins is minimized, and heat-bearing blood plasma can be routed to the skin, where heat is transferred to the environment through conduction, radiation, convection, and evaporation. Panting also dissipates heat, and body heat is transferred to the environment via the moisture carried out by each exhalation. The vaporization of one liter of water at 20°C constitutes the loss of 585 kcal of heat (Kleiber, 1975; Askew, 1996).

WATER CONTENT OF THE BODY

Of all the molecules in the animal body, water makes up about 99% (MacFarlane and Howard, 1972). That high molecular percentage is a consequence of the size of the water molecule—which is smaller than molecules of carbohydrate, protein, and fat—and water's high percentage of body mass. Of fat-free body mass of the adult animal, water is said to make up a relatively constant 68-72% (National Research Council, 1974). A study of the developmental body composition of squirrel monkeys (*Saimiri sciureus*) examined changes in water, fat, protein, and ash concentration in 51 animals from birth through the age of 156 weeks. Tissues analyzed at necropsy included the eviscerated carcass and fatty and connective tissue trimmings from the brain, thyroids, thymus, heart, lungs, liver, pancreas, spleen, kidneys, gut, and reproductive organs that were removed and not included in the analysis. It was found that fat in the carcass plus trimmings was low at birth (2.7%); on a fat-free basis, water in the carcass plus trimmings was 76.4% in the newborn and declined to 68.9% in the adult (Russo et al., 1980). When expressed as a percentage of whole-body mass, water concentrations in a wide array of species vary inversely with body fat, from 40% in the obese adult to 85% in the neonate (Robbins, 1993).

Percentage of body water differs among humans according to sex, age, and reproductive stage (Askew, 1996). Because women tend to have less muscle and more adipose tissue than men and adipose tissue has about 10% water compared with about 76% water in muscle, men usually have a higher percentage of body water (about 60%) than women (about 50-55%). A human infant has about 77% body water, whereas an elderly person can have as little as 45%. Pregnancy usually increases blood volume and alters relative water distribution between intracellular and extracellular compartments (Southgate, 1987).

About 62% of body water in humans is in cells, including erythrocytes (Askew, 1996). If the roughly 7% of total body water in joints, eyeballs, and spinal column is included in a transcellular compartment, the remaining extracellular compartment accounts for about 31% of total body water. About 75% of the extracellular fraction is found in the interstitial space and about 25% in blood plasma. Thus, blood plasma accounts for about 7% of total body water. Although it is considered outside the body, substantial water can be found in the gastrointestinal tract. In animals with foregut fermentation, such as the dairy cow, gut water may constitute 15-35% of live body mass, with lower values in late gestation and lactation (National Research Council, 2000). Bauchop and Martucci (1968) reported that the

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contents of the foregut of a langur accounted for 12% of live body mass, and foregut contents were 85% water.

The percentage of total body water (by tritiated-water dilution) in adult chimpanzees has been found to average 67%, slightly higher than the average in adult humans because of the lower body fat in the chimpanzees studied (9%) than in the adult humans (20%) with which they were compared (Angus, 1971). On the basis of tritiated-water dilution, comparable mean concentrations of body water (64%) were found in adult female cynomolgus (*Macaca fascicularis*) and rhesus (*M. mulatta*) macaques (Azar and Shaw, 1975).

In 13 normal male pigtailed macaques (*Macaca nemestrina*) with a mean age of 70 months, body water by tritium dilution was 72.6%. In 12 normal female pigtailed macaques with a mean age of 90 months, body water was 70.1%. In five obese female pigtailed macaques with a mean age of 130 months, body water was 52.5% (Walike et al., 1977).

Nonhuman primates in captivity can differ dramatically in percentage of body water and corresponding percentage of body fat—hence their degree of obesity—just as humans do. In a study of 23 adult baboons (*Papio* sp.), fat in 10 males was 2.4-17.6% and in 13 females 3.7-33.0% of body mass (Lewis et al., 1986). In another study, fat in 24 adult male rhesus macaques was 5.9-49.0% of body mass (Jen et al., 1985). Kemnitz and Francken (1986) also found a wide range of adiposity in adult male rhesus macaques. Body fat ranged from 30-61% of body weight and was located most prominently in the abdomen. Glucose tolerance was normal, but blood insulin concentrations and insulin response to glucose loading increased with increasing adiposity. The authors concluded that obese monkeys, like obese humans, are at risk for diabetes mellitus and its complications.

With antipyrine dilution, total body water was estimated in 16 adult nonpregnant female baboons (*Papio cynocephalus*) 4-14 years old and weighing 11.0-13.9 kg (Brans et al., 1985). Although mean total body water was reported to be 798 $L \cdot kg^{-1}$ of body mass, it is assumed that the authors meant 798 $ml \cdot kg^{-1}$. Thus, total body water would have been about 80% of body mass. That value is higher than expected and higher than mean values (770 and 769 $ml \cdot BW_{kg}^{-1}$) reported for newborn (day 1) and 29-day-old baboons, again on the basis of the antipyrine dilution technique (Brans et al., 1986b). In a study of the effects of extracorporeal membrane oxygenation (as used in intracardiac surgery) on body water content and distribution, total body water, extracellular water, and plasma volume were measured simultaneously with antipyrine, bromide, and T-1824 (Evans blue) dilution in neonate baboons 17-28 days old and weighing 820-1,478 g (Brans et al., 1986a). Measurements were made before and after 8 hours of extracorporeal membrane oxygenation. Estimates ($\pm$ SE) of antipyrine space were 843 $\pm$ 37.4 and 787 $\pm$ 80.5 $ml \cdot BW_{kg}^{-1}$, respectively, and were not significantly different. Estimates of corrected bromide space were 361 $\pm$ 47.6 and 409 $\pm$ 47.6 $ml \cdot BW_{kg}^{-1}$ respectively, and of plasma volume 53 $\pm$ 8.2 and 58 $\pm$ 19.2 $ml \cdot BW_{kg}^{-1}$; and they were also not significantly different. Calculated mean volumes of intracellular water, interstitial water, and blood were 482 and 379, 308 and 350, and 84 and 95 $ml \cdot BW_{kg}^{-1}$, respectively. When estimated with antipyrine dilution on the day of birth in newborn baboons with mean weights of 923 and 624 g, total body water volumes were 773 and 874 $ml \cdot BW_{kg}^{-1}$ (Brans et al., 1986c). Body water content and distribution were estimated before, during, and after 32 pregnancies in baboons weighing 10-22 kg (Brans et al., 1990b). It was concluded that mean plasma volume and blood volume were higher during pregnancy than before or after. In a later study comparing $H_2{}^{18}O$ dilution with antipyrine dilution in neonatal baboons, Brans et al. (1990a) concluded that antipyrine dilution is of doubtful reliability for estimating total body water.

Lewis et al. (1986) measured the total body water, triacylglycerol mass, and lean body mass of 13 female and 10 male 5-year-old baboons (*Papio* sp.) at necropsy. Total body water was calculated as the wet weight of the baboon (body weight minus contents of the gut and bladder) minus the dry weight of the tissues and organs. Male baboons were heavier than females (20.4 kg vs 15.9 kg) and had less triacylglycerol (6.1% vs 16.9%), and more total body water (67.4% vs 64.8%) per unit of body mass.

Because of concern expressed by Sheng and Huggins (1979) that tritiated-water dilution overestimates total body water by 4-15% compared with determination with desiccation, a nuclear magnetic resonance (NMR) method was tested by Lewis et al. (1986a) on 21 18-week-old baboons (*Papio* sp.). Mean total body water concentration was 71% with NMR and 70% with desiccation. When another 19 young baboons were studied, estimates of total body water were higher in 16 and lower in three when determined with tritiated-water dilution than with desiccation. In a study of 10 adult male rhesus monkeys (*Macaca mulatta*), weighing 6.79-12.35 kg, Baer et al. (2000) found that body-water space with deuterium oxide dilution was overestimated by 10% as compared with direct determination by desiccation. Hydration of lean body mass was 71.2 $\pm$ 0.52% (mean $\pm$ SE) with a range of 67.9-77.3%.

Chwals et al. (1992) studied the utility of magnetic resonance imaging (MRI) for determination of body water with eight *Macaca fascicularis*. The two measures had a correlation of 0.81 ($P < 0.02$), and mean total body water determined with MRI was 72.1% of body mass vs 73.8% of body mass with tritiated-water dilution.

The intracellular and extracellular distribution of water and concentrations of lipid and the electrolytes sodium, potassium, and chloride in 14 tissues of six normal male

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rhesus macaques were determined at necropsy (Liu and Griffin, 1978). The tissues examined included the cerebral cortex, cerebellum, thalamus and hypothalamus, medulla oblongata, spinal cord, heart (left ventricle), lung, liver, renal cortex, renal outer medulla, renal inner medulla, diaphragm, skeletal muscle (gastrocnemius), and hair-shaved skin. Mean total water concentrations in those tissues (on a fat-free, wet basis) ranged from 75.8% in skin to 86.8% in the medulla oblongata. The mean concentration of intracellular water as a percentage of total tissue water was lowest in the skin (33.2%) and highest in the thalamus and hypothalamus (82.0%). Pivarnik and Palmer (1994) have reported similar data on humans.

Alterations in body-fluid distribution have been reported in rhesus macaques inoculated with *Rickettsia rickettsii*, the agent that causes Rocky Mountain spotted fever (Liu et al., 1978). There was no change in total body water concentration, but there was a shift of intracellular water to the extracellular space. The shift had little effect on the amount of interstitial fluid but mainly increased plasma volume. However, there were selective alterations in concentrations of water and electrolytes in several tissues with intracellular overhydration of the medulla oblongata. It was suggested that the localized swelling has the potential to depress the cardiovascular and respiratory centers and to lead to circulatory shock and respiratory arrest.

Effects of Activity Restriction

Total body water concentration, extracellular and intracellular distribution, and water intake and excretion were affected by prolonged restriction of the motor activity of rhesus macaques (Zorbas et al., 1997). Over a 90-day period of activity restriction, changes in fluid metabolism could be divided into three phases. Overall, mean total body water concentrations declined from 62.7% to 50.1% of body mass. The decline was associated with a decrease in water intake, an increase in urine excretion, and increased hematocrit and specific plasma resistance.

Effects of Cold

Acclimation to cold results in adjustments of body-fluid distribution (Oddershede and Elizondo, 1980a, 1982). Exposure of six adult male non-cold-acclimated rhesus macaques to a cold environment (6°C, 85% relative humidity) for 35 days resulted in a mean increase in total body water from 66.7% to 70.8% of body mass. During the pre-cold-exposure control period, intracellular, extracellular, and interstitial fluid volumes in relation to body mass were 47.2%, 19.5%, and 15.1%, respectively. Mean increases in these measures during cold exposure were 3.8%, 3.2%, and 1.0% of body mass.

Prosimians generally have a low basal metabolic rate, which makes it difficult for them to deal with a cool environment (Müller, 1983). The slow loris (*Nycticebus coucang*) has the lowest basal metabolic rate among normothermic primates reported so far, about 40% of the mass-specific mammalian standard (Müller, 1975, 1979; Whittow et al., 1977). Although mainly an inhabitant of tropical rain forests with relatively constant high temperatures, the slow loris has morphologic features of a cold-adapted homeotherm: thick fur, short nose, small ears, stumpy tail, and short, stout limbs. Those features and vascular bundles in the extremities that function as countercurrent heat exchangers (Müller, 1979) limit loss of heat, because of the insulation of fur, the minimum surface area per unit of mass, and redirection of fluids (and the heat they carry) to the body core. Thus, core temperatures can be sustained during moderate cold exposure, even with modest basal heat production.

The slender loris (*Loris tardigradus*) is found in tropical rainforests but also lives in deciduous forests that experience drought and heat seasonally. It has a long body, a long nose, large ears, very long, thin limbs, and a basal metabolic rate that is about 50% of the mass-specific mammalian standard. When exposed to cold, the slender loris diverts body fluids to maintain a high temperature only in a small body core; large parts of the body are allowed to cool. However, the lower limit of its thermoneutral zone was found to be only 32.5°C, and the slender loris was unable to increase heat production sufficiently to sustain vital functions at low temperatures (Müller et al., 1985). Other findings support the conclusion that this species is better adapted to high than to low temperatures—a circumstance that is consistent with its natural environment.

Effects of Heat and Water Deprivation

Heat acclimation of rhesus macaques from 24°C and 65% relative humidity to 35 days at 35°C and 30% relative humidity was characterized by a fluid shift from interstitial space to the cardiovascular system and the intracellular compartment. Water input via drinking increased from 95 to 118 $ml \cdot BW_{kg}^{-1} \cdot d^{-1}$, and total water input via drinking, metabolic water, and moisture in food increased from 120 to 140 $ml \cdot BW_{kg}^{-1} \cdot d^{-1}$. Total body water, determined by tritiated-water dilution, increased by 4.8% during heat exposure (Oddershede and Elizondo, 1980b).

Hamadryas baboons (*Papio hamadryas*) are found in desert regions of the Horn of Africa and southern Arabia. In contrast with nondesert species, these baboons were able to maintain normal activity after 2 days of water deprivation in a warm environment by conserving blood-plasma volume at the expense of losses from other fluid compartments (Zurovsky and Shkolnik, 1982). Withholding drinking water for 48 hours during midsummer (22-32°C, 70%

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relative humidity) induced dehydration. Total body water was determined with tritiated-water dilution, and plasma volume was determined with Evans blue dilution (before and after water deprivation). The procedure was repeated six or seven times in each of three animals over a 2-year period. After 2 days of water deprivation, 10% of body mass and 12.5% of body water, but only 4% of plasma volume, were lost. The ability to sustain plasma volume was related to an increase in plasma colloidal osmotic pressure through efficient retention of albumin and an increase in the rate of albumin synthesis (Zurovzky et al., 1984).

Adolescent male baboons (*Papio cynocephalus* and *P. anubis*) weighing 11.9-16.5 kg were subjected to water deprivation for 64-68 hours, and the effects of dehydration on blood and plasma volumes, plasma constituents, and weight were measured (Ryan and Proppe, 1990). In addition, the effect of interaction of increased environmental temperature (38-42°C vs 22-24°C) and dehydration on hindlimb blood flow was explored. Plasma osmolality and concentrations of blood hemoglobin and plasma sodium and total proteins were significantly increased by dehydration. Blood volume, plasma volume, and weight were significantly decreased. Dehydration attenuated the cutaneous vasodilatory response to heat stress in the hindlimb, and studies of intravenous fluid replacement suggested that the attenuation was associated with a local mechanism in the vascular smooth muscle cell that was triggered by interstitial-fluid volume depletion.

Crab-eating macaques (*Macaca fascicularis*) are found along the southeastern coast of the Asian continent and on Southeast Asia islands. On the Indonesian island of Bali, the species has adapted to a region of considerable rainfall (72-98 mm per month) and to a region with a dry season when there is no water in the rivers and monthly rainfall is only 7-12 mm. They were free-ranging monkeys, so it was possible to study shifts in body fluids in response to dehydration only by collecting single blood samples from each animal. Hematologic data on 85 crab-eating macaques in the two regions revealed that blood-plasma protein, creatinine, and sodium ion concentrations were increased in monkeys in the region with low water supply (Takenaka, 1986).

The morphology and behavior of the slow loris equips this species better for dealing with an occasional cool environment as opposed to a hot one. It has a thermal neutral zone between 24-33°C (Müller, 1975), and exposure to an environmental temperature above 35°C usually leads to a rapid rise in rectal temperature (Müller, 1979). Although respiration rate increased to 140 breaths·min^{-1} at an ambient temperature of 40°C, evaporative cooling at 35°C was sufficient only to dissipate about 50-60% of metabolic heat production (Müller, 1983). The potto (*Perodicticus potto*) exhibits similar limitations (Hildwein and Goffart, 1975). In contrast, the respiration rate of the slender loris at an environmental temperature of 35°C increased to 200-300 breaths·min^{-1}, and about 80% of metabolic heat production was dissipated by evaporation (Müller et al., 1985). When the water content of surrounding air (75% relative humidity) and ambient temperatures (35°C) were high, the efficiency of evaporative cooling was reduced. However, evaporative cooling was supported by a cardiovascular response that increased transport of body heat from the core to the surface. As a consequence, deep-rectal temperatures rose only slightly above ambient temperature, even after prolonged heat exposure.

WATER SOURCES

Water to meet requirements comes from three sources: free or liquid water, as in dew, rain, snow, terrestrial and arboreal pools, streams, and lakes; preformed water in food; and metabolic water from oxidation of organic compounds in body tissues.

Liquid-Water Intake

What it eats, ambient temperatures and humidity, activity, and other factors influence the amount of water that a primate drinks. Maintenance of body water balance is the ultimate homeostatic objective. Diets low in moisture or high in fiber, salt, sodium bicarbonate, or protein will increase water consumption (Harris and Van Horn, 1992). Increased air temperatures and aridity will increase water loss and the amount of water consumed for replacement. Some conditions can induce abnormal water intake. A deficiency of n-3 fatty acids in rhesus macques was shown to result in polydipsia, even though the kidneys retained their ability to concentrate urine and there was no evidence of diabetes insipidus (Reisbick et al, 1990, 1991).

Although water, consumed as such, is the major water source for humans in large areas of the world, much of the human water intake in the United States comes from consumption of beverages, such as soft drinks, juices, milk, tea, and coffee (Askew, 1996). Nonhuman primates in the wild drink from running and standing water sources, either by crouching and sipping, by dipping their hand in the water and drinking from their hand or fingers, or by using chewed leaves as sponges to soak up and direct water into the mouth (Angus, 1971). They also have been observed licking moist rocks and plants moist with dew or rain (Nishida, 1980). In a study of free-ranging New World monkeys, mantled howlers (*Alouatta palliata*) were never seen drinking from terrestrial water sources but rather drank from arboreal cisterns (such as depressions at junctures of tree limbs and trunk) during the wet season. During the dry season, when arboreal cisterns were empty, the howlers

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maintained their water balance by selecting a diet comprising largely succulent new leaves (Glander, 1978).

Quantitative data on liquid-water consumption are available for few species of nonhuman primates. Pace et al. (1964) reported that three adult pig-tailed macaques (*Macaca nemestrina*) fed a dry commercial diet consumed gross energy (GE) at 70 $kcal \cdot kg^{-1}$ of body weight and water at 1 $ml \cdot kcal^{-1}$ of GE. Kerr (1972) concluded that consumption of water at 1 $ml \cdot kcal^{-1}$ of GE was a reasonable estimate of liquid-water intake. Schroederus et al. (1999) measured baseline water intakes in adult rhesus monkeys of both sexes. Older monkeys (20-36 years) drank 380 ± 63 $ml \cdot d^{-1}$, significantly less ($P < 0.05$) than the 679 ± 92 $ml \cdot d^{-1}$ consumed by middle-aged (13-17 years) monkeys or the 750 ± 128 $ml \cdot d^{-1}$ consumed by young adults (7-9 years).

Patterns of eating and drinking were studied in five adult male rhesus macaques housed in individual cages and provided food and water ad libitum. Animal weights and ambient temperatures and relative humidity were not given, but the light:dark cycle was 12:12. Purina Monkey Chow 5040® providing metabolizable energy (ME) at an estimated 4 $kcal \cdot g^{-1}$ (air-dry) was fed. Mean daily food consumption was 126.8 g and mean daily liquid-water consumption was 440 ml. Thus, daily liquid-water consumption was 3.5 $ml \cdot g^{-1}$ of air-dry diet or 0.87 $ml \cdot kcal^{-1}$ of ME consumed (Natelson and Bonbright, Jr., 1978).

Six rhesus macaques were housed in individual cages at an ambient temperature of 24-29°C, a relative humidity of 75-80%, and a light:dark cycle of 12:12 (Zorbas et al., 1997). They were 3-4 years old and had a mean body weight of 5.58 kg. They had ad libitum access to a commercial dry diet and liquid water. Food intake was not reported, but mean water intake was 679 $ml \cdot d^{-1}$ or 122 $ml \cdot BW_{kg}^{-1} \cdot d^{-1}$.

Daily food and water intakes of 253 wild-origin cynomolgus macaques (*Macaca fascicularis*) kept in individual cages were determined (Suzuki et al., 1989). Mean (± SD) body weight of 61 males was 6.5 ± 1.3 kg and of 192 females 3.4 ± 0.9 kg. They were fed a dry commercial primate diet plus apples and oranges. Mean (± SD) drinking-water intake by males was 50 ± 33 $ml \cdot BW_{kg}^{-1} \cdot d^{-1}$ and by females 49 ± 48 $ml \cdot BW_{kg}^{-1} \cdot d^{-1}$. Mean (± SD) total water intake from drinking water and food by males was 76 ± 35 $ml \cdot BW_{kg}^{-1} \cdot d^{-1}$ and by females 100 ± 51 $ml \cdot BW_{kg}^{-1} \cdot d^{-1}$.

Preformed-Water Intake

Preformed-water concentration in ingested food varies greatly with the diet but accounts for about one-third of water intake by humans (Askew, 1996). Most foods contain some water, and water in the edible portions of cultivated fruits and vegetables generally makes up 80-95% of their mass (National Research Council, 1989; Holland et al., 1991). Preformed water in the foods of free-ranging nonhuman primates can be as little as about 2-3% of air-dried seeds in hot deserts or over 70% of the fresh weight of succulent plant parts in a tropical rainforest (Baranga, 1982; Calvert, 1985; Rogers et al., 1990; Barton et al., 1993; Robbins, 1993; Edwards, 1995).

Metabolic Water

The gross yield of metabolic water from oxidation of 100 g of carbohydrate, protein, and fat is about 60, 41, and 107 g, respectively (Askew, 1996). However, excretion of the urea produced during protein oxidation requires nearly all the metabolic water released. Thus, there is no net water yield from oxidation of protein. Metabolic water furnishes about 8-10% of the water needs of humans (Askew, 1996). If 100 g of a nonhuman-primate diet contained 16% digestible protein, 10% digestible fat, and 50% digestible carbohydrate, complete oxidation of these three fractions would have a net yield of about 40 ml of metabolic water, or about 1 ml per 8.8 kcal of ME.

Metabolic water is also generated during muscular activity through catabolism of stored glycogen and fat. However, the anaerobic metabolism of glucose to lactate (associated with intense effort) yields only one-third as much water as does complete glucose oxidation, and the metabolic-water contribution from either anaerobic or aerobic effort is still a small proportion of total body water (Askew, 1996).

WATER LOSS

Water is lost from the body mainly via the lungs, skin, intestine, and kidneys, although losses also occur via menstruation and lactation (Widdowson, 1987; Harris and Van Horn, 1992; Askew, 1996).

In the absence of sweating, about 44% of total water loss from the human body is insensible water vapor from the lungs or from diffusion through the skin (National Research Council, 1989). These insensible losses increase under conditions of high ambient temperature, high altitude, and low relative humidity. Perspiration increases human water loss further, but there is little information on the presence of sweat glands and sweating in nonhuman primates.

Water concentration of feces varies with diet but in healthy adult humans is about 70% (Askew, 1996). In the absence of sweating, water in the normal human stool makes up about 3-4% of total daily water loss; diarrhea can greatly increase this figure (National Research Council, 1989). Cotton-top tamarins (*Saguinus oedipus*) frequently exhibit colitis in a laboratory environment, and daily fecal output of tamarins with mild, moderate, or severe colitis was 6.0, 7.6, or 8.1 $g \cdot BW_{kg}^{-1}$, respectively. Water concentrations were 49.4% or 55.0% in the feces of tamarins with mild or moderate colitis (Stonebrook et al., 1996). Suzuki

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et al. (1989) reported that mean daily fecal outputs of captive cynomolgus macaques were 3.0 and 3.9 $g \cdot BW_{kg}^{-1}$ for males and females, respectively, but they did not report fecal moisture concentrations. Mean daily total water intakes (drinking water plus water in food) by males and females were 76 and 100 $g \cdot BW_{kg}^{-1}$, respectively. If these primates were in water balance, water intakes plus metabolic water would be equaled by water loss. Assuming fecal water concentrations of 50-70%, fecal water loss would be equivalent to 2-3% of total water intake. If it were possible to account for the contribution of metabolic water to water balance, fecal water loss presumably would be a still lower percentage of total water loss.

The majority of total water loss in nonsweating humans, about 53%, is lost as urine (National Research Council, 1989). Because the concentrating ability of the adult human kidney is limited to about 1,400 $mOsm \cdot L^{-1}$, the amount of waste that must be excreted by the kidneys dictates the minimal volume of water required for urine formation. Much of the waste comes from products of protein catabolism, such as urea, sulfates, phosphates, and other electrolytes. Several studies have found that rhesus macaques fed a dry commercial diet excreted urine at about 20-50 $ml \cdot BW_{kg}^{-1} \cdot d^{-1}$ (National Research Council, 1978). Male and female cynomolgus macaques fed a dry commercial diet plus apples and oranges excreted urine at 21 and 27 $ml \cdot BW_{kg}^{-1} \cdot d^{-1}$, respectively, or about 27% of the total water intake from drinking water and food (Suzuki et al., 1989). Common marmosets (*Callithrix jacchus*) were placed in metabolism cages for 24 hours without food but with ad libitum access to water. Mean water intakes during 161 observations were 11.7 ml, whereas mean urine volumes were 12.6 ml (Lunn, 1989).

In controlled laboratory studies with adult male lesser mouse lemurs (*Microcebus murinus*), it has been demonstrated that photoperiod and diurnal variations in activity can influence water loss (Perret et al., 1998). This lemur is a small, arboreal, nocturnal prosimian found near the south coast of Madagascar. Its winter environment is dry and up to 20°C cooler (considering both diurnal and seasonal differences), and more limited in resources than the rainy summer environment. Daylength at the winter solstice is 10 hours 50 minutes and at the summer solstice is 13 hours 20 minutes. As days shorten and preparation for winter begins, the animals fatten and decrease their locomotor activity, whereas reproduction occurs during the lengthening days of late spring and early summer. Lesser mouse lemurs were subjected in the laboratory to a constant temperature (24-26°C), 55% relative humidity, and short days (light:dark ratio, 8:16) for 14 weeks, followed by long days (L:D, 14:10) for 22 weeks. Initial mean ($\pm$ SEM) body mass was 97 $\pm$ 3 g; it increased to a maximum of 125 $\pm$ 4 g after exposure to short days. After exposure to long days, mean body mass declined to 77 $\pm$ 3 g. Total water loss declined during short-day exposure to 38 $\pm$ 0.3 $mg \cdot BW_g^{-1} \cdot day^{-1}$ after 3 months and increased during long-day exposure to 87 $\pm$ 7 $mg \cdot BW_g^{-1} \cdot day^{-1}$ after 2 months. When measured in a post absorptive state (no food or water during 24 hours), water in feces accounted for less than 0.5% of total water loss and water in urine about 37%, and the remainder was presumably evaporative water loss. Urine was voided only at the beginning of the nocturnal active period, and total water loss at night was always greater than during the daily sleeping period.

Dehydration is a common cause of fluid and electrolyte imbalance in elderly humans and, if not properly managed, can lead to central nervous system dysfunction, convulsions, coma, and death (Miller, 1987). It has been suggested that this susceptibility to dehydration resides in impaired regulation of thirst, impaired urine-concentrating ability, or both. The issue has been studied in monkeys by Schroederus et al. (1999). Although elderly rhesus macaques (20-36 years old) drank less during a baseline period than did younger macaques (7-17 years old), the elderly macaques responded to 24-hour water deprivation by eating less and concentrating their urine to the same degree as the younger macaques. During a postdeprivation compensation period, water intakes of elderly and younger macaques returned to predeprivation levels.

According to Harris and Van Horn (1992), animals can lose nearly all the fat and about half the protein of the body and still survive, but a loss of about one-tenth of total body water results in death. Even moderate restriction of water sources will generally diminish food consumption (National Research Council, 1981, 1986).

WATER QUALITY

Analyses of surface water and groundwater by geologic, agricultural, and public-health agencies have established the presence of variable concentrations of essential and nonessential mineral elements (National Research Council, 1974). In some cases, concentrations of essential minerals can be high enough to contribute substantially to meeting total nutrient needs (National Research Council, 1974, 1980). In others, mineral concentrations can be infinitesimal or excessive and potentially toxic. Because streams, lakes, and private wells are widely used by agricultural interests, these issues are of particular importance to farm families and their livestock. Water-quality guidelines for livestock and poultry were developed (National Research Council, 1974); they are commonly updated in publications in the National Research Council Nutrient Requirements series as they are revised.

In contrast with agricultural animals, captive nonhuman primates usually get their water from municipal water systems just as do most humans in the United States. Although

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the composition of water can vary among municipal systems, all such systems are required, at a minimum, to meet national primary drinking-water standards (National Primary Drinking Water Regulations [NPDWR]) established by the US Environmental Protection Agency (EPA). These primary standards protect drinking-water quality by setting limits on levels of specific contaminants that can adversely affect public health and that are known to occur or can be expected to occur in public water systems. The contaminants are divided into inorganic chemicals, organic chemicals, radionuclides, and microorganisms. EPA has included two levels in the NPDWR for each contaminant. The first is the Maximum Contaminant Level Goal (MCLG), defined as the maximal level of a contaminant in drinking water at which no known or expected adverse effect on human health would occur; MCLGs are nonenforceable public-health goals. The second is the Maximum Contaminant Level (MCL), defined as the maximal permissible level of a contaminant in water delivered to any user of a public water system; MCLs are enforceable standards. MCLGs are equal to or lower than MCLs, with margins of safety that ensure that slightly exceeding the MCL does not pose a substantial risk to public health.

EPA also has established secondary drinking-water standards (National Secondary Drinking Water Regulations) that are nonenforceable guidelines related to contaminants of drinking water that might cause cosmetic effects (such as skin or tooth discoloration) or aesthetic effects (such as taste, odor, or color). Although the EPA does not require compliance with these secondary regulations, some states comply.

It is not experimentally verified, but water-quality standards established for humans would probably be satisfactory for nonhuman primates. Detailed information on the EPA drinking-water standards for US public water systems can be obtained at http://www.epa.gov/safewater/mcl.html. Composition of the water from specific municipal water supplies can usually be obtained from public-works departments or state departments of health.

WATER REQUIREMENTS

Requirements for liquid-water intake are dictated by the need to balance total water intake and water loss when metabolic water and water from food are inadequate for that purpose. Thus, liquid-water requirements will vary with food composition, intake, and metabolism and with activity and the need to dissipate body heat. The efficiency of the latter process varies with environmental circumstances, particularly ambient temperature and relative humidity, which in turn affect food intake.

Thirst is the body's clue that something is amiss with water balance, and it encourages the thirsty subject to seek and consume water. Little has been reported on the physiology of thirst in various species of nonhuman primates, and the issue is complicated by observations that the mechanisms involved can be different in different nonprimate species (Wood et al., 1982).

Homeostatic regulation of body fluid volumes has received major attention in humans because of its importance for normal subjects and for clinical patients (Oh and Uribarri, 1999). Body fluid is an aqueous solution containing many electrolytes in intracellular and extracellular compartments. Intracellular fluid occupies not a single large compartment but myriad cell compartments, which have their characteristic environments and communicate with each other via interstitial fluid and plasma. Although cells in different tissues can vary in the solutes present and in solute concentrations, osmotic equilibrium is maintained so that the same number of water molecules surrounds each particle of solute throughout the body. Cell membranes are so permeable to water that osmolality is normally the same throughout the body fluid.

Most of the metabolic reactions of the body take place in cells. For normal operation of these reactions, optimal ionic strengths must be maintained in the cellular compartment, and the homeostatic mechanisms of the body are constantly at work to provide such an environment. Extracellular fluids (ECFs), in contrast, are not sites of major metabolic activity. Therefore, there can be substantial alterations in ionic strength of ECFs without adverse effects. The primary function of ECFs is to serve as a conduit between cells and between organs. The interstitial fluid surrounds cells and allows for slow but efficient intercellular solute exchange. Plasma is a conduit for rapid solute exchange between organs. ECFs thus regulate intracellular volume and ionic strength.

The kidneys and central nervous system are jointly responsible for maintaining the homeostasis of body fluids. When water loss exceeds water intake, increases in extracellular fluid osmolality shrink the hypothalamic osmoreceptor cells, which then signal the thirst center in the cerebral cortex and the antidiuretic hormone (ADH) releasing center in the supraoptic and paraventricular nuclei. ADH release is also regulated by nonosmotic factors, such as low effective arterial volume. ADH is released from the posterior pituitary, is carried in the plasma to the kidneys, and stimulates tubular resorption of water from the renal glomerular filtrate. At the same time or shortly thereafter, the thirst center responds by increasing the thirst drive and consequently promotes water intake (Askew, 1996; Oh and Uribarri, 1999).

Because of the complexity and interrelationships of factors affecting water requirements and the dearth of information from studies of nonhuman primates, water needs can be most safely met by providing ad libitum access. It should be noted that in group-housing situations, competi-

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tion for the water supply can require special measures to ensure that access (Weisbard and Goy, 1976).

When research protocols make ad libitum access to water impossible, preliminary studies should be conducted under similar environmental circumstances and conditions of management to ensure that a limited water supply will not alter research findings or adversely affect animal health. A starting point for an estimate of the daily water needs of adult primates might be 1 ml·kcal^{-1} of ME expenditure, on the basis of studies with humans (National Research Council, 1989), adult pig-tailed macaques (Pace et al., 1964), and adult rhesus macaques (Natelson and Bonbright, Jr., 1978).

Small species of nonhuman primates might have higher water requirements, on the basis of 161 observations of adult common marmosets (*Callithrix jacchus*) that consumed a mean of 11.7 ml of water per day (Lunn, 1989). Because of a larger surface area per unit of mass, a higher percentage of body water, a high rate of water turnover, the increased solute load from the high protein intakes required for growth, and an inability to express thirst, water intakes of 1.5 ml·kcal^{-1} of ME expenditure have been recommended for human infants (National Research Council, 1989). The same concerns apply to infant nonhuman primates.

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9 Pathophysiologic and Life-Stage Considerations

BODY WEIGHT

Data on body weight are routinely collected as part of captive-animal management. The mean body weights of individual animals are often used as summary measures of body size and in the assessment of health status (Terranova and Coffman, 1997). These data can be used to monitor relationships among environment (including diet), genetics, and such diverse biologic issues as metabolic rate, growth, reproduction, and longevity (Lundrigan, 1996). The opportunity to collect systematic, repeated measurements on the same animal is rarely available in work with free-ranging specimens. However, such measures can be used to help identify health problems, evaluate the effect of changes in management practices, and establish standards for normal growth and development of captive primates (Lundrigan, 1996; Terranova and Coffman, 1997).

The effects of captivity on body weight should be considered in direct comparisons of captive and noncaptive animals (Lundrigan, 1996; Leigh, 1994; Terranova and Coffman, 1997). Within anthropoid primate species, correlations between wild and captive weights are high ($r = 0.95$) (Leigh, 1994). However, captive lemurs (*Eulemur*, *Hapalemur*, and *Varecia*) were found to be, on the average, heavier than noncaptive conspecifics (Terranova and Coffman, 1997). The data on adult body weight in Table 9-1 are derived largely from studies of captive animals. For inclusion in this table, the data were required to meet the following criteria: actual weights only, no estimates; animal's age and sex were known; weighed animals were alive, non-gravid, and physiologically normal (that is, no evidence of clinical disease); and animals were in good body condition (not emaciated or obviously obese). For comparisons with free-ranging primates, users might wish to refer to Silva and Downing (1995).

In comparison with many other mammals, primates typically grow slowly (Oftedal, 1991), and rates of growth within a species or subspecies can be influenced by birth weight, rearing method (maternal vs hand-rearing), and sex (Ausman et al., 1985). Squirrel monkeys attained the body weights ($\pm$ SD) of their dams and sires by the age of 3 years, 665 $\pm$ 122 and 990 $\pm$ 212 g, respectively (Ausman et al., 1985). Weight data on five model species for specific age categories from birth to adulthood are presented in Table 9-2.

Obesity—as a consequence of excessive food intake, limited physical activity, or altered thermogenesis—can influence body weight measures. Adult body weights ($\pm$ SD) of 14 male and 18 female squirrel monkeys classified as obese were 1,527 $\pm$ 246 g and 1,032 $\pm$ 229 g, respectively (Ausman et al., 1985). Chimpanzees were described as obese when mean adult weights were 68 kg in males and 61 kg in females (Smith et al., 1975). Judgments of obesity in captive primates have been made by comparing their body weights with those of noncaptive conspecifics. However, the weights of free-ranging primates might not be ideal, and other measures associated with fat accumulation, such as increased body-mass index, should also be considered. Animals in any species can exhibit obesity; the species seemingly at greater risk in captive surroundings are listed in Table 9-3.

NUTRITION FROM BIRTH TO WEANING

Growth

"Normal" growth of infants is commonly considered a good indicator of adequate nutrition, whereas inadequate nutrition can, but does not always, result in suboptimal growth. Most early researchers, rearing infant nonhuman primates on milk replacers, strived to achieve growth patterns similar to those of infants reared by their mothers. Changes in body weight were commonly used measures of growth, but crown-rump length, limb length, and head circumference have also been used. Observer-to-observer variations in the latter measures tend to be greater, but

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TABLE 9-1 Body Weight of Captive Adult Primates

Taxon	Sex[a]	Mean ± SD (kg)	Min (kg)	Max (kg)	*n*	Location	Country	Reference
Lorisidae								
Perodicticus potto	b	1.280 ± 0.170	1.10	1.50	4	Midland, MI	US	Cowgill et al., 1989
Lemuridae								
Hapalemur griseus	b	0.940 ± 0.145	0.66	1.55	25	Durham, NC	US	Terranova and Coffman, 1997
Varecia variegata rubra	f	4.295 ± 0.494	3.60	5.30	4	San Diego, CA	US	Edwards, 1995
Varecia variegata variegata								
	f	4.350 ± 0.475	3.80	5.00	2	San Diego, CA	US	Edwards, 1995
	b	3.524 ± 0.465	2.51	5.62	53	Durham, NC	US	Terranova and Coffman, 1997
Eulemur coronatus	b	1.660 ± 0.238	1.12	2.98	30	Durham, NC	US	Terranova and Coffman, 1997
Eulemur fulvus rufus	b	2.261 ± 0.341	1.59	3.59	41	Durham, NC	US	Terranova and Coffman, 1997
Eulemur fulvus sanfordi	b	2.128 ± 0.205	1.72	2.90	17	Durham, NC	US	Terranova and Coffman, 1997
Eulemur macaco flavifrons	b	2.339 ± 0.185	1.73	3.11	21	Durham, NC	US	Terranova and Coffman, 1997
Eulemur macaco macaco	b	2.473 ± 0.260	1.59	4.00	66	Durham, NC	US	Terranova and Coffman, 1997
Eulemur mongoz	b	0.618 ± 0.222	0.52	0.82	67	Durham, NC	US	Terranova and Coffman, 1997
Eulemur rubriventer	b	2.060 ± 0.178	1.58	2.63	15	Durham, NC	US	Terranova and Coffman, 1997
Galagonidae								
Galago senegalensis	m	0.235	0.215	0.257	—	East Lansing, MI	US	Holmes et al., 1968
	f	0.215	0.177	0.237	—	East Lansing, MI	US	Holmes et al., 1968
Otolemur crassicaudatus	m	1.300	—	—	—	Kensington, MD	US	Valerio et al., 1972
	f	1.100	—	—	—	Kensington, MD	US	Valerio et al., 1972
Tarsiidae								
Tarsius bancanus	m							
	f							
Callithricidae								
Callithrix jacchus	u	0.355	—	—	8	Bethesda, MD	US	Power and Oftedal, 1996
Cebuella pygmaea	u	0.133	—	—	3	Washington, DC	US	Power and Oftedal, 1996
Leontopithecus rosalia	u	0.678	—	—	7	Washington, DC	US	Power and Oftedal, 1996
Saguinus fuscicollis	u	0.310	—	—	7	Oak Ridge, TN	US	Power and Oftedal, 1996
Saguinus oedipus	m	0.490	—	—	—	Bristol	England	Kirkwood, 1983
	f	0.481	—	—	—	Bristol	England	Kirkwood, 1983
	u	0.472	—	—	10	Oak Ridge, TN	US	Power and Oftedal, 1996
Cebidae								
Alouatta caraya	m	10.70	—	—	1	Cleveland, OH	US	Edwards, 1995
	f	7.033 ± 2.139	4.72	8.94	3	Cleveland, OH	US	Edwards, 1995
Alouatta villosa	m	6.192 ± 0.653	5.15	6.85	2	San Diego, CA	US	Edwards, 1995
Alouatta seniculus	m	8.140 ± 0.698	7.50	9.15	2	San Diego, CA	US	Edwards, 1995
Cebus albifrons	m	3.252 ± 0.858	—	—	24	Boston, MA	US	Ausman et al, 1981
	f	2.130 ± 0.564	—	—	43	Boston, MA	US	Ausman et al, 1981
Cebus apella	f	2.35 ± 0.160	—	—	11	Athens, GA	US	Fragaszy and Adams-Curtis, 1998
	f	4.40	—	—	13	Yemassee, SC	US	Fragaszy and Bard, 1997
Siamiri sciureus (Leticia)	m	0.990 ± 0.212	—	—	7	Boston, MA	US	Rasmussen et al., 1980
	f	0.665 ± 0.132	—	—	129	Boston, MA	US	Rasmussen et al., 1980

(continues)

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TABLE 9-1 *(continued)*

Taxon	Sex[a]	Mean ± SD (kg)	Min (kg)	Max (kg)	*n*	Location	Country	Reference
Cercopithecidae								
Cercocebus galeritus	m	10.000 ± 0.361	9.60	10.30	1	San Diego, CA	US	Edwards, 1995
Colobus guereza	m	10.750 ± 0.132	10.65	10.90	1	San Diego, CA	US	Edwards, 1995
	f	11.34	—	—	1	San Diego, CA	US	Edwards, 1995
Macaca mulatta	m	8.8 ± 0.3	—	—	9	Poolesville, MD	US	Baer et al., 1998
Mandrillus leucophaeus	f	9.700 ± 0.700	8.90	10.20	1	San Diego, CA	US	Edwards, 1995
Pygathrix nemaeus	m	12.083 ± 0.325	11.75	12.40	1	San Diego, CA	US	Edwards, 1995
Trachypithecus francoisi	m	6.734 ± 0.869	5.75	7.78	3	San Diego, CA	US	Edwards, 1995
	f	5.955 ± 0.478	5.67	6.67	2	Cleveland, OH	US	Edwards, 1995
Hylobatidae								
Symphalangus syndactylus	m	12.8 ± 2.5	6.80	19.40	89	Various	Various	Orgeldinger, 1994
	f	10.5 ± 1.7	6.80	15.70	87	Various	Various	Orgeldinger, 1994
Pongidae								
Gorilla gorilla gorilla	m	147.05	117.90	174.60	4	Various	Various	Cousins, 1979
	f	67.30	54.90	77.10	5	Various	Various	Cousins, 1979
Pan troglodytes	m	53.20	—	—	4	Kumamoto	Japan	Hamada et al., 1996
	f	42.70	—	—	4	Kumamoto	Japan	Hamada et al., 1996
	m	53.40	—	—	—	Atlanta, GA	US	Gavan, 1953
	f	47.70	—	—	—	Atlanta, GA	US	Gavan, 1953
	f	55.00	—	—	—	Atlanta, GA	US	Fragaszy and Bard, 1997
	f	47.0 ± 4.9	—	—	6	Atlanta, GA	US	Milton and Demment, 1988

[a] Male = m, female = f, both sexes = b, sex unreported = u.

linear measures involving the skeleton are not as distorted by accumulations of fat as are body weights.

MOTHER-REARED INFANTS

Growth rates of captive, breast-fed, infant primates have been published in a number of handbooks and research articles (Jacobson and Windl, 1960; Long and Cooper, 1968; Sackett et al., 1979). For some species, there appear to be substantial differences in growth rates among animals raised at different US Regional Primate Research Centers. Growth rates of animals maintained in one of these centers, the Wisconsin Regional Primate Research Center, have been published (Goy and Kemnitz, 1983). The reasons for variation in growth rates of captive primates among centers have not been identified, but differences between colonies in genetic background, maternal nutrition during pregnancy and lactation, early availability of supplemental or weaning foods, and different rearing practices have been suggested.

ARTIFICIALLY REARED INFANTS

Published data on growth rates of formula-fed infants vary considerably (Blomquist and Harlow, 1961; Fleishman, 1963; Kaye et al., 1966; Vice et al., 1966; Kerr et al., 1969a, 1969b; Buss et al., 1970; King and King, 1970; Ausman et al., 1970, 1972, 1976, 1977, 1986, 1989; Kaplan, 1970, 1979; Samonds et al., 1973; Cicmanec et al., 1979; Moore and Cummins, 1979: Ruppenthal, 1979; Sackett et al., 1979; Golub et al., 1990). In some studies, growth rates of formula-fed infants were lower than those of nursing infants. Limited access to food (less-frequent feeding), low nutrient or caloric density of formulas, and lack of social contacts were offered as explanations for the differences. In other studies, artificially reared primates grew faster than mother-reared infants; in most of these cases, formula was available around the clock or very frequently, allowing on-demand feeding. Some mother-reared infants, particularly as early neonates, had difficulty in obtaining sufficient breast milk because of the low productivity of the mother's mammary glands. That result is similar to what is sometimes seen in humans when formula-fed infants gain weight much faster than breast-fed infants because milk is more available.

Milk Volume and Composition

VOLUME

Nutrient requirements of infants have been estimated by analyzing mothers' milk and estimating the volume of milk consumed (Neville, 1986). Amounts of nutrients ingested per unit of infant body weight per day can then be determined. The determinations are sometimes used as minimal nutrient requirements when milk replacers are

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TABLE 9-2 Body Weight of Captive Primates at Various Stages of Development

Taxon	Sex[a]	Age	BW (kg)	Min (kg)	Max (kg)	n	Location	Country	Reference
Galagonidae									
Otolemur crassicaudatus	u	0 d	0.047 ± 0.006	—	—	77	Kensington, MD	US	Valerio et al., 1972
Galago senegalensis zanzibaricus	u	1 d	0.015	—	—	1	Wroclaw	Poland	Gucwinska and Gucwinski, 1968
		2 d	0.014 ± 0.001	0.013	0.014	2	Wroclaw	Poland	Gucwinska and Gucwinski, 1968
		6 d	0.023 ± 0.001	0.022	0.023	2	Harpenden	England	Brown, 1979
		7 d	0.024 ± 0.003	0.022	0.026	2	Wroclaw	Poland	Gucwinska and Gucwinski, 1968
		12 d	0.025	—	—	1	Wroclaw	Poland	Gucwinska and Gucwinski, 1968
		14 d	0.044 ± 0.007	0.039	0.048	2	Wroclaw	Poland	Gucwinska and Gucwinski, 1968
		22 d	0.053	—	—	1	Wroclaw	Poland	Gucwinska and Gucwinski, 1968
		28 d	0.046 ± 0.008	0.041	0.052	2	Wroclaw	Poland	Gucwinska and Gucwinski, 1968
		31 d	0.040 ± 0.001	0.035	0.045	2	Wroclaw	Poland	Gucwinska and Gucwinski, 1968
		39 d	0.063	—	—	1	Wroclaw	Poland	Gucwinska and Gucwinski, 1968
Callithricidae									
Saguinus oedipus oedipus	m	>2 y	0.490	—	—	—	Bristol	England	Kirkwood, 1983
	f	>2 y	0.481	—	—	—	Bristol	England	Kirkwood, 1983
Cebidae									
Cebus albifrons	m	3080 d	3.252 ± 0.858	—	—	24	Boston, MA	US	Ausman et al., 1981
	f	0 d	0.226 ± 0.006	—	—	10	Boston, MA	US	Wilen and Naftolin, 1978
		>1245 d	1.617 ± 0.033	—	—	10	Boston, MA	US	Wilen and Naftolin, 1978
		2940 d	2.130 ± 0.564	—	—	43	Boston, MA	US	Ausman et al., 1981
Cebus apella	b	0 d	0.210	0.170	0.260	7	Athens, GA	US	Fragaszy and Adams-Curtis, 1998
	b	0 d	0.210 ± 0.012	—	—	5		Argentina	Patiño et al., 1997
	b	0 d	0.197 ± 0.020	—	—	10		Argentina	Patiño et al., 1997
	b	28 d	0.317 ± 0.440	—	—	5		Argentina	Patiño et al., 1997
	b	28 d	0.355 ± 0.035	—	—	10		Argentina	Patiño et al., 1997
	b	56 d	0.472 ± 0.082	—	—	5		Argentina	Patiño et al., 1997
	b	56 d	0.460 ± 0.110	—	—	10		Argentina	Patiño et al., 1997
	b	84 d	0.597 ± 0.094	—	—	5		Argentina	Patiño et al., 1997
	b	84 d	0.537 ± 0.097	—	—	10		Argentina	Patiño et al., 1997
	b	112 d	0.678 ± 0.108	—	—	5		Argentina	Patiño et al., 1997
	b	112 d	0.647 ± 0.110	—	—	10		Argentina	Patiño et al., 1997
	b	140 d	0.779 ± 0.131	—	—	5		Argentina	Patiño et al., 1997
	b	140 d	0.772 ± 0.166	—	—	10		Argentina	Patiño et al., 1997
Siamiri sciureus, Leticia	m	0 d	0.116 ± 0.014	—	—	37	Boston, MA	US	Russo et al., 1980
		0 d	0.112	0.092	0.129	10	San Diego, CA	US	Long and Cooper, 1968
		1 m	0.200	0.161	0.232	10	San Diego, CA	US	Long and Cooper, 1968
		2 m	0.272	0.234	0.311	10	San Diego, CA	US	Long and Cooper, 1968
		3 m	0.343	0.309	0.391	8	San Diego, CA	US	Long and Cooper, 1968
		4 m	0.398	0.364	0.422	4	San Diego, CA	US	Long and Cooper, 1968
		5 m	0.451	0.445	0.455	3	San Diego, CA	US	Long and Cooper, 1968
		6 m	0.467	0.441	0.496	3	San Diego, CA	US	Long and Cooper, 1968
		7 m	0.502	0.480	0.520	3	San Diego, CA	US	Long and Cooper, 1968
		8 m	0.546	0.528	0.564	3	San Diego, CA	US	Long and Cooper, 1968
		9 m	0.556	0.531	0.582	3	San Diego, CA	US	Long and Cooper, 1968
		10 m	0.600	0.562	0.624	3	San Diego, CA	US	Long and Cooper, 1968
		11 m	0.624	0.588	0.653	3	San Diego, CA	US	Long and Cooper, 1968
		12 m	0.640	0.621	0.662	3	San Diego, CA	US	Long and Cooper, 1968
		13 m	0.654	0.611	0.698	2	San Diego, CA	US	Long and Cooper, 1968
		14 m	0.680	0.663	0.701	3	San Diego, CA	US	Long and Cooper, 1968
		15 m	0.703	0.665	0.770	4	San Diego, CA	US	Long and Cooper, 1968

(continues)

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TABLE 9-2 *(continued)*

Taxon	Sex[a]	Age	BW (kg)	Min (kg)	Max (kg)	n	Location	Country	Reference
		16 m	0.709	0.677	0.756	4	San Diego, CA	US	Long and Cooper, 1968
		17 m	0.729	0.694	0.788	4	San Diego, CA	US	Long and Cooper, 1968
		18 m	0.731	0.660	0.797	4	San Diego, CA	US	Long and Cooper, 1968
		19 m	0.751	0.698	0.808	4	San Diego, CA	US	Long and Cooper, 1968
		20 m	0.758	0.713	0.814	4	San Diego, CA	US	Long and Cooper, 1968
		21 m	0.758	0.716	0.829	4	San Diego, CA	US	Long and Cooper, 1968
		22 m	0.779	0.730	0.827	4	San Diego, CA	US	Long and Cooper, 1968
		23 m	0.792	0.760	0.822	4	San Diego, CA	US	Long and Cooper, 1968
		24 m	0.817	0.765	0.868	4	San Diego, CA	US	Long and Cooper, 1968
		25 m	0.853	0.816	0.885	4	San Diego, CA	US	Long and Cooper, 1968
		26 m	0.862	0.843	0.894	4	San Diego, CA	US	Long and Cooper, 1968
		27 m	0.867	0.839	0.895	3	San Diego, CA	US	Long and Cooper, 1968
		28 m	0.905	0.863	0.966	3	San Diego, CA	US	Long and Cooper, 1968
		29 m	0.911	0.866	0.964	3	San Diego, CA	US	Long and Cooper, 1968
		30 m	0.900	0.849	0.965	3	San Diego, CA	US	Long and Cooper, 1968
		31 m	0.906	0.835	0.973	3	San Diego, CA	US	Long and Cooper, 1968
		32 m	0.913	0.837	0.978	3	San Diego, CA	US	Long and Cooper, 1968
		33 m	0.921	0.854	0.985	3	San Diego, CA	US	Long and Cooper, 1968
		34 m	0.916	0.867	0.962	3	San Diego, CA	US	Long and Cooper, 1968
		35 m	0.931	0.907	0.959	3	San Diego, CA	US	Long and Cooper, 1968
		36 m	0.942	0.918	0.962	3	San Diego, CA	US	Long and Cooper, 1968
		>36 m	0.990 ± 0.212	—	—	—	Boston, MA	US	Rasmussen et al., 1980
	f	0 d	0.108 ± 0.014	—	—	32	Boston, MA	US	Russo et al., 1980
		0 d	0.106	0.084	0.144	11	San Diego, CA	US	Long and Cooper, 1968
		1 m	0.191	0.156	0.235	10	San Diego, CA	US	Long and Cooper, 1968
		2 m	0.269	0.222	0.324	9	San Diego, CA	US	Long and Cooper, 1968
		3 m	0.316	0.271	0.389	6	San Diego, CA	US	Long and Cooper, 1968
		4 m	0.359	0.307	0.447	6	San Diego, CA	US	Long and Cooper, 1968
		5 m	0.397	0.353	0.465	6	San Diego, CA	US	Long and Cooper, 1968
		6 m	0.425	0.368	0.507	6	San Diego, CA	US	Long and Cooper, 1968
		7 m	0.452	0.389	0.552	6	San Diego, CA	US	Long and Cooper, 1968
		8 m	0.471	0.395	0.563	6	San Diego, CA	US	Long and Cooper, 1968
		9 m	0.487	0.415	0.577	5	San Diego, CA	US	Long and Cooper, 1968
		10 m	0.507	0.427	0.607	5	San Diego, CA	US	Long and Cooper, 1968
		11 m	0.522	0.460	0.610	5	San Diego, CA	US	Long and Cooper, 1968
		12 m	0.548	0.475	0.618	5	San Diego, CA	US	Long and Cooper, 1968
		13 m	0.570	0.503	0.647	3	San Diego, CA	US	Long and Cooper, 1968
		14 m	0.620	0.567	0.673	2	San Diego, CA	US	Long and Cooper, 1968
		>36 m	0.665 ± 0.122	—	—	—	Boston, MA	US	Rasmussen et al., 1980
Cercopithecidae									
Macaca fascicularis	m	0 d	0.369 ± 0.005	—	—	166	Clamart	France	Dang et al., 1992
	f	0 d	0.339 ± 0.005	—	—	156	Clamart	France	Dang et al., 1992
Macaca mulatta	m	0 d	0.498 ± 0.066	—	—	255	Madison, WS	US	Kemnitz, 1994
		0 d	0.453	—	—	16			Bowman and Lee, 1995
		336 d	1.880	—	—	—			Bowman and Lee, 1991
	f	0 d	0.464 ± 0.063	—	—	255	Madison, WS	US	Kemnitz, 1994
		0 d	0.473	—	—	16			Bowman and Lee, 1995
		336 d	1.805	—	—	—			Bowman and Lee, 1991
Papio cynocephalus	m	0	0.910	—	—	9	San Antonio, TX	US	McMahan et al., 1976
	f	0	0.820	—	—	15	San Antonio, TX	US	McMahan et al., 1976
Pongidae									
Pan troglodytes	b	0	1.800			42	Atlanta, GA	US	Gavan, 1953
		0	1.820			77			Graham et al., 1985
		0	1.770 ± 0.260			18	Kumamoto	Japan	Udono et al., 1989
		0	1.830 ± 0.253			41	Kumamoto	Japan	Hamada et al., 1996
	m	0	2.130			5	Holloman AFB	US	Smith et al., 1975
	f	0	2.100			4	Holloman AFB	US	Smith et al., 1975

[a] Male = m, female = f, both sexes = b, sex unreported = u.

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TABLE 9-3 Primate Species Identified as Potentially at Increased Risk of Obesity in Captive Environments (Leigh, 1994; Terranova and Coffman, 1997)

Species	
Eulemur coronatus	*Macaca cyclopis*
Eulemur macaco flavifrons	*Macaca mulatta*[a]
Hapalemur griseus griseus	*Macaca arctoides*
Mandrillus leucophaeus	*Cercopithecus neglectus*[a]
Mandrillus sphinx	*Cercopithecus torquatus atys*[a]

[a] Only aged adults of these species appear to be at risk.

being formulated for artificial rearing. In reality, some nutrients appear to be present in breast milk at concentrations higher than required. Thus, such estimates can provide margins of safety for nutrients that are poorly absorbed from synthetic milk and ensure that milk replacers will be nutritionally complete.

Milk volumes ingested by mother-reared infant primates are difficult to measure, and few data have been published (Oftedal, 1984). The commonly used weigh-suckle-weigh method, in which an infant is weighed before and after each nursing bout during a 24-hour (or longer) period, is not particularly applicable to primates, because an infant primate nurses often and might hold the nipple in its mouth when not nursing. As a consequence, it is difficult to determine when nursing starts and stops. Other methods for measuring milk consumption, such as the use of isotope dilution, have been used little with nonhuman primates, although Buss and Voss (1971) used such a technique with baboons (*Papio cynocephalus*).

Formula intakes by artificially reared infants can be determined with reasonable accuracy by measuring volumes consumed over a long period (to modulate diurnal variations). Caution is urged because large holes in artificial nipples and the manipulative skills of young primates often lead to substantial losses of formula and overestimates of intake. If formula spillage is observed and "nonspillers" are selected for study, reliability of intake data can be enhanced. Caloric density of the formula must be taken into account because it will affect volumes of milk ingested. Some early researchers concluded that neonates of several species are incapable of handling nursing bottles and should be hand-fed at frequent intervals up to the age of 30-60 days. Other studies have found that newborn infants adapt quickly to the bottle and will self-feed soon after birth.

COMPOSITION OF MOTHER'S MILK

There are several reports on the gross nutrient composition of milk of nonhuman primate species (Van Wagenen et al., 1941; Pilson and Cooper, 1967;Buss 1968a, b, 1975; Buss and Cooper, 1970, 1972; Taylor and Tomkinson, 1975; Buss et al., 1976; Nishikawa et al., 1976; Turton et al., 1978; Lonnerdal et al., 1984) (Table 9-4). Many of the reports were published years ago, and some of the analytic methods are different from those of today. In some cases, the method of milk collection was such that samples obtained were not representative of milk consumed during a complete nursing bout; thus, a sampling bias was introduced (Oftedal, 1984). For example, fat concentrations in milk at the beginning of mammary evacuation can be one-third or less of concentrations near the end of mammary evacuation (Erb et al., 1977). Ideally, milk sampling replicates normal suckling behavior. It should include the normal interval for accumulation of milk before suckling and the normal amount of milk removed by suckling. If milk samples represent less than normal expression of the contents of the mammary gland, concentrations of fat and other nutrients can be in error.

The stage of lactation also affects milk composition. As lactation progresses and infants are weaned, the volumes of milk produced per nursing bout decrease, and concentrations of fat and protein dramatically increase. Maternal diet can also affect some composition values if nursing mothers have been fed diets that are not nutritionally complete. Finally, excessively vigorous manual milking can result in bleeding that is insufficient to color the milk noticeably but sufficient to affect its composition. Various milking devices have been developed to obtain milk samples without causing trauma to the breast (Buss and Kriewaldt, 1968). Ketamine as a sedative and oxytocin to promote milk ejection have been helpful in the collection of milk samples and appeared to have no effect on milk composition (Buss, 1968b), but nonphysiologic doses and repeated injections of oxytocin might result in spurious values (Oftedal, 1984).

There are reports on specific components of nonhuman-primate milk, including individual milk proteins (Davidson and Lonnerdal, 1986; Kunz and Lonnerdal, 1994), amino acids (Hayes et al., 1980; Buss and Cooper, 1970), oligosaccharides, triglycerides (Turton et al., 1978; Myher et al., 1994; Buss et al., 1976), cholesterol (Mott et al., 1982, 1985, 1990, 1993a,b), and minerals (Lonnerdal, 1984; Buss et al., 1976; Turton et al., 1978; Buss and Cooper, 1970). In chapter 5, detailed information about fatty acid composition of milk from different primates, and the effect of fat thereon, is provided. In many cases, the information was sought to explore the applicability of nonhuman primates as models for study of issues in human pediatric nutrition.

Nutrient Intakes with Milk Replacers

Nutrient intakes by artificially reared infants can be estimated by multiplying the volume of milk replacer ingested by the concentration of nutrients in the formula. Estimates of nutrient intake in commercial products will be more accurate if the milk replacer is analyzed, as opposed to

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TABLE 9-4 Proximate Composition of Milk from Several Primate Species

Species	No. of Samples	Lactation Stage, Days	Dry Matter, %	Fat, %	Crude Protein, %	Carbo-hydrates, %	Ash, %	References
Lemuridae								
Brown lemur (*Eulemur fulvus*)	6	28-74	9.6	0.9	1.3	8.5	0.2	Tilden and Oftedal, 1997
	2	90	—	2.75	1.95	6.2	0.295	Buss et al, 1976
Black lemur (*Eulemur macaco*)	7	30-82	10.1	1.1	1.5	8.4	0.3	Tilden and Oftedal, 1997
	2	2-5 h; 184 d	—	0.8 2.6	6.0 4.8	5.5 5.0	0.60 0.59	Buss et al, 1976
Lemur (*Lemur catta*)	3	7-161	—	2.5	3.23	6.43	0.37	Buss et al, 1976
Red-bellied lemur (*Eulemur rubriventer*)	3	26-57	10.3	0.8	1.1	8.9	0.2	Tilden and Oftedal, 1997
Mongoose lemur (*Eulemur mongoz*)	4	45-81	9.8	0.7	1.3	7.9	0.2	Tilden and Oftedal, 1997
Ruffed lemur (*Varecia variegata*)	5	17-48	14.0	3.2	4.2	7.7	0.4	Tilden and Oftedal, 1997
Galagidae								
Garnett's bushbaby (*Otolemur garnettii*)	14	14-73	18.5	7.3	5.2	6.6	0.6	Tilden and Oftedal, 1997
Thick-tailed bushbaby (*Otolemur crassicaudatus*)	8	19-60	18.6	8.0	4.8	6.4	0.6	Tilden and Oftedal, 1997 Pilson and Cooper, 1967
Lorisidae								
Slow loris (*Nycticebus coucang*)	4	18-90	16.3	7.0	3.9	6.6	0.7	Tilden and Oftedal, 1997
Callitrichidae								
Golden lion tamarin (*Leontopithecus rosalia*)	1	3	—	5.8	5.7	6.9	0.78	Buss, 1975;
	4	10-55	19.4	10.2	3.0	6.8	—	Oftedal and Iverson, 1995
Common marmoset (*Callathrix jacchus*)	4	14-75	—	7.14	3.56	7.5	0.26	Turton et al, 1978
Cotton-top tamarin (*Saguinus oedipus*)	3	—	13.1	3.1	3.8	5.8	0.4	Jenness and Sloan, 1970
Cebidae								
Red howler (*Alouatta seniculus*)	7	30-150	11.3	1.1	1.9	6.6	—	Oftedal and Iverson, 1995
Mantled howler (*Aloutta palliata*)	7	30-150	11.7	1.6	2.2	6.7	—	Oftedal and Iverson, 1995
Squirrel monkey (*Saimiri sciureus*)	13	—	—	5.1	3.5	6.3	0.3	Buss and Cooper, 1972
Squirrel monkey (*Saimiri sciureus*)	2-7	—	—	3.3	4.3	0.1	—	Hopf, 1970
Squirrel monkey (*Saimiri sciureus*)	2	—	—	1.0	3.0	7.0	0.2	Jenness and Sloan, 1970
Cercopithecidae								
Talapoin monkey (*Cercopithecus talapoin*)	5	17-38	12.3	2.9	2.1	7.2	0.28	Buss and Cooper, 1970
Crab-eating macaque (*Macaca fascicularis*)	8	44-119	12.2	5.2	1.6	—	0.4	Nishikawa et al., 1976
Japanese macaque (*Macaca fuscata*)	7	35-56	14.0	4.2	1.6	6.2	—	Ota et al., 1991
Rhesus macaque (*Macaca mulatta*)	13-18	16-35	15.6	4.6	2.3	7.9	0.8	Lönnerdal et al., 1984;
	45			3.0	2.1	5.9	0.26	Wagenen et al., 1941
Baboons (*Papio anubis, Papio cynocephalus, Papio papio*)	24	21-63	14.0	4.5	1.5	7.8	0.3	Buss, 1968a; Roberts et al., 1985
Lowland gorilla (*Gorilla gorilla*)	1	13	.	2.05	3.0	3.60	0.28	Taylor and Tomkinson, 1975
Humans (*Homo sapiens*)		Mature	11.6	3.2	0.89	7.4	0.143	Fomon, 1993
Humans (*Homo sapiens*)	1160	>10	12.4	4.1	0.8	6.8	0.2	Jenness, 1979

depending upon the product label. To ensure that label claims will be met, manufacturers often incorporate excesses of some nutrients to account for loss during production, storage, and use.

Formulas Used for Artificially Rearing Infant Nonhuman Primates

Early on, it was found that milk formulas intended for human infants could be used to rear some newborn nonhuman primates (Table 9-5). Originally, human-infant formulas were used to ensure survival of newborn monkeys that had lost their mothers. That was successful, and it was soon recognized that artificially reared (formula-fed) nonhuman primates could be used as animal models for studies of nutrition, growth, and development of human infants (Ausman et al., 1977, 1986, 1989; Samonds and Hegsted, 1973, 1978). For some nonhuman-primate species, however, the proportion of metabolizable energy provided by protein (usually 5-10%) was too low, and protein malnutrition was induced, since those species normally produce milk in which protein accounts for 12-16% of metabolizable energy. Later, higher-protein diets that successfully nourish these infants were developed (Samonds and Hegsted, 1978; Ausman et al, 1989).

It is difficult to prepare liquid diets in the laboratory that keep nutrient sources in a homogeneous suspension. Some particles precipitate and others float, causing varia-

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TABLE 9-5 Composition of Nonhuman-Primate Milk, Human Milk, and Human-Infant Formula

Constituent	Rhesus[a]	Infant Formula[b]	Human Milk	Baboon[c]
Lipids, %	4.6-5.4	3.6	4.6	4.6-5.8
Protein, %	2.3-2.5	1.5	1.3	1.5-1.7
Carbohydrate, %	7.8-8.1	7.2	7.1	7.4-7.7
GE, kcal·L^{-1}	820-910	670	670	770-900
Calcium, mg·L^{-1}	364-420	420	270	
Magnesium, mg·L^{-1}	31-33	45	34	
Iron, mg·L^{-1}	1.1-1.2	1.5, 12[d]	0.2-0.6	
Zinc, mg·L^{-1}	1.8-2.4	5.4	0.5-3.0	
Copper, mg·L^{-1}	0.5-1.2	0.5	0.2-0.4	
Sodium, mg·L^{-1}	82-96	150	184	
Potassium, mg·L^{-1}	242-276	560	470	

[a] Mature milk (Lönnerdal et al., 1984).
[b] SMA® (Wyeth-Ayerst).
[c] Buss (1968b).
[d] Unfortified/iron-fortified formula.

tions in caloric and nutrient intake. Thus, if self-fed, a nutritionally dilute formula might be consumed during some hours, and a thick, nutrient-dense diet at others. Other reports indicate that the vitamin D content of some human infant formulas may be too low to support normal bone growth in some nonhuman primates; the use of vitamin D supplement drops would be required. A variety of options for preparation of milk replacers that match the milk composition of many mammal species has been developed by commercial manufacturers.

Long-Term Consequences of Different Modes of Infant Feeding

Development of feeding regimens that produced satisfactory growth in artificially reared infant nonhuman primates led to studies of the long-term physiologic and metabolic consequences of early nutrition. Examples of long-term, carefully controlled studies include those focusing on effects of dietary taurine on development of visual and brain function (Hayes et al., 1980; Stephan et al., 1981; Sturman et al., 1984, 1988), the relationship of cholesterol intake and plasma lipoproteins, bile acid metabolism, and atherosclerosis (see Chapter 5), and the effect of marginal zinc deficiency on growth, immune function, and behavior (Hendrickx, 1984; Strobel and Sandstead, 1984; Golub et al., 1984, 1985, 1991; Haynes et al., 1985; Keen et al., 1989: Lonnerdal et al., 1990a, b; Liu et al., 1992; Polberger et al., 1996). Not only has important information regarding the specific nutrients being studied been obtained, but the studies provide important lessons for long-term management of nonhuman-primate research facilities and for conduct of primate research.

It is important to recognize that the composition of commercial infant formulas is only as good as our current knowledge of human infant nutrition. For example, taurine was not added to infant formulas until the 1980s, although it is a major free amino acid in human milk and has specific metabolic roles. In fact, nonhuman-primate studies were instrumental in gaining approval for taurine supplementation of human-infant formulas in the 1990s.

Another important consideration, despite the fact that formula rearing can lead to growth patterns similar to those of mother-reared infants, is that mode of feeding (natural vs formula) can lead to long-term differences in metabolism of nutrients and in health and development (Lucas, 1990). That is illustrated by a series of experiments performed on breast-fed and formula-fed baboons (Mott et al., 1982, 1985, 1990, 1993 a, b; Jackson et al., 1993; Lewis et al., 1988, 1993). Although many metabolic indices were similar in the two groups during infancy, plasma lipoprotein patterns, cholesterol levels and forms, arterial plaque formation, and bile acid conjugation were considerably different in both juvenile and adult baboons. This metabolic "imprinting" suggests that infant nonhuman primates that have been artificially reared might respond to some study conditions quite differently from animals that have been breast-fed.

Furthermore, even though growth and development of infant nonhuman primates fed diets marginally deficient in single nutrients appear to be normal, subtle, less apparent impairments can have long-term consequences. For example, the marginally zinc-deficient pregnant rhesus monkey can deliver an infant that is apparently normal but has defects in immune function and in behavior that are not overcome by consumption of a zinc-sufficient diet (Golub et al., 1984; Haynes et al., 1985). The association of such signs with a prenatal or early postnatal nutritional insult is particularly difficult to diagnose because marginal zinc deficiency usually does not affect plasma zinc concentration or other potential indicators of zinc status.

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Weaning Foods and Strategies

Weaning hand-reared infant primates of the usual laboratory species from a bottle to solid food is not particularly difficult. For infants fed semipurified milk replacers, the same ingredients can be formulated into solid diets with gelling agents, such as agar. Sugars, such as lactose or glucose, can be used in place of the starch, dextrins, and dextromaltose that are so commonly used in semipurified diets for adults. Provision of a solid diet simultaneously with the liquid diet allows infants to become accustomed to the novelty of a new food, providing opportunities to smell, touch, taste, and carry it around long before appreciable quantities are consumed. By the age of 2-4 months, infant monkeys still consuming liquid diets with lactose or glucose as a carbohydrate can be converted to solid diets containing "adult" carbohydrates or any of a variety of natural-ingredient-based products. Older monkeys generally prefer to handle and chew their food rather than drink it.

NUTRITION AND AGING

Dietary Restriction

Humans share many age-related phenomena with great apes and Old World monkeys. If biologic aging of nonhuman primates is studied longitudinally, data representing a substantial portion of the human life span can be obtained within relatively few years (Short et al., 1987). Because of their close genomic relationship, the most relevant models of human aging may be chimpanzees (*Pan troglodytes*) or bonobos (*P. paniscus*), but the costs of acquisition and care of these species, combined with longevities of more than 5 decades in captivity, renders their use prohibitive.

Perhaps rhesus (*Macaca mulatta*), pigtail (*Macaca nemestrina*), and celebes (*M. nigra*) macaques are more practical; all have been used as models for studies of aging (Hansen et al., 1981; Howard, 1983; Kemnitz et al., 1993; Lane et al., 1996). They share aging maladies with humans, including atherosclerotic vascular disease, altered plasma lipid metabolism, signs of Alzheimer's disease, menopause, diabetes mellitus, rheumatoid arthritis, obesity, and osteoporosis (Brown et al., 1974; Howard, 1983; Kaplan et al., 1985; DeRousseau, 1985a,b; Willcox et al., 1986; Sumner et al., 1989; Hansen, 1992; vom Saal et al., 1994; DeRousseau, 1994; Austad, 1997; Cefalu et al., 1997; Colman and Kemnitz, 1998). Early reviews described age-related changes in old primates (Bowden, 1979; Davis and Leathers, 1985; Short et al., 1987). Many current studies in primate gerontology are focused on age-related disorders that are influenced by nutrition.

Undoubtedly, many factors accelerate aging, but alterations in diet composition and limitations in the amount of food consumed have proved to be effective modulators of this process. Diet restriction, in the absence of essential-nutrient deficiencies, plays a positive and fundamental role in increasing survival and in delaying the onset and slowing the development of degenerative aging conditions (McCay et al., 1935; Tannenbaum, 1940; Merry and Holehan, 1979; Bodkin et al., 1995; Lane et al., 1996; Cefalu et al., 1997; Verdery et al., 1997). It is the only intervention consistently shown to extend both median and maximal life span in mammals (Weindruch and Walford, 1988; Weindruch et al., 1995; Roth et al., 1995). Many types of diets work. Both highly purified diets and commercial diets increase maximal life span when fed in reduced amounts, provided that all essential nutrients are present and moderate reductions in caloric intake are achieved (Weindruch, 1995).

It is probable that experimentally increasing the maximal age of research animals at death will yield important insights into the systematic processes of aging (Hayflick, 1985). Likewise, increasing the life span of research subjects will assist in the definition of biomarkers of aging, attributes that generally change with age and could help in predicting health and length of life (Ingram et al., 1993).

A preliminary aging study with 30 male rhesus macaques (*M. mulatta*) 0.6-25 years old and 30 male squirrel monkeys (*Saimiri sciurius*) 1 to more than 10 years old, representing Old World and New World species, respectively, was begun in 1987 for the National Institute on Aging (NIA) at the National Institutes of Health (NIH) Primate Unit of the National Center for Research Resources in Poolesville, MD (Ingram et al., 1990; Lane et al., 1992; Moon and Taylor, 1994; Roth et al., 1995). These species have natural life spans of about 40 and 20 years, respectively. The study was later expanded to include 120 female and male rhesus macaques and 30 male squirrel monkeys of various ages. All except the oldest animals, were caged as pairs (Weindruch et al., 1995).

Separate pelleted natural-ingredient diets were fed to each species. The proximate proportions of components of the diets (by weight) for rhesus and squirrel monkeys, respectively, were as follows: 15.4% and 20.3% crude protein; 5.0% and 8.0% crude fat; and 5% and 5% crude fiber. Gross energy (GE) concentrations in the rhesus and squirrel monkey diets were 3.77 $kcal \cdot g^{-1}$ and 4.03 $kcal \cdot g^{-1}$, respectively. Each diet was supplemented with vitamins and minerals at concentrations 40% above recommended allowances (Ingram et al., 1990; Weindruch et al., 1995). Diet-restricted primates were fed about 30% less than normally fed controls of each species and were adapted to the lower intakes over a 3-month period. Daily diet allotments during the preliminary study were based on National Research Council (National Research Council, 1978) estimates of GE requirements in kilocalories per kilogram of body weight (BW). Daily GE intakes by juvenile, adult, and old rhesus macaques fed ad libitum were

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216, 145, and 93 kcal·kg^{-1} of BW, respectively, and by diet-restricted juvenile, adult, and old rhesus macaques were 153, 102, and 66 kcal·kg^{-1} of BW. Daily GE intakes by juvenile, adult, and old squirrel monkeys fed ad libitum were 341, 264, and 229 kcal·kg^{-1}of BW, respectively, and for diet-restricted squirrel monkeys 242, 188, and 160 kcal·kg^{-1} of BW, respectively. Those values were calculated on the basis of measured daily dietary intakes in grams, GE concentrations of the diets, and average BW of the animal groups (Ingram et al., 1990).

A second aging primate study, done at the University of Wisconsin Regional Primate Research Center, was initiated concurrently (Kemnitz et al., 1993; Weindruch, 1996; Ramsey et al., 1997, 2000). An original group of 30 adult male rhesus macaques (*M. mulatta*) 8-14 years old, divided into 15 fed ad libitum and 15 that were diet-restricted to 30% below ad libitum intake, was expanded to include 16 additional male and 30 female rhesus macaques (Moon and Taylor, 1994). The monkeys were individually caged to control access to diet and to allow accurate daily measurement of dietary intake and feed waste. All monkeys were fed a defined, pelleted diet containing (by weight) 15% lactalbumin, 10% corn oil, about 65% carbohydrate, and 5% cellulose (Kemnitz et al., 1993; Ramsey et al., 1997). Ad libitum-fed controls were given free access to this semipurified diet for 6-8 h·d^{-1} while diet-restricted monkeys were fed the diet at 70% of their baseline intake, predetermined individually. A piece of fresh fruit was provided daily (kind and energy contribution not identified). The semipurified diet furnished ME at an estimated 3.98 kcal·g^{-1} using the percentages and ME values of individual ingredients in the formula as provided by Merrill and Watt (1955).

A third aging primate study, done at the University of Maryland, examined the effects of ME restriction and its relation to obesity and signs of diabetes in adult rhesus macaques (*M. mulatta*) (Hansen and Bodkin, 1993; Bodkin et al., 1995). After the macques reached full maturity, ME intake was restricted by weekly diet-intake adjustments to maintain a stable adult weight of 10-12 kg (Hansen and Bodkin, 1993). That method of caloric titration retarded middle-age-onset obesity (which is common in rhesus monkeys) and resulted in lower blood insulin concentrations and higher glucose tolerance in the diet-restricted animals (Hansen and Bodkin, 1993). After 9 years of diet restriction, the daily ME intake required to maintain a stable adult BW proved to be 40% less than the ME intake by ad libitum-fed controls.

Seven older (average, 20.7 years) male rhesus macaques (*M. mulatta*) were kept on a restricted diet for about 9 years. Seven male rhesus of similar age (average, 21 years), with no evidence of diabetes or impaired glucose tolerance served as ad libitum-fed controls (Bodkin et al., 1995). Four of the ad libitum-fed males were offered a standard commercial monkey diet with a composition (by weight) of 17% protein, 70% carbohydrate, 13% fat, and ME at 3.5 kcal·g^{-1}. Three ad libitum-fed males were provided a complete liquid diet (Ensure®, Ross Laboratories, Columbus, OH) designed for human consumption, containing 14% protein, 55% carbohydrate, 31% fat, and ME at 4.9 kcal·g^{-1} of DM. In dilute form, this product provided ME at 1.0 kcal·ml^{-1}. The diet-restricted monkeys were fed the commercial monkey diet three times per day. Restrictions in diet intake resulted in an average 35% reduction in ME intake compared with the ad libitum-fed controls, or ME at 582 and 894 kcal·d^{-1}, respectively (Bodkin et al., 1995).

After 1 year of the NIA study, diet restriction appeared to have had a greater effect on BW gain among squirrel monkeys than among rhesus when absolute BW gain in diet-restricted animals was expressed as a percentage of that in controls (Ingram et al., 1990). When juvenile and adult rhesus macaques were diet restricted, absolute BW increases were 48% and 29% of those observed in ad libitum-fed controls, respectively. The absolute BW increases in the diet-restricted squirrel monkey juveniles and adults were only 35% and 24% of those in ad libitum-fed controls, respectively. When rates of BW gain in diet-restricted animals were expressed as a percentage of those in ad libitum-fed controls, relative gains were 46% and 49% for juvenile and adult rhesus macaques, respectively. For juvenile and adult squirrel monkeys, these estimates were 32% and 20%, respectively. Absolute diet consumption was reduced by 23% and 24% in diet-restricted juvenile and adult rhesus, respectively; the corresponding reductions in squirrel monkeys were 22% and 24%. Old monkeys of both species continued to gain BW when fed their respective diets.

After 1 year of diet restriction, the adult rhesus macaques in the Wisconsin study were in apparent good health and had no clinical evidence of detrimental effects. The adult ad libitum-fed controls had dietary intakes below National Research Council (1978) recommendations (Ingram et al., 1990), but average BW increased by 9% during the first year of the study (Kemnitz et al., 1993). The diet-restricted monkeys did not gain BW and had 33% less body fat than the controls, but there were no lean body mass differences until after 2 years (Ramsey et al., 1997). Dual-energy x-ray absorptiometry (DEXA) was used to measure the effect of 20-30% dietary restriction on body composition at baseline and after 6, 12, and 18 months (Colman et al., 1998). At baseline, males had significantly ($P < 0.05$) greater values than females for BW, body mass index, total body lean tissue mass, appendicular skeletal mass, and total body bone mineral concentration. When analyzed longitudinally through 18 months, ad libitum-fed females had significantly increased BW, total body fat tissue mass, total body percent fat tissue mass, total body lean tissue mass, appendicular skeletal muscle mass, total body bone mineral concentration, and abdominal fat tissue mass relative to diet-

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restricted females. Ad libitum-fed males had significantly increased BW, total body fat tissue mass, total body bone mineral concentration, and abdominal fat tissue mass relative to diet-restricted males. The primary effect of dietary restriction in both sexes was on total body fat tissue mass.

The diet-restricted monkeys were restricted further after 18 months to re-establish a 30% difference in food intake between the two groups because the ad libitum-fed controls had voluntarily decreased their food intake. After 3 years of diet restriction (70% of the ME intake of controls), body fat mass and lean body mass were significantly ($P < 0.05$) lower than in the ad libitum-fed control group (Ramsey et al., 1997). A comparison of DEXA with traditional somatometric measures for determining body fat in adult male rhesus monkeys was made at various time points over a 4-year period (Colman et al., 1999). Additionally, the precision of these methods was assessed by repeated measures on the same individuals. DEXA estimates of body fat were positively correlated with body weights, body fat mass indices, body circumferences, and abdominal skinfold thicknesses. DEXA assessments of soft-tissue composition were precise, with low coefficients of variation. The majority of observed variability in somatometric measures was explained by subject variance rather than by inter- or intraobserver variability or observer experience level. These researchers concluded that noninvasive DEXA technology provides precise estimates of body composition that correlate well with the somatometric measures traditionally used in primate studies.

No significant differences in physical activity were apparent between diet-restricted and ad libitum-fed rhesus macaques during the first 30 months of the Wisconsin study (Weed et al., 1997). This was similar to the finding of DeLany et al. (1998), at the University of Maryland, who reported that physical activity was similar for ad libitum-fed and diet-restricted male rhesus macaques when matched for age and BW. Nevertheless, Weed et al. (1997) reported that there were clearly discernable differences in diurnal and circadian activity in diet-restricted rhesus macaques after 6 years on the Wisconsin study. Some diet-restricted individuals exhibited increased pacing and grooming behaviors. These changes in activity were not, however, related to measured alterations in 24-hour energy balance.

After 4.5 years, body composition and energy balance of 30 male rhesus in the NIA study were measured. The data were grouped by primate age: juveniles (6.5-7 years old), adults (8.5-10 years old), and old (over 24 years old). Both diet-restricted and ad libitum-fed monkeys were represented in the juvenile and adult groups, but all the old monkeys were ad libitum-fed (Lane et al., 1995a). Absolute body fat was not significantly altered by diet restriction, but the percentage of lean body mass decreased with age as the percentage of body fat increased. Despite substantial differences in food intake, the percentage of dietary energy that was apparently digestible (83%) was similar in all groups.

The anti-aging effects of diet restriction are believed to be associated with changes in energy metabolism. Rectal body temperature decreased progressively with age from 2 to 30 years in rhesus macaques fed ad libitum but was about 0.5°C lower in age-matched monkeys subjected to 6 years of diet restriction (Lane et al., 1996). During short-term diet restriction, 24-hour energy expenditure was reduced by about 24% (Lane et al., 1996). Absolute energy expenditures (as determined by the doubly labeled water method) over 24 hours were consistently lower in diet-restricted monkeys; but when expressed as a function of metabolic mass, 24-hour energy expenditures and energy balances were not different between long-term diet-restricted and ad libitum-fed monkeys (Lane et al., 1995a). DeLany et al. (1998) found, however, that energy expenditure (also determined by the doubly labeled water method) was lower in rhesus monkeys that were diet-restricted for more than 10 years than in ad libitum-fed controls, even with correction for differences in body size with BW, surface area, or lean body mass as a covariate. Weekly adjustments of energy intake to maintain a stable BW over the long term were shown to prevent obesity and the onset of type II diabetes, a disease that develops in many middle-aged rhesus monkeys (Hansen and Bodkin, 1993). Ramsey et al. (1996) reported that nighttime energy expenditures (determined by indirect calorimetry) were significantly ($P < 0.001$) lower in rhesus macaques at the 24- and 30-month assessments of diet restriction than in ad libitum-fed controls after adjustment for lean body mass. However, morning, afternoon, and total energy expenditures did not differ between groups.

Dietary intakes and morphologic measurements of the NIA rhesus macaques and squirrel monkeys were reported after 5 years on the study. The target diet restriction was to 70% of ad libitum intake; the average diet restriction for the two younger groups of rhesus macaques was to 67%, whereas the average diet restriction for the two younger groups of squirrel monkeys was to 78% (Weindruch et al., 1995). Nutritionally adequate restricted diets reduced BW and crown-rump length by 10-20% in rhesus monkeys. However, the influence of diet restriction on squirrel monkeys was less obvious, probably because the restriction did not reach the target for this species. Such health measures as body temperature, adiposity, blood pressure, and blood concentrations of glucose, insulin, and triglycerides were reduced, and there was a trend toward lower blood concentrations of glycosylated hemoglobin in the diet-restricted rhesus monkeys in the Wisconsin study after 5 years (Moon and Taylor, 1994; Weindruch, 1996). Insulin sensitivity, however, increased in the diet-restricted monkeys, and this was linked to changes in BW and abdominal girth.

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Growth rates were lower in diet-restricted animals than in controls (Ingram et al., 1990; Lane et al., 1992), and diet restriction delayed maturational changes in circulating testosterone levels; food restriction apparently retarded sexual maturation in prepubertal rhesus monkeys by at least 1 year (Roth et al., 1993). Postmaturation serum concentrations of the adrenal androgen dehydroepiandrosterone sulfate decreased in ad libitum-fed young adult male rhesus monkeys at a rate twice that seen in humans (Lane et al., 1997), but diet restriction slowed the postmaturation decline, and this suggests that aging rate, as indexed by adrenal steroid production, can be retarded by nutritional intervention.

Bone

Some age-related changes in the skeleton are common to humans and rhesus macaques (*M. mulatta*) that are more than 6 years old and are significantly related to BW in both sexes (DeRousseau, 1985a). Although absolute degenerative joint disease in rhesus can differ between populations, rates of age-related decline in skeletal integrity tend to be similar in all age groups examined (DeRousseau, 1985b).

The effect of maturation and subsequent aging on bone mineral content and two dimensional bone area was examined in female rhesus macaques aged 2.8-34.6 years (Champ et al., 1996). Total body, lumbar spine, and distal radial DEXA scans were performed. At all sites bone mineral content was correlated with bone area, which was positively correlated with BW and age. Total body and lumbar spine bone mineral concentration and bone area increased with maturation until age 11 and then stabilized. Significant bone loss at older ages was observed only at radial sites. The skeletal effects of aging and menopausal status were studied in female rhesus macaques ranging in age from 4-30 years (Colman et al., 1999a). Total body and posterior-anterior spinal bone masses were lower in growing than in adult premenopausal females. Postmenopausal females had lower total body, distal radius, and spinal bone masses than premenopausal females. Serum osteocalcin concentrations (marker of bone turnover) were higher in post- than in premenopausal females. Spinal osteoarthritis became common in older females, causing an increase in DEXA-measured bone mass in lumbar spinal posterior-anterior projections. The skeletal effects of aging in male rhesus macaques include reaching peak bone mass at about 10 years of age, after which bone mass is lower at the lateral spine and distal radius (Colman et al., 1999b). Markers of bone turnover, such as serum concentrations of osteocalcin and carboxyterminal telopeptide of type I collagen, decline with age. With advancing age, the prevalence of lumbar spine osteoarthritis increases dramatically, as in females, and may mask decreases in posterior-anterior spinal bone mass. Diet restriction to 30% below ad libitum-fed controls for more than 6 years affects bone growth and skeletal aging in male rhesus monkeys even if daily mineral and vitamin intakes exceed recommended intakes by 40% (Lane et al., 1995c).

Long-term food restriction of younger monkeys resulted in a significant delay in the developmental decline (to adult concentrations) in serum alkaline phosphatase concentrations, slowed skeletal growth (as reflected by shorter crown-rump length), and significantly reduced total body bone-mineral content but not bone-mineral density (as measured by DEXA absorptiometry). Serum calcium and phosphorus concentrations declined significantly with age ($P < 0.005$) but were not significantly altered by diet restriction. Those findings suggest that long-term diet restriction delays skeletal development among male rhesus monkeys while allowing the development of a shortened but otherwise normal skeleton.

Standard laboratory monkey diets have significantly higher calcium and vitamin D concentrations than do typical American human diets. Consequently, "age-associated" reductions in vitamin D status and the hyperparathyroidism commonly observed in humans were not found in postmenopausal rhesus females (Champ and Brinkley, 1996). Although bone-mineral turnover was increased in the rhesus females, there was no observed difference in bone density as measured with DEXA absorptiometry at the lumbar spine and distal radius.

Immunology

After 7 years, several immunologic measures were evaluated in the NIA monkeys. As in diet-restricted mice, lymphopenia was observed in diet-restricted monkeys, and peripheral blood lymphocyte numbers were significantly ($P < 0.05$) reduced compared with those in ad libitum-fed, age-adjusted controls (Weindruch et al., 1997). At the Wisconsin Regional Primate Research Center, reduced immune responses were reported (Roecker et al., 1996) in rhesus monkeys that were first subjected to dietary restriction as adults in 1989. After 2-4 years of dietary restriction, natural killer cell activity, antibody responses to influenza vaccine, and responses to concanavalin A and pokeweed mitogens were reduced ($P < 0.01$) compared to ad libitum-fed controls.

Wound Healing

Wound healing has been observed to become increasingly impaired with advancing age in various species (Roth et al., 1997). Concentrations of the glycation product pentosidine increase in skin collagen during aging at rates inversely proportional to life span in a large variety of mammalian species. Pentosidine accumulation is retarded

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by diet restriction in rats (Sell et al., 1996), and despite the lack of statistical significance, diet-restricted male Wistar rats and male rhesus monkeys generally exhibited a trend toward faster healing than their ad libitum-fed controls (Roth et al., 1997).

Atherosclerosis

Atherosclerosis remains one of the most important age-associated diseases in humans. Most studies that use nonhuman primates to examine the relation of diet to atherosclerotic risk include diets that are isocaloric but with modifications in concentrations of cholesterol, in fatty acid distribution, or in the relative proportions of energy from fat, carbohydrate, and protein (Verdery et al., 1997). Studies with the adult diet-restricted monkey model (intake reduced by 30%, 5% dietary fat, and cholesterol at 4.5 mg per 100 g) have produced decreased plasma concentrations of triglycerides and increased concentrations of HDL_{2b}, the high-density lipoprotein subfraction associated with protection from atherosclerosis. Differences in plasma lipid and lipoprotein concentrations occurring with diet restriction could be accounted for, in part, by decreased BW and improved glucose regulation. The results suggest that diet restriction, as mediated by its beneficial effects on body composition and glucose metabolism, could affect human longevity by decreasing atherosclerotic incidence. Plasma concentrations of low-density lipoprotein (LDL) cholesterol were similar in ad libitum-fed and diet-restricted rhesus monkeys more than 5 years old (82 vs 72 $mg \cdot dl^{-1}$, respectively [Edwards et al., 1998]). However, LDL particles from diet-restricted animals had a significantly lower molecular weight (2.9 vs 3.2 $g \cdot \mu mol^{-1}$, respectively) and were depleted in triglyceride (249 vs 433 $mol \cdot particle^{-1}$, respectively) and phospholipid (686 vs 837 $mol \cdot particle^{-1}$, respectively). Thus, diet restriction might be an intervention that retards the consequences of aging, in part by altering factors that contribute to atherogenesis.

BODY COMPOSITION

Although it is well documented in the human-nutrition literature, relatively few studies have been conducted to determine the variability of body composition of nonhuman primates. Body composition is typically described in terms of body fat and lean body mass. Lean body mass (LBM) is defined as body weight minus ether-extractable fat and is thus synonymous with fat-free mass (Forbes, 1990). A number of factors influence body composition, including nutrient and energy intake, sex, age, and level of activity.

Total dissections of pygmy chimpanzees suggest that males have a higher proportion of muscle relative to body weight than females (McFarland and Zihlman, 1994). Young adult (6-9 years old) and middle-age (13-19 years old) male rhesus macaques had more lean soft tissue and less body fat than females in the same age classes (Hudson et al., 1996). The percentage of body fat was greatest during middle age in females and during older adulthood (20-36 years old) in males. There was progressive loss of weight and lean body mass during older adulthood in both sexes in the same animals (Kemnitz, 1994). In adult rhesus macaques the androgenic hormones, testosterone and dihydrotestosterone, promote increases in body mass, which is largely attributable to accretion of lean tissue (Kemnitz et al., 1988).

When body composition was measured in squirrel monkeys during growth, moisture and protein concentrations were found to be linearly related to body mass, but fat and ash were not (Russo et al., 1980). No sex differences were detected.

The effects of nutrient and caloric intakes on body mass and composition are of particular interest. The influence of moderate caloric restriction (to 70% of ad libitum intake) on body mass and composition have been evaluated in *Macaca mulatta* (Wolden-Hanson et al. 1992). After 12 months of caloric restriction, body weights of restricted animals were 89% of weights of controls; the difference was attributed to reductions in body fat (65% of that in controls). After 24 months, restricted animals weighed 75% as much as control animals, with body fat and LBM 40% and 93% of those in controls, respectively. Similar differences in body weight and LBM were observed in animals that were ad libitum-fed or calorie-restricted (to 70% of ad libitum) over a 4.5-year period (Baer et al., 1998). However, there were no statistically significant differences in body fat (Table 9-6).

Body composition was determined in lean (control) male squirrel monkeys, fatted controls, and obese monkeys. The mean body composition of lean animals, with body weights of 733-950 g, was 64.3% water, 21.7% protein, 7.0% fat, and 7.0% ash and miscellaneous.

The validity of body-composition data is strongly related to the methods used to obtain them. Advantages and disadvantages of the various techniques used in human studies have been reviewed (Forbes, 1990). The animal-care

TABLE 9-6 Physical Characteristics (Mean ± SD) of Control (Ad Libitum-Fed) and Diet-Restricted (30% Restriction) *Macaca mulatta* after 4.5 Years (Baer et al., 1998)

	Control (n = 9)	Diet-Restricted (n = 10)
Body weight, kg	8.8 ± 0.3	7.4 ± 0.3[a]
Body mass index, $kg \cdot m^{-2}$	27.3 ± 0.8	22.6 ± 0.7[a]
Lean body mass, %	7.7 ± 0.3	6.3 ± 0.3[a]
Body fat, %	12.1 ± 2.2	14.2 ± 2.0

[a] Means in the same row were different ($P < 0.05$).

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restrictions associated with use of nonhuman primates as study subjects limit the techniques that can be used. Meehan et al. (1989) evaluated deuterium oxide (D_2O) dilution, bioelectric impedance (BIA), and skinfold thickness for assessing body composition in western lowland gorillas (Table 9-7).Body-composition estimates based on D_2O dilution were not statistically different from those based on the BIA method. Skinfold measurements were highly variable and could not be correlated with either method.

OBESITY

Growth of primates includes changes in body composition (Alberts and Altmann, 2001). True growth can be defined as an increase in the size of muscles, bones, internal organs, and other associated parts of the body, as contrasted with fat deposition. After adult dimensions are reached, body remodeling continues; and during aging, the body tends to accumulate fat and lose lean. With a persistently positive energy balance, accumulations of adipose tissue cause body weights to increase, and this ultimately leads to obesity.

A natural tendency for captive rhesus monkeys to develop obesity was observed first by Hamilton et al. (1972) and later by Kemnitz and co-workers (Kemnitz et al., 1989; Schwartz et al., 1993; Wolden-Hanson, et al., 1993) and by Jen et al. (1985). The incidence of obesity in free-ranging, provisioned rhesus monkeys on the Puerto Rico island of Cayo Santiago was 7% (Schwartz et al., 1993), which was about 20% less than observed in laboratory rhesus monkeys (Jen et al., 1985; Kemnitz et al., 1989). The frequency of obesity in rhesus monkeys in the wild is unknown but is believed to be lower (Kemnitz et al., 1989).

Studies on development of spontaneous obesity in other macaque species have been reviewed (Kemnitz, 1984). The incidence and degree of obesity in bonnet macaques, stumptailed macaques, and pigtailed macaques appear to be similar to those in the much more extensively studied rhesus monkey. A rather high incidence (20-60%, depending on age) of spontaneous obesity has been noted in squirrel monkeys raised in the laboratory on semipurified liquid diets (Ausman et al., 1981). In contrast with squirrel monkeys, cebus monkeys (*Cebus albifrons*) did not exhibit a trend toward obesity before or after sexual maturation when maintained and fed similarly for a 7-year period (Ausman et al., 1981). In all settings, it is apparent that only some animals become obese. The data suggest there may be an individual genetic predisposition to obesity in the monkey, as in humans. Furthermore, in monkeys, the predisposition might be species-specific. When unlimited calories are available, only some animals—those with a genetic predisposition—develop obesity. The genetic components of this phenomenon are not understood.

TABLE 9-7 Body Fat (%) Determined with Three Methods in Western Lowland Gorillas (Meehan et al., 1989)

Method	Mean ± SD	Min	Max
Female			
D_2O	29.5 ± 4.1[a]	6.7	44.5
BIA	35.4 ± 2.3[a]	27.0	50.4
Skinfold	20.3 ± 1.1[b]	16.8	25.9
Male			
D_2O	15.9 ± 2.2[a]	8.1	19.8
BIA	22.1 ± 3.1[a]	12.4	30.2
Skinfold	19.9 ± 0.7[b]	18.1	22.1

[a,b] Statistically significant difference among methods ($P < 0.05$, Tukey test).

The rhesus monkey has been used as a model for studies of the causes and effects of obesity in humans by both Wisconsin and Maryland groups. The measures used to describe obesity include a variety of combinations of somatometric, compositional, and body weight data. The definition of obesity in one study was based on body weight: obese monkeys were those which had body weights greater than 2 standard deviations (SD) above the mean for their sex (Kemnitz et al., 1989). A remarkably high correlation ($r = 0.978$) has been found between body mass index (body mass [or weight] in kilograms divided by the square of crown-rump length in meters) and body fat mass in a group of seven obese and seven normal-weight males and females. Body fat was estimated with tritiated water (for method, see Kemnitz and Francken, 1986). Jen et al. (1985) developed a similar measure, termed the obesity index Rh (body mass [or weight] in kilograms divided by the square of crown-rump length in centimeters), to characterize the fatness of individual rhesus macaques. This measurement was chosen as an appropriate descriptor of obesity based on its high correlation with body weight and blood concentrations of insulin and glucose and its lack of correlation with height. When fat constituted over 25% of body mass, Jen et al. (1985) defined the monkeys as obese. All monkeys had body weights over 13 kg. Monkeys weighing 13-15 kg varied in fatness, but in all monkeys weighing over 15 kg, more than 25% of body mass was fat.

The obese rhesus monkeys in most studies have been fed ad libitum. There was a natural tendency for such monkeys to gradually fatten so that by the age of about 9 years some were obese (Kemnitz, 1984). In the studies of Hansen and colleagues (Hansen and Bodkin, 1993; Hansen et al., 1995) with nonobese animals in the 9-year age range, two groups of animals were selected for longitudinal study. One group of six monkeys had their weights measured and kept constant by food restriction in what was termed "a body weight clamp"; food intake was measured at the start of the study, and then only the amount of food required to maintain constant body weights was fed for the rest of the study. A comparison group of six age- and sex-matched

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animals were fed ad libitum. Food for these groups was either a dry extruded commercial monkey diet or a commercial liquid diet for humans (Ensure®, Ross Laboratories, Columbus, OH). In analysis of the results, distinctions were not made for the diet used. Complete 3-year data sets on all animals were examined after the animals had been in the study for 9 years (Hansen et al., 1995). Remarkably, food intakes by the ad libitum and the weight-stabilized groups were relatively constant over the 3 years of data reporting; the weight-stabilized group consumed ME at an average (± SEM) of 591 ± 32 $kcal \cdot d^{-1}$ and the ad libitum group at 1,001 ± 79 $kcal \cdot d^{-1}$. Body weights were significantly different between the two groups, and these values remained relatively constant and near the mean weights (± SEM) at the age of 20 years of 11.0 ± 0.5 kg and 18.0 ± 1.5 kg in the weight-stabilized and ad libitum groups, respectively. Body fat (± SEM), estimated with the tritiated-water technique, was 21.3 ± 3.3% for the weight-stabilized group and 33.6 ± 4.0% for the ad libitum group. The energy consumed by both groups was essentially the same, ME at 54-55 $kcal \cdot kg^{-1}$ of body weight, and appeared to remain nearly constant throughout the 3 years of observation, although a trend for a slight decrease (about 10% over 3 years) was evident in the weight-stabilized group. The data indicate that the caloric intake per unit lean body mass was higher in obese than in nonobese animals (ME at 84 vs 68 $kcal \cdot BW_{kg}^{-1}$). However, it was not established whether that represented a difference between groups in the efficiency of energy use, inasmuch as the mass of adipose tissue was over twice as great in the ad libitum group and the energy required to carry and maintain this extra weight is unknown.

Social rank among monkeys in a group may be associated with obesity (Kemnitz, 1984). The dominant animal tends to determine the time that others spend in feeding in any particular location. In captive groups, subordinate animals eat only after the dominant animal is satisfied. That pattern of hierarchic behavior might result in excessive energy intake by more dominant animals; their obesity could be partly a result of social organization. Furthermore, when social order is disrupted, as when animals co-exist in an urban environment with humans or when social groups are altered by the addition of new members, obesity might be inhibited by disruption of the dominance hierarchy. In one study of male cynomolgus macaques, disruption of social order by substitution of new monkeys for former group members was used to induce stress; although obesity was not defined, regional distribution of fat was altered in such a way that stressed monkeys accumulated more intra-abdominal fat (Jayo et al., 1993).

The distribution of body fat varies among animals. Central obesity occurs when the predominant site of adipose-tissue accumulation is the abdomen and upper body. Central obesity, typically including intra-abdominal fat accumulation, represents the distribution of adipose tissue that has been most strongly associated with defects in lipid and carbohydrate metabolism, including insulin resistance and glucoregulatory dysfunction (Kemnitz and Francken, 1986; Hansen et al., 1995), and with cardiovascular disease (Shively and Clarkson, 1988; Cefalu and Wagner, 1997) in monkeys. In a recent study (Coleman et al., 1999), adipose-tissue distribution shifted as body-weight differences increased between ad libitum-fed rhesus monkeys and diet-restricted monkeys. The percentage of body fat present in the abdomen of ad libitum-fed animals progressively increased for about 90 months of observation. At the start of the study, the average monkey weight was 11 kg, and about 40% of the body fat was in the abdomen. Ad libitum-fed monkeys grew to over 14 kg, and abdominal fat increased to 45% of body fat. In contrast, the body weight of diet-restricted monkeys decreased from 11 kg to about 9 kg, and the percentage of total body fat present in the abdomen decreased to about 35%. After 90 months, the mass of total body fat was about 3 times higher in ad libitum-fed than in diet-restricted animals.

Assuming an analogy with humans, the central obesity that occurs spontaneously in rhesus monkeys appears to confer increased cardiovascular-disease risk, although measurements of cardiovascular-disease end points themselves have not been extensively studied. Hamilton et al. (1972) first reported that plasma cholesterol, triglycerides, and β-lipoproteins were increased in obese rhesus monkeys. Hannah et al. (1991) later analyzed the plasma-lipoprotein profile and demonstrated an increase in plasma concentration of very-low-density lipoprotein cholesterol and triglycerides and a decrease in HDL cholesterol in obese, insulin-resistant rhesus monkeys. Both those changes in lipoproteins would tend to increase the risk of coronary heart disease. Conversely, by inhibiting the development of obesity with diet restriction, Edwards and co-workers (1998) showed that, although LDL cholesterol concentrations were unchanged, LDL particles were modified in composition and had a decreased tendency to interact with arterial proteoglycans. Diet restriction thus appeared to block one of the proposed mechanisms of atherosclerosis, or "hardening of the arteries", in which LDL particles are trapped in the arterial intima and effectively stimulate inflammatory responses. No direct measurements of atherosclerosis have been reported in obese, diabetic rhesus monkeys, although experimental atherosclerosis in this species has been well characterized (Armstrong, 1976). The use of Western (fat- and cholesterol-enriched) diets to induce hyperlipidemia is a prerequisite for promoting the development of atherosclerosis, and the likelihood that effects of obesity on atherogenesis will be observed in the absence of this dietary background seems small. Most of the studies on obesity have not used this type of diet.

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High intakes of energy-dense diets by immature animals can result in a high growth rate that potentially induces obesity as these animals mature. Overfeeding during infancy apparently does not result in increased fat-cell numbers but rather promotes increased fat-cell size, particularly in female baboons (Lewis et al., 1989). Newborn baboons (*Papio cynocephalus*) were fed a commercial milk-replacer diet modified to contain ME at 40.5, 67.5, and 94.5 kcal per 100 g to produce underfed, normally fed, and overfed male and female infants at the age of 4 months. From the age of 4 months to 5 years, male and female baboons were fed a similar diet formulated to contain 40% of ME calories as lard, 39% as carbohydrate, and 21% as protein. Cholesterol was supplemented at 1.7 $mg \cdot kcal^{-1}$ of ME. At 5 years, females that had been overfed as infants had a significantly greater percentage of body mass that was fat, and mean fat cell volume was greater, when compared with females that were underfed or normally fed as infants. However, infant food intake did not significantly influence body composition or fat-cell number in 5-year-old male baboons. Nevertheless, in the context of the fat cell studies in baboons, it should be noted that obesity has not been described in this species. Such a fat-cell response in baboons might not be applicable to a species that develops spontaneous obesity, such as the rhesus monkey.

Regulation of Glucose Metabolism

Reductions in fasting blood glucose resulting from diet restriction first became apparent in the Wisconsin rhesus macaques *(M. mulatta)* after 24 months (Kemnitz et al. 1994a), and in the NIH rhesus males after 36 months (Lane et al., 1995b). Differences in age at initiation of diet restriction, relative fractions of life span on diet restriction, severity of diet restriction, differences in body composition, and concentrations of sucrose in the diet were regarded as potential contributors to that discrepancy between studies (Lane et al., 1995b). It was noted, however, that differences in blood glucose concentration between ad libitum-fed and diet-restricted monkeys were observed in the Wisconsin monkeys shortly after the imposition of additional diet restriction 18 months into the study (Kemnitz et al., 1994a). After 8.5 years, a longitudinal study of semiannual glucose tolerance tests in the Wisconsin rhesus monkeys revealed that diet-restricted monkeys had increased insulin sensitivity, increased plasma glucose disappearance rate, reduced fasting plasma insulin concentration, and reduced insulin response to glucose compared to ad libitum-fed controls (Gresl et al., 2001). Chronic dietary restriction appeared to protect against development of insulin resistance in aging rhesus macaques and also might have improved glucoregulatory measures compared with those of otherwise normoinsulinemic monkeys.

Cefalu et al. (1997) reported that insulin sensitivity, as measured with frequent intravenous glucose-tolerance tests, was increased in purchased, feral adult cynomolgus macaques *(M. fascicularis)* after 1 year of diet restriction (target of 30% below ad libitum-fed, 34% actual). BW, total abdominal fat, and intra-abdominal fat, determined by computed tomographic scan, were all lower in diet-restricted than in ad libitum-fed cynomolgus monkeys. Those results demonstrate that diet restriction can ameliorate pathologic fat deposition; this change might be associated with a substantial improvement in peripheral-tissue insulin sensitivity.

Reductions in fasting blood glucose became apparent in NIH diet-restricted rhesus macaques (*M. mulatta*) after 3-4 years of restriction (Lane et al., 1995b). Maximal glucose concentrations, reached during intravenous glucose-tolerance tests, increased with age but were lower in diet-restricted monkeys than in ad libitum-fed controls. Several measures of the insulin response (baseline, maximum, and integrated areas under the curve) increased with age and were lower in diet-restricted monkeys. The age-related increase in maximal blood glucose concentration in ad libitum-fed monkeys, after intravenous glucose challenge, was probably related to decreased insulin sensitivity, inasmuch as insulin levels measured concurrently with glucose peaks during intravenous infusions were significantly increased among older, heavier animals. The age-related increase in the maximal glucose peak was inhibited in monkeys subjected to long-term diet restriction, and this difference between dietary treatments might be linked to increased insulin sensitivity in diet-restricted monkeys. Hansen and Bodkin (1993) reported that glucose disappearance rate was greater in diet-restricted rhesus monkeys than in ad libitum-fed controls, and insulin resistance was lower in diet-restricted, older rhesus (Bodkin et al., 1995). Those findings suggest that long-term diet restriction can be an effective means of mitigating the development of potentially pathologic insulin resistance in older rhesus monkeys.

Diabetes

Captive orangutans (*Pongo* spp.) have a propensity to become obese and develop diabetes (Gresl et al., 2000). Intravenous glucose tolerance tests performed on 30 orangutans ranging in age from 3.5-40.5 years revealed two diabetic and two potentially prediabetic individuals. Mean $\pm$ SE fasting plasma or serum glucose and insulin concentrations were 113 ± 16 $mg \cdot dl^{-1}$ and 45 ± 7 $\mu U \cdot ml^{-1}$, respectively. The two diabetic orangutans had fasting glucose concentrations of 380 and 562 $mg \cdot dl^{-1}$ and fasting insulin concentrations of 21 and 14 $\mu U \cdot ml^{-1}$. Their insulin responses during the intravenous glucose tolerance tests were low or non-detectable. Nearly half of all orangutans exhibited delayed or attenuated acute insulin responses.

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The development of obesity in rhesus monkeys appears to be necessary, if not sufficient, for the development of insulin resistance and later non-insulin-dependent diabetes (type II diabetes) (Ausman et al., 1981; Hansen and Bodkin, 1986; Bodkin et al., 1995). Hansen and Bodkin (1986) characterized the development of obesity and diabetes in 42 male rhesus monkeys 3-28 years old and weighing 5-31.7 kg. All animals were fed ad libitum, and the diet was either a commercial monkey diet (Monkey Chow®, Purina Mills Inc., St. Louis, MO) or a liquid diet for humans (Ensure®, Ross Laboratories, Columbus, OH). Rhesus monkeys appeared to advance through a series of eight stages in which age, body weight, and percentage of body fat progressively increased, insulin resistance increased, and the plasma-glucose disappearance rate decreased. In about the sixth stage, when the monkeys' average age was about 16 years, body weight had increased to over 17 kg, body fat was near 35% of body weight, and fasting plasma insulin had risen almost tenfold to over 415 $\mu U \cdot ml^{-1}$ of plasma. Glucose disposal rate, measured as the slope of the impaired glucose-tolerance test disappearance curve, had decreased by 33%. In the final two stages of progression to frank diabetes, plasma glucose disappearance rate fell another 30%, fasting plasma-glucose rose to over 10 $mmol \cdot L^{-1}$, body weight fell, and body fat decreased. In this study of 3-6 years, seven of 42 monkeys progressed to overt diabetes, and 14 showed transitions suggesting that they would eventually become diabetic. Although all monkeys were obese before the onset of type II diabetes, some monkeys with similar degrees of obesity showed no progression toward the disease. Thus, obesity appears to be necessary but not sufficient for diabetes development.

Whether intervention and weight reduction after the development of obesity might reduce the incidence of diabetes development was not examined. However, dietary restriction that prevents the development of obesity does prevent the development of impaired glucose tolerance, hyperglycemia, and hyperinsulinemia (Kemnitz et al., 1994b; Bodkin et al., 1995; Gresl et al., 2001) and of type II diabetes (Hansen and Bodkin, 1993). In the Hansen and Bodkin study (1993), eight adult male rhesus monkeys (average age, 11 years) were diet-restricted (just enough diet to maintain constant body weights) for an average of 7 years, whereas a group of 19 age-matched controls were fed ad libitum. At the end of the study, the diet-restricted group had an average body weight of 10.4 kg, whereas the ad libitum-fed group had an average body weight of 16.1 kg, with a range of values that were up to 100% greater than in the diet-restricted group. In the ad libitum group by the end of the study, four animals were frankly diabetic, and six had developed impaired glucose tolerance and hyperinsulinemia and were considered to be prediabetic. None of the animals that maintained normal weight in the diet-restricted group developed any of those changes in glucose metabolism. As the data indicate, diet restriction was effective in preventing both obesity and diabetes; again, the two disease syndromes are closely linked, although the molecular basis is unclear.

Examination of potential molecular interactions that might underlie the development of insulin resistance and type II diabetes in the rhesus monkey has been attempted. The insulin receptor has two isoforms that are derived from alternate splicing of exon 11 in the insulin-receptor gene, and this splice variation has been examined in obese, hyperinsulinemic rhesus monkeys (Huang et al., 1994; Huang et al., 1996). A patterned increase in the proportion of the shorter, exon 11-negative insulin-receptor mRNA in liver was described in rhesus monkeys as they progressed from normal through prediabetic to frank diabetic status (Huang et al., 1996). The pattern is similar to that seen in muscle (Huang et al., 1994), although the percentage of the exon 11-negative form of the insulin-receptor mRNA in muscle was almost twice that seen in liver, and the pattern of increase in this form of the insulin receptor is apparently similar to the pattern seen in humans (Huang et al., 1996). The functional significance of such a modification of the insulin receptor is not understood.

The presence of hyperleptinemia in obese, hyperinsulinemic rhesus monkeys has been reported (Bodkin et al., 1996). Leptin is a hormone made in adipose tissue; its absence has been found to be the cause of obesity in the genetically obese ob/ob mouse model by Friedman and colleagues (Zhang et al., 1994). The function of leptin is not completely understood, but it appears that when it is absent, satiety is not sensed and food consumption continues in an uncontrolled manner, leading to the gross obesity observed in the ob/ob mouse. Paradoxically, increased blood concentrations of leptin have been observed in obese humans (Maffei et al., 1995), presumably as a result of the increased mass of adipose tissue. The observation of increased leptin in obese rhesus monkeys, therefore, does not define the role of leptin in the development of obesity; it only shows similarities to the observations made in humans. The monkey studies did show a strong correlation between leptin concentrations and body fat and fasting plasma insulin concentrations (Bodkin et al., 1996), but correlations with glucose disposal were less remarkable. Ramsey et al. (2000) reported a correlation of 0.8-0.9 between body fat and blood leptin concentrations.

Other studies in rhesus monkeys showed that the response of the brain to leptin can be modulated by the ability of the hormone to cross the blood-brain barrier (Ramsey et al., 1998). Leptin directly infused into the brain decreased food intake by as much as 50%, whereas leptin injections into plasma had no effect on food intake, although plasma concentrations of leptin increased by as much as a factor of 100. The mechanism that facilitates leptin movement across the blood-brain barrier needs to

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be found because it could play a key role in the brain's signal to limit food intake in response to leptin. Thus, the role of leptin in the development of obesity in the monkey remains unclear, but its identification has led to many new experimental approaches that might eventually facilitate a better understanding of the causes of obesity.

Studies have been done to identify the potential roles of expression of the nuclear hormone receptors, termed peroxisome proliferator-activated receptors (PPAR γ1 and PPAR γ2), in obesity in rhesus monkeys (Hotta et al., 1998). These transcription activators were selected for study because it was observed that they are highly expressed in adipocytes (Hotta et al., 1998), that thiazolodinedione ligands for the receptors are effective antidiabetics and sensitize target tissues to insulin (Kemnitz et al., 1994a), and that the ratio of PPAR γ1 to PPAR γ2 was altered in obesity in humans (Vidal-Puig et al., 1997), although not in rodents (Vidal-Puig et al., 1996). When the abdominal subcutaneous adipose tissue of 28 normal, obese, and type II diabetic rhesus monkeys was examined, the mRNA abundance of PPAR γ did not correlate with body weight, but the ratio of PPAR γ1 to PPAR γ 2 mRNA correlated highly with body weight and with fasting plasma insulin concentration (Hotta et al., 1998). The difference between the two forms of PPAR γ results from alternative splicing that modifies the n-terminal portion of the protein. The mechanism that leads to a difference in insulin sensitivity is not known. One study has shown that insulin sensitivity and blood concentrations of glucose, insulin, and lipids were reduced in a dose-dependent fashion in obese rhesus monkeys by pioglitazone, a member of the thiazolodinedione class of compounds (Kemnitz et al., 1994a). Those outcomes presumably result from the drug interactions with PPAR γ receptors—but, again, the mechanism(s) through which the various end-point alterations occur are not fully explained. PPAR γ responses to pioglitazone in muscle, adipose tissue, liver, and pancreas might all contribute to the phenotype of the response.

Collectively, the studies done thus far suggest the presence of a molecular basis of insulin resistance, obesity, and diabetes. However, the players and their interrelationships are not all determined. The use of mouse genetics, molecular biology to understand nuclear hormone receptors, and the monkey models of obesity and diabetes might well all be key components in the search that will eventually lead to an understanding of the molecular mechanisms of these diseases. Appropriate nutrition of the research subjects will be essential for derivation of the needed information.

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10 Diet Formulation, Effects of Processing, Factors Affecting Intake, and Dietary Husbandry

DIET FORMULATION

The goals of diet formulation are to integrate natural dietary habits, digestive morphology and physiology, nutrient requirements, and the physical characteristics and nutrient composition of potential feedstuffs to make diets that will be eaten in amounts sufficient to meet nutrient needs.

Natural Dietary Habits

Information on natural dietary habits is derived from field studies of free-ranging primates in their natural habitat (see Chapter 1). Such studies have been conducted with a number of species, and the results are published in varied detail in research journals, books, and theses (Clutton-Brock, 1977; Milton, 1980; Newton, 1992; Edwards, 1995; Nijboer and Dierenfeld, 1996; Mowry et al., 1997; Dierenfeld and McCann, 1999; Silver et al., 2000).

Digestive System Morphology and Physiology

Descriptions of primate digestive systems (Langer, 1988; Stevens and Hume, 1995) have been derived opportunistically from necropsies performed for other purposes or from necropsies conducted specifically to gather this information. Data on digestive physiology are usually obtained from studies of living primates in captivity (Bauchop, 1978; Edwards, 1995).

Nutrient Requirements

Estimated nutrient requirements derived from a review of published research are presented in Chapter 11, Table 11-1. However, the values listed there represent minimal needs in that they were derived largely from studies with purified diets in which biologic availability was assumed to be 100%. In general, the bioavailabilities of nutrients in natural-ingredient diets are lower (Ammerman et al., 1995), and it might be necessary to compensate for their lower availability by increasing nutrient concentrations above minimal requirements, as recommended in Table 11-2. Factors influencing nutrient requirements are described in relevant chapters of this report dealing with specific nutrients and general considerations regarding adequate dietary nutrient concentrations are described in Chapter 11.

Feedstuffs

Feedstuffs with potential for use in primate diets are shown in Chapter 12, Tables 12-1 through 12-6. Ultimately, it is necessary to match the nutrient composition and physical characteristics of feedstuffs with the nutrient requirements and the structural and physiologic characteristics of the gastrointestinal tract of the primate in question.

Diet Formulation

Although the calculations required in formulating diets can be made with a calculator, diet formulation is easier and faster with a computer that uses software designed specifically for the purpose. Diet-formulation software is available (Anonymous, 1999), and commercial programs are commonly designed to select and incorporate feedstuffs on a least-cost basis. If a consistent, unvarying formula is desired, that option is also available.

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Commercial feed manufacturers offer a variety of closed-formula diets for nonhuman primates. Although the specific amounts of each ingredient in the formula are not usually revealed, most manufacturers will furnish estimates of typical nutrient content in printed form or on a Web site. The information from the manufacturer can then be compared with the estimated nutrient requirements listed in Table 11-1. However, commercial feed manufacturers routinely alter feed formulations based on the quality and availability of feed ingredients, and customers are typically not notified when these formulation changes occur (Knapka, 1997). Although changes might only involve alterations in the ratios of the ingredients listed, in order to control the variation in the dietary nutrients of interest and perhaps permit use of low cost ingredients, changes might also occur in dietary constituents that are not being measured. For example, dietary ingredient changes can result in alterations of phytoestrogen concentrations, which are not typically reported, but can have a significant effect on reproductive efficiency and tumor rates in laboratory animals. These changes in feed composition can have potential impacts on the health of the animals being fed and the quality of research conducted with experimental animal colonies. Because of the potential variation in nutrient composition and other nonnutrient factors that may have physiologic effects, closed formula diets are not recommended for many research situations. If closed formula diets are used in research, they should be used with extreme caution and the researcher should conduct independent analyses of the diets throughout the experimental period. Researchers and caretakers should maintain detailed knowledge of the composition of diets, and those dietary constituents—nutrients and nonnutritive components—that may be of special interest.

Persons conducting research with primates often use an open-formula diet, publishing the amount and identity of each ingredient. Information on diet composition has utility in the interpretation of research findings, but one should be wary of uncritically adopting diets based on formulas published in the past. The definitions of feed ingredients (and their nutrient compositions) tend to change, and it might be difficult or even impossible to formulate diets as originally specified. For example, an open formula might specify the use of a fishmeal containing 70% protein. Fishmeal containing 70% protein has traditionally been derived from processing of sardines and is no longer widely available. The fishmeal used in most feed mills today is derived either from menhaden (60% protein) or from anchovies (65% protein), and few commercial feed mills have more than one type of fishmeal on hand. Another example is related to the use of wheat in an open-formula diet. The many types of wheat (such as soft white winter, hard red winter, and durum) vary in protein concentration from 10% to 15%. Most feed manufacturing plants will have only one type of wheat, and that makes it difficult to meet specifications that require a particular type of wheat or wheat with a particular protein level. An example of an ingredient specification that is not consistent with current technology is related to the form of vitamin C. Most older published diet formulations specify ascorbic acid, whereas modern formulas use L-ascorbyl-2-polyphosphate, a biologically active vitamin C form that is much more stable.

Because of concern that natural-ingredient diet formulas published in this document would be used without critical consideration of the issues raised above, we have chosen instead to refer the reader to relevant literature. A National Institutes of Health open-formula high-fiber diet that was developed to study the effect of fiber on rhesus monkeys during quarantine has been used as a maintenance ration in a number of colonies (Morin et al., 1978; Knapka et al., 1995). Diets used for longevity studies with rhesus and squirrel monkeys, in which food was restricted, have been published by Ingram et al. (1990). Diets for marmosets (Flurer et al., 1983; Barnard et al., 1988) and diets for lemurs, howlers, colobus, langurs, mangabeys, and drills (Edwards, 1995) also have been described.

A number of investigators have used purified diets in their research, and these diets are referred to in many of the studies cited in this report. Purified-diet formulas for macaques *(Macaca* spp.*)* (Kark et al., 1974; Kemnitz et al., 1993; Thornberg et al., 1995), African green monkeys *(Cercopithecus aethiops)* (Scobey et al., 1992), and squirrel monkeys *(Saimiri sciureus)* (Rasmussen et al., 1979; Martin et al., 1972) and a liquid diet used for alcohol investigations with baboons *(Papio* spp.) (Leiber and DeCarli, 1974) have been published. They can be used as a starting point by those wishing to formulate a diet for a specific purpose. The original publications should be studied carefully and formulas modified as appropriate. Adjustment of nutrient levels is particularly important for diets that were used to produce nutrient deficiencies.

EFFECTS OF PROCESSING

Feed processing typically includes grinding of dietary ingredients to produce particles of approximately equal size suitable for mixing and then pelleting or extrusion. Such processing promotes diet homogeneity and reduces the likelihood that primates will select and consume only the ingredients that appeal to them, regardless of their relative nutritional importance. Many primates manipulate their food and generally prefer the physical characteristics of extrusions or pellets to ground meals.

Manufactured diets for nonhuman primates usually are prepared by extrusion. This process involves passing steam-moistened feed through a high-pressure, high-temperature chamber and forcing it through a small opening. The pres-

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sure is sufficiently high that steam is formed and the starches are gelatinized and made more digestible (Camire et al., 1990; Knapka et al., 1995). Thus, difficult-to-digest starches are less likely to escape endogenous digestion in the upper gastrointestinal tract of simple-stomached primates and are less likely to produce digestive disturbances as a consequence of excessively rapid microbial fermentation in the lower gut. Variable effects on lipids, proteins, and minerals have been noted (Camire et al., 1990); much of this variability is associated with the sources and chemical nature of these nutrients and variations in the conditions of extrusion. The temperatures and pressures of extrusion are high enough to greatly reduce dietary microbial concentrations, although in most commercial operations recontamination occurs to some degree during cooling and bagging. If the conditions are proper, the final product will expand or "puff" so that a low-density biscuit is formed; this low-density extrusion tends to be more palatable than pellets.

If diets are prepared by pelleting, sources of carbohydrate that provide sugars or gelatinized starch should be used to ensure adequate carbohydrate digestibility. Such a pelleted diet was formulated by Barnard et al. (1988). If extruding or pelleting equipment is not available, baked diets can be prepared (Knapka et al., 1995).

Some primate diets are canned. The general procedure includes grinding of the major ingredients, precooking in a continuous cooker with live steam, addition of mineral and/or vitamin mixes, blending of all ingredients, and filling of cans while hot. The cans are vacuum sealed and transferred to a retort for sterilization. Temperature and time of cooking depend upon steam pressure, size of can, can contents, and rate of can movement. After retorting, the cans are rapidly cooled to about 38° C, dried, labeled, and placed in cases (Ockerman and Hansen, 2000). The canning process significantly reduces potential for microbial contamination.

Extruding, pelleting or baking can have destructive effects on the vitamins in feed. Some nutrients—for example, vitamin A, vitamin D, vitamin E, vitamin C, thiamin, and folacin—are particularly susceptible to destruction during feed manufacture and storage unless included in the proper form.

Vitamin A is quite unstable in its free form, retinol, and is commonly stabilized by creating an ester, retinyl palmitate, and by microencapsulation within a coating that contains antioxidants. Vitamin D also is stabilized by microencapsulation. The ester form of vitamin E, α-tocopheryl acetate, that is commonly added to manufactured feeds is much more stable than α-tocopherol. Protective coatings also have been used to stabilize vitamin C, but creation of the ester L-ascorbyl-2-polyphosphate has been even more successful. Thiamin and folacin each have a free amino group that makes them susceptible to losses in activity during heat treatment in the presence of reducing sugars, such as glucose and lactose; these losses can be exaggerated by close association with some mineral mixes and must be compensated for by supplementation. Thiamin mononitrate appears to be more stable than thiamin hydrochloride (Gubler, 1991).

The most labile vitamin is ascorbic acid; 40-70% of ascorbic acid can be destroyed during extrusion (Lovell and Lim, 1978; Grant et al., 1989). Ascorbic acid in a manufactured diet continues to be lost during storage. The rate of loss depends on feed composition and on the temperature and humidity at which the feed is stored. The traditional recommendation is that primate feeds be used within 90 days of the date of manufacture unless a stable form of vitamin C is used or a supplementary form of ascorbic acid is provided. Vitamin pills, fresh fruit, or orange-flavored drinks containing additional ascorbic acid have been used as supplements.

L-Ascorbyl-2-polyphosphate, a form of vitamin C that is stable to oxidation, is now available. It is a phosphate ester of ascorbic acid, and has full biologic activity in primates (Machlin et al., 1979). The phosphate stabilizes the ascorbate molecule in feed, but the ester is cleaved by intestinal phosphatases when consumed and releases ascorbic acid for absorption. Although there can be some loss of ascorbyl polyphosphate during extrusion, that present in the final manufactured feed is quite stable (Grant et al., 1989); manufactured feeds containing the polyphosphate form of vitamin C may be stored for 180 days or longer before feeding.

If high-quality, stable forms of vitamins are added at concentrations sufficient to compensate for manufacturing and storage losses and the feed is stored under cool, dry conditions, manufactured diets can be held for several months (Coehlo, 1996).

FACTORS AFFECTING INTAKE

The feeding ecology of several wild primate species has been studied, but the methods of study generally provide an idea of *what* rather than *how much* is eaten. For primates living in the wild, the adequacy of the food supply varies with the health of the ecosystem and with the season. Wild primates must identify what is food, avoid toxicants, and distinguish between edible and inedible items. Experience and the organoleptic senses are both important (Lang, 1970). Visual, olfactory, taste, and tactile clues are used, and young primates commonly mimic the foraging behavior of adults, such as the mother and older family members.

In captivity, the supply and quality of food are under the control of humans, but unless it is eaten, its nutrient composition is of limited significance. Observations of other primates consuming a food, including trusted

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humans, can encourage tasting by a primate for which consumption of the food is a novel experience.

Influence of Visual, Olfactory, Taste, and Tactile Clues on Food Acceptance

Color vision in nonhuman primates has been little explored, but some colors or shadings of food can influence acceptance. Color preferences probably have a role in selection of foods in the wild; in captivity, juvenile orangutans consumed more of colored extruded diets, and adults took less time to consume the colored food (Barbiers, 1985).

Olfactory and taste characteristics also seem important, and it is common to see some primates responding to tastes and odors, particularly citrus and other fruity flavors and odors (Wene al., 1982). There is evidence that nonhuman primates have taste responses to sweet substances, as do humans. Most, but not all, primate species like the sweetness associated with sucrose, fructose, and glucose (Glaser, 1979; Kemnitz et al., 1986; Simmen, 1992a; Laska, 1996), and it is common to add sugar to commercial primate diets composed of natural ingredients. Sweet and fruity tastes generally enhanced dietary palatability for Callitrichidae (*Callithrix jaccus*, *Saguinus fuscicollis*, *S. labiatus*, *S. mystax*, and *S. oedipus*) but not when the fruity flavors were artificial (Flurer et al., 1983). Banded leaf monkeys (*Presbytis melalophos*) and red (*P. rubicunda*) leaf monkeys were found to favor seeds and fruits that had high concentrations of storage carbohydrates or fats but not those rich in simple sugars (Davies and Bennett, 1988). Taste-preference studies with spider monkeys (*Ateles geoffroyi*) and squirrel monkeys (*Saimiri sciureus*) showed a preferential response to sugar concentrations that were lower than those detected by other nonhuman primates and suggest that these species use sweetness as a criterion for food selection that is correlated with their dietary specialization (Laska et al., 1996; Laska, 1996). Squirrel monkeys preferred sucrose over starch-derived polysaccharides when taste preferences were compared with those of bonnet macaques (*Macaca radiata*). The latter preferred the starch-derived sugars maltose and polycose (Sunderland and Sclafani, 1988). Taste-preference profiles were consistent with the natural food preferences of those two species. When near-threshold concentrations of fructose solutions (30-60 mM) were provided, they were strongly preferred by Goeldi's monkeys (*Callimico goeldii*) and tamarins, whereas most marmosets, especially *Cebuella pygmaea*, were least attracted (Simmen, 1992b). Those findings are consistent with the dietary strategies exhibited by tamarins (*Saguinus* and *Leontopithecus*) and Goeldi's monkeys, which are predominantly frugivores and nectarivores that feed mainly on foods rich in soluble sugars, and the marmosets (*Cebuella pygmaea* and *Callithrix jaccus*), which meet much of their energy requirement from plant exudates.

Captive and free-living gentle lemurs (*Hapalemur griseus alaotrensis*) exhibited a hierarchy of food preference based on the age of plant parts. New growth, containing greater crude-protein and lower indigestible-fiber concentrations, was preferred to mature growth (Fidgett et al., 1966). When damaged plant parts were encountered, they remained untouched.

Quinine hydrochloride added to the drinking water of *Macaca fascicularis* was rejected. However, these monkeys did not find moderate concentrations of hydrochloric acid aversive (Pritchard et al., 1994).

Mouth "feel" and tactile responses during food manipulation appear to influence food acceptability. Special attention should be paid to the final form of extruded and pelleted diets. If a pellet or extruded biscuit is too hard or too dense, an animal might not be able to bite it comfortably. The final hardness or density can be controlled through manipulation of manufacturing procedures. The size of the extruded biscuit or pellet is also important, particularly for the smaller species of primates. A feed morsel should be small enough to be readily held and taken into the mouth.

To promote intake, some animal caretakers soak extruded biscuits in water or juice to make them softer. That practice is not recommended: soaking the biscuits can result in loss or destruction of some vitamins (particularly ascorbic acid), facilitate spoilage by molds and bacteria, and increase the incidence of oral health problems.

Regulation of Food Intake

Normal feeding behavior appears to involve adjustment of oral intakes to balance the energy acquired with the energy needed. When rhesus macaques (*M. mulatta*) received an intragastric infusion of food energy during a meal, oral energy intakes were reduced by an amount equivalent to the energy provided by the infusate (Hansen et al., 1977). After being rendered obese by intragastric hypercaloric feeding, male rhesus macaques orally consumed fewer kilocalories of metabolizable energy (ME) per kilogram of body weight (BW) during restabilization to pre-overfeeding weights than they had consumed before induction of obesity (Jen and Hansen, 1984). When a liquid diet providing ME at 1.35 $kcal \cdot ml^{-1}$ was diluted with water to create four diets with ME densities of 1.35-0.5 $kcal \cdot ml^{-1}$, rhesus macaques were able to maintain a constant average ME intake of 84 ± 0.7 $kcal \cdot kg^{-1}$ of BW for a period of 15 d (Hansen et al., 1981a). However, if the liquid diets were very dilute or were offered for only a limited time, the animals were unable to ingest enough food to meet the day's needs (Hansen et al., 1981b).

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Although, in general, primates eat to meet their energy requirements, some captive primates seem to consistently eat in excess of immediate energy needs and become obese. Thus, it might be necessary to limit intake of diets that are energy-dense and very palatable. Long-term studies (Ingram et al., 1990) exploring the effects of restricted energy intake on life span have demonstrated that primates can adjust to moderate energy restriction as long as nutrient intakes are sufficient to maintain basic body functions. They do it either by decreasing accretion of body tissue, particularly fat, or by decreasing physical activity to match energy consumption.

High protein intakes can have satiating effects beyond the calories provided. When Jen et al. (1985) administered a liquid intragastric infusate containing casein as 36% of ME calories, satiation of rhesus macaques receiving the infusate and consuming a nutritionally adequate solid diet occurred more quickly than when the same percentage of ME in the infusate was provided by either carbohydrate or fat. The putative effects of high-protein diets in suppressing appetite were concluded to have potential for weight control. When adult male rhesus macaques received 50% of their ME intake as protein (oral plus intragastric infusion) compared with 14%, a doubling in plasma branched-chain amino acid (valine, isoleucine, and leucine) concentration and a consistently reduced caloric intake (by 24.7%) were noted (Hannah et al., 1990). Gibbs and Smith (1977) found that gastric preloads of L-phenylalanine, but not of D-phenylalanine, produced large reductions in meal size among rhesus monkeys, as did intravenous infusions of cholecystokinin, a gut hormone released in response to L-phenylalanine and regarded as an endogenous "satiety signal." Young adult male baboons (*Papio cynocephalus*) responded with a 44% decrease in meal size when cholecystokinin octapeptide at 25 $ng \cdot kg^{-1}$ of BW was given intravenously before a 30-min meal (Figlewicz et al., 1995).

Plasma concentrations of glucose and insulin modulate feeding behavior, and blood concentrations of these compounds can be influenced by diet composition. When solutions of maltose, sucrose, or glucose (molar concentrations not specified) were provided to rhesus macaques at the beginning of a 24-h feeding period, the intake of a commercially prepared complete diet was significantly reduced, and total energy intake matched need. However, when fructose solutions were offered, reduction in food intake was only 37% of that induced by the other sugars. The difference in food intake was evident 3 h after presentation of the sugar solutions; this suggested an association with absorptive or immediate postabsorptive events and was presumably due to the failure of fructose to increase plasma glucose concentrations, as do the other sugars, or to elicit an insulin response (Kemnitz and Neu, 1986).

Variations in the concentrations of essential vitamins and minerals and the presence of aversive compounds, can also influence food intake and animal performance substantially (Newberne, 1975).

DIETARY HUSBANDRY

Primary Food Source

Most feeding programs for nonhuman primates in captivity use dry extrusions as the chief source of nutrients. In some management systems, food is offered ad libitum; in others, a fixed amount of food is presented one or more times per day. Some animal caretakers feed the same number or volume of extrusions. However, the densities and sizes of extrusions vary, not only between products made by different manufacturers but between batches of the same product. Thus, feeding by number or volume can lead to unintended changes in energy and nutrient intake. Weight is the recommended measure upon which the amount of food offered should be based.

The nutritional implications of feeding pellets ad libitum or in amounts limited to what can be consumed in 1 h, twice a day, to baboons (*Papio cynocephalus*) have been explored by Phillips and Clemens (1981). Food consumption and digestibility were not significantly different, nor were there differences in total transit times of fluid and particulate digesta markers. However, ad libitum-fed baboons passed 2-mm and 10-mm particulate markers more quickly and had a shorter 85% marker-recovery interval than did limit-fed baboons.

Supplements

Extrusions can make the entire diet or be supplemented with other foods, such as nutritionally complete treats, vegetables, fruits, and insects. Such supplements often are more palatable than the extrusions, and supplement intake must be controlled lest overall intake become nutritionally unbalanced (Shimwell et al., 1979).

With the exception of browse for such primates as colobus monkeys (*Colobus* spp.), langurs (*Presbytis* spp.), and howlers (*Alouatta* spp.), which have a well-developed digestive capacity for fermenting fiber, supplemental foods are commonly fed for environmental enrichment rather than for nutritional reasons. When used, such foods should be nutritionally complete or result in minimal nutritional distortion of the diet. In some cases, nutritionally complete "treats" are available from commercial manufacturers, but care should be taken to assure that the supplement is nutritionally complete before incorporating it into a feeding program. Aside from nutritionally complete supplements or treats, appropriate environmental enrichment food choices would be those high in moisture and low in calories, such as vegetables and some fruits, rather than

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TABLE 10-1 Plant Species Used in Feeding Captive Primates

Plant Species	Reference
Alder (*Alnus* spp.)	Dierenfeld et al., 1992; Kirschner et al., 1999
Alfalfa (*Medicago sativa*)	Bauchop and Martucci, 1968
American holly (*Ilex opaca*)	Dierenfeld and McCann, 1999
Bamboo (*Pseudosasa* spp., *Phyllostachys* spp.)	Gould and Bres, 1986
Beech (*Fagus* spp.)	Gould and Bres, 1986
Blackberry (*Rubus betuifolius*)	Dierenfeld and McCann, 1999
Brush cherry (*Syzgium paniculatum*)	Griner, 1977; Ullrey et al., 1982; Janeke, 1995
Buckthorn (*Bumelia tena*)	Dierenfeld and McCann, 1999
Cabbage palm (*Sabel palmetto*)	Dierenfeld and McCann, 1999
Carolina cherry laurel (*Prunus caroliniana*)	Dierenfeld and McCann, 1999
Chinaberry (*Melia azedarach*)	Dierenfeld and McCann, 1999
Common nightshade (*Solanum nigrum*)	Dierenfeld and McCann, 1999
Cup-of-gold (*Solandra guttata*)	Griner, 1977
Fig (*Ficus carica*)	Janeke, 1995
Fig (*Ficus glomerata*)	Janeke, 1995
Fig (*Ficus macrophylla*)	Janeke, 1995
Fig (*Ficus nittida*)	Janeke, 1995
Fig (*Ficus retusa*)	Janeke, 1995
Fig (*Ficus rubiginosa*)	Janeke, 1995
Fig (*Ficus rumphii*)	Janeke, 1995
Fig (*Ficus thonningii*)	Janeke, 1995
Flowering dogwood (*Cornus florida*)	Dierenfeld and McCann, 1999
Grape (*Vitis* spp.)	Hill, 1964; Dierenfeld et al., 1992
Giant cane (*Arundinaria gigantean*	Dierenfeld and McCann, 1999
Hackberry (*Celtis occidentalis georgiana*)	Dierenfeld and McCann, 1999
Hercules' club (*Zanthoxylum clava-herculis*)	Dierenfeld and McCann, 1999
Hibiscus (*Hibiscus rosa-sinensis*)	Hill, 1964; Griner, 1977; Ullrey et al., 1982; Janeke, 1995
Kudzu (*Pueraria hirsuta*)	Gould and Bres, 1986
Live oak (*Quercus virginiana*)	Dierenfeld and McCann, 1999
Loblolly pine (*Pinus taeda*)	Dierenfeld and McCann, 1999
Mangrove (*Rhizophora* spp.)	Dierenfeld et al., 1992
Maple (*Acer* spp.)	Gould and Bres, 1986
Mexican tea (*Chenopodium ambrosiodes*)	Dierenfeld and McCann, 1999
Mistletoe (*Phoradendron flavescens*)	Dierenfeld and McCann, 1999
Mulberry (*Morus* spp.)	Hill, 1964; Gould and Bres, 1986; Dierenfeld et al., 1992; Janeke, 1995
Muscadine grape (*Vitis rotundifolia*)	Dierenfeld and McCann, 1999
Mushrooms (unkown spp.)	Dierenfeld and McCann, 1999
Nut muscadine (*Vitis cinerea*)	Dierenfeld and McCann, 1999
Persimmon (*Diospyros virginiana*)	Dierenfeld and McCann, 1999
Red bay (*Persea borbonia*)	Dierenfeld and McCann, 1999
Red cedar (*Juniperus silicicild*)	Dierenfeld and McCann, 1999
Resurrection fern (*Polypodium polyploides*)	Dierenfeld and McCann, 1999
Small pignut (*Carya ovalis*)	Dierenfeld and McCann, 1999
Southern bayberry/wax myrtle (*Myrica cerifera*)	Dierenfeld and McCann, 1999
Southern magnolia (*Magnolia grandiflora*)	Dierenfeld and McCann, 1999
Spanish moss (*Tillandsia usneoides*)	Dierenfeld and McCann, 1999
Sparkleberry (*Vaccinium arboreum*)	Dierenfeld and McCann, 1999
Sugarberry (*Celtis laevigata*)	Dierenfeld and McCann, 1999
Virginia creeper (*Parthenocissus quinquefolia*)	Dierenfeld and McCann, 1999
Weeping Chinese banyan (*Ficus benjamina*)	Janeke, 1995
Willow (*Salix* spp.)	Höllihn, 1973; Gould and Bres, 1986; Dierenfeld et al., 1992; Kirschner et al., 1999
Yaupon (*Ilex vomitoria*)	Dierenfeld and McCann, 1999

energy-dense and nutritionally incomplete foods, such as raisins and nuts.

Cultivated fresh fruits and vegetables typically contain about 80-93% moisture. If the contribution of produce is restricted to 40% of dietary wet weight, it will furnish less than 10% of total dietary dry matter (DM) and will distort nutrient balance minimally. However, if that restriction is exceeded, it might be necessary to take special steps to ensure that nutritional needs are met.

Browse

The diets of some captive primates may include plant materials propagated or harvested as a source of nutritional

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and behavioral stimulation (Gould and Bres, 1986; Woods, 1992). Plant materials may include leaves, twigs, shoots, flowers, and fruits (Oftedal et al., 1996). These materials are collectively referred to as browse. In most situations, browse includes plant species indigenous to the geographic location where the primates are housed. Some institutions have made efforts to propagate plant species that are consumed in natural ecosystems by the free-ranging counterparts of the primates under their care.

Regardless of the source, prospective users of browse must recognize two key points: nutrient composition varies greatly among plant species and among plant parts within a species (one plant species or part is not necessarily analogous to another) and plants have various protective mechanisms (some toxic) that have evolved as feeding deterrents to limit or prevent "predation" by herbivores (Kingsbury, 1964; Harris, 1970; Rosenthal and Janzen, 1979; Cheeke, 1985).

Free-ranging primates are highly selective in their feeding. Captive-born primates do not have the same experience as wild primates in food selection and avoidance of potentially hazardous material. The presumption that naive animals are innately capable of recognizing nutrient concentrations or toxicants within a food source (nutritional wisdom) is not supported by evidence (Ullrey, 1989). Even if nutrition is not the primary reason for providing browse, the plant species offered should be evaluated as though they will be consumed.

The morbidity and mortality related to primate-browse interactions have increased proportionately with the inclusion of browse in diets of captive primates (Ensley et al., 1982; Robinson et al., 1982; Janssen, 1994). The relatively high concentration of indigestible lignin (23.6% acid-detergent lignin, DM basis) in *Acacia longifolia* and *A. saligna* leaves contributed to the formation of gastrointestinal obstructions (phytobezoars) and death when these browse species were offered to leaf-eating primates (*Presbytis entellus* and *Pygathrix nemaeus*). Similar problems might be expected when browse species with lower leaf lignin concentrations are fed in restricted amounts, thus encouraging leaf-eating primates to eat not only leaves but also high-lignin plant parts, such as bark.

Ingestion of indigenous plants containing toxic secondary plant compounds has resulted in poisoning of nonhuman primates. Some secondary plant compounds may be bitter or cause mild digestive disorders, whereas others may be acutely toxic and lead rapidly to death (Oftedal et al., 1996). Three ruffed lemurs (*Varecia variegata variegata*) exhibited signs of alkaloidal glycoside exposure—including depression, lethargy, ataxia, diarrhea, and death—after consuming hairy night shade (*Solanum sarrachoides*) (Drew and Fowler, 1991). A capuchin monkey (*Cebus apella*) consumed fruits of English ivy (*Hedra helix*) and died 3 days later with severe gastroenteritis (Fowler, 1980). The lethal dose of dried oleander leaf for capuchin monkeys (*Cebus apella*) was found to be 30-60 $mg \cdot kg^{-1}$ of BW (Swartz et al., 1974). The alkaloid senecionine in *Senecio* spp. produced toxicity in nonhuman primates (Wakim et al., 1946), and rhesus macaques (*Macaca mulatta*) were found to be susceptible to pyrrolizidine alkaloids in *Crotalaria spectabalis* (Allen et al., 1965).

With those warnings, appropriately selected browse can be an important dietary supplement for captive primates, especially highly folivorous species. Griner (1977) suggested that fresh vegetation should make up a major portion of the daily diet of captive proboscis monkeys (*Nasalis larvatus*), especially during high-stress periods, such as quarantine and acclimation to captivity. Table 10-1 lists some plant species that have been offered to captive primates or that were consumed by provisioned, semi-free ranging primates (with published documentation).

Although the use of browse can be both behaviorally and nutritionally beneficial, the uncertainties concerning nutrient composition and the presence of toxicants suggest caution (Oftedal et al., 1996). Considerable research will be required to assess the nutritional benefits of and potential toxic risks posed using fresh plant materials in feeding captive primates.

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11 Nutrient Requirements

Table 11-1, which lists estimated minimum nutrient requirements in diets (dry matter basis) for model primate species in six categories, was generated from information presented in the earlier chapters of this volume. Data were sought on model species from eight categories (suborder Strepsirrhini; families Hominidae and Pongidae, Hylobatidae, Cercopithecidae, Cebidae, Callitrichidae, and Tarsiidae; and subfamily Colobinae), but useful data on Hylobatidae and Tarsiidae were not found. The requirement estimates apply to primates fed purified or semipurified diets and assume a high nutrient bioavailability, little to no adverse interaction of nutrients, and an apparent metabolizable energy of 4 $kcal \cdot g^{-1}$ of dietary dry matter. Energy requirements, as estimated by a variety of techniques, are presented in Chapter 2.

As noted by Knapka (2000), many factors influence estimates of nutrient requirements, including genetics, the stage of the life cycle, the rearing environment, the presence of stress, amounts of food consumed, nutrient bioavailability, loss of nutrients between diet formulation and consumption, and criteria of nutritional adequacy. In the studies used to generate Table 11-1, environmental circumstances and the criteria of nutritional adequacy varied greatly. In some instances only one nutrient concentration was tested, or tested nutrient concentrations were very far apart, and that limited the accuracy of the nutrient requirement estimates.

Table 11-2 lists estimated dietary nutrient concentrations (dry matter basis) proposed as adequate in diets containing conventional feed ingredients and intended for postweaning primates. The estimated nutrient concentrations in Table 11-2 were based upon primate research reported in previous chapters; nutrient requirements of other herbivorous, omnivorous, and carnivorous mammals published in the National Research Council nutrient requirement series; and the composition of research and commercial primate diets that have successfully supported adult maintenance, reproduction, and growth of young after weaning. The estimates in Table 11-2 are intended to be target levels at the time the diet is fed, and do not account for all potential losses in processing and storage, which can sometimes negatively affect dietary nutrient levels. The nutrient concentrations in Table 11-2 are estimated as adequate but should be used with caution because they may not be appropriate for all species or all postweaning physiologic stages.

Nutrient concentrations in Table 11-2 tend to be higher than those in Table 11-1 because the bioavailabilities of nutrients in conventional feed ingredients are usually lower, and nutrient interactions are more likely to require compensation, than when purified or semipurified ingredients are used. Although the bioavailability of all nutrients in natural-ingredient diets should be considered, special attention should be given to phosphorus, zinc, niacin, and biotin. Some of the phosphorus in cereal grains, oilseeds, and their byproducts is found as phytate and is poorly available to simple-stomached animals because of the absence of endogenous digestive enzymes that release phosphorus from its bound form. Phytate also forms complexes with zinc, which render it unavailable for absorption, and additional zinc might be required when phytate is present in the diet. Iron deficiency also has been noted when isolated soy protein replaced casein in semipurified diets fed to rhesus macaques (*Macaca mulatta*), presumably because of binding by phytate (Fitch et al., 1964).

Some natural fiber sources reportedly reduce the activity of amylase, lipase, trypsin, and chymotrypsin in the intestinal tract of human patients with pancreatic insufficiency, although the basis for the inhibition is not entirely clear (Gallaher and Schneeman, 1996). Likewise, some natural sources of fiber reportedly reduce absorption of calcium, magnesium, iron, copper, and zinc; the presence of phytate, rather than fiber itself, might account for some of this reduction (Gallaher and Schneeman, 1996; Jenkins et al., 1999).

Some vitamins are bound in organic combinations of limited availability (Ammerman et al., 1995; Jacob and Swendseid, 1996; Mock, 1996). Much of the niacin in cereal

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TABLE 11-1 Estimated Nutrient Requirements (in Dietary DM) of Primate Model Species Fed Purified or Semipurified Diets[a]

	Cercopithecidae		Cebidae			Callitrichidae	Colobinae	Strepsirrhini	Pongidae and Hominidae[b]	
Nutrient	Macaque	Baboon	Squirrel monkey	Cebus	Howler	Marmoset, Tamarin	Colobus, Langur	Lemur	Chimpanzee	Humans
Crude protein, %[c]	8_m	—	$8\text{-}21_g$	7_m $7\text{-}10_g$		7_m $12\text{-}18_g$	—	—	14_g[d]	6
Taurine, %[e]	—	—	—	—	—	—	—	—	—	—
Essential n-3 fatty acids, %[f]	0.5	—	0.5	0.5	—	—	—	—	0.5	—
Essential n-6 fatty acids, %[g]	2	—	2	2	—	—	—	—	2	—
NDF, %[h]	10	—	—	—	30	10	30	20	20	—
ADF, %[i]	5	—	—	—	15	5	15	10	10	—
Ca, %	0.55_m	—	—	—	—	—	—	—	—	0.22
P, %	0.33_m	—	—	—	—	—	—	—	—	0.14
Mg, %	0.04_m	—	—	—	—	—	—	—	—	0.074
K, %	—	0.24_m[d]	—	—	—	—	—	—	—	—
Na, %	—	0.25_m[d]	—	—	—	—	—	—	—	—
Cl, %	—	0.27_m[d]	—	—	—	—	—	—	—	—
Fe, $mg\cdot kg^{-1}$	100_g	—	—	—	—	—	—	—	—	16
Cu, $mg\cdot kg^{-1}$	15[d]	—	—	—	—	—	—	—	—	1.8
Mn, $mg\cdot kg^{-1}$	44[d]	—	—	—	—	—	—	—	—	4.1
Zn, $mg\cdot kg^{-1}$	20_g 13_m	—	17_g	—	—	—	—	—	—	19
I, $mg\cdot kg^{-1}$	—	—	—	—		0.65[d]	—	—	—	0.3
Se, $mg\cdot kg^{-1}$	0.11	—	0.11	—			—	—	—	0.11
Cr^{+3}, $mg\cdot kg^{-1}$	—	—	>0.09	—			—	—	—	0.06
Vitamin A, $IU\cdot kg^{-1}$	5,000	—	12,000[d]	—	—	—	—	—	—	5,333
Vitamin D_3, $IU\cdot kg^{-1}$	1,000	—	1,250[d]	1,000	—	2,400[d]	—	—	—	800
Vitamin E, $mg\cdot kg^{-1}$[j]	68[d]	—	—	—	—	>95-130[l]	—	—	—	30
Vitamin K, $mg\cdot kg^{-1}$[k]	>0.06-3.0[l]	—	—	—	—	—	—	—	—	0.3
Thiamin, $mg\cdot kg^{-1}$	1.1	—	—	—	—	—	—	—	—	2.3
Riboflavin, $mg\cdot kg^{-1}$	1.7	—	—	1.7	—	—	—	—	—	2.4
Pantothenic acid, $mg\cdot kg^{-1}$	20[d]	—	20[d]	—	—	—	—	—	—	10
Niacin, $mg\cdot kg^{-1}$	16	—	—	—	—	—	—	—	—	30
Vitamin B_6, $mg\cdot kg^{-1}$	4.4[d]	3.1[d]	—	$2\text{-}4_g$	—	—	—	—	—	2.9
Biotin, $mg\cdot kg^{-1}$	0.11	—	—	—	—	—	—	—	—	0.06
Folacin, $mg\cdot kg^{-1}$	1.5[g]	—	1.5_g 3.3_r	1.5_g 3.3_r	—	—	—	—	—	0.8
Vitamin B_{12}, $mg\cdot kg^{-1}$	0.011	0.011	—	—	—	—	—	—	—	0.005
Vitamin C, $mg\cdot kg^{-1}$	110	—	—	—	—	—	—	—	—	170

[a] Estimated from published data in prior chapters, assuming apparent metabolizable energy at 4.0 $kcal g^{-1}$ of dry matter, high nutrient bioavailability, and little to no adverse nutrient interactions. Values with following subscripts were derived from studies concerned with maintenance (m) of adults, reproduction (r), or growth (g) of young. Values without a subscript were presumed adequate for all life stages.

[b] For comparison, recommended dietary allowances or adequate intakes for humans (approximate means of non-reproducing adult age and sex categories), assuming a daily intake of 500 g of dietary dry matter (NRC, 1989 [protein only]; Institute of Medicine, 1997, 1998, 2000, 2001).

[c] Protein requirement depends on amounts and proportions of essential amino acids. Growth requirements decline with age.

[d] Lowest concentration tested.

[e] Taurine appears to be required in the diet during the first post-natal year.

[f] Essential n-3 fatty acid requirements met by indicated concentration of α-linolenic acid. If supplied by eicosapentaenoic acid and/or docosahexaenoic acid, required concentration may be less (see Chapter 5).

[g] Essential n-6 fatty acid requirements met by indicated concentration of linoleic acid.

[h] Neutral-detergent fiber. Not a nutrient, but indicated or higher concentration appears to promote gastrointestinal health in indicated primates after weaning (see Chapter 3).

[i] Acid-detergent fiber. Not a nutrient, but indicated or higher concentration appears to promote gastrointestinal health in indicated primates after weaning (see Chapter 3).

[j] As all-*rac*-α-tocopheryl acetate.

[k] As phylloquinone.

[l] Lower concentration inadequate, higher concentration adequate.

grains and a considerable amount of the niacin in oil seeds is bound and unavailable to simple-stomached animals. Bioavailability of biotin in corn is near 100%, but it is bound and only about 50% available in wheat, barley, triticale, and sorghum grain.

Diets comprised of conventional feed ingredients often contain items such as ground grains, grain byproducts, oilseed meals, forage meals, animal byproducts, fats or oils, calcium and phosphorus sources, salt, and vitamin and trace mineral premixes. These or other items are combined

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TABLE 11-2 Estimated Adequate Nutrient Concentrations (Dry Matter Basis) in Diets Containing Conventional Feed Ingredients Intended for Post-weaning Nonhuman Primates, Accounting for Potential Differences in Nutrient Bioavailabilities and Adverse Nutrient Interactions, But Not Accounting for Potential Losses in Feed Processing and Storage[a]

Nutrient	Concentration
Crude protein, %	15-22[b]
Essential n-3 fatty acids, %	0.5
Essential n-6 fatty acids, %	2
NDF, %	10-30[c]
ADF, %	5-15[c]
Ca, %	0.8
Total P, %	0.6[d]
Non-phytate P, %	0.4
Mg, %	0.08
K, %	0.4
Na, %	0.2
Cl, %	0.2
Fe, $mg \cdot kg^{-1}$	100[e]
Cu, $mg \cdot kg^{-1}$	20
Mn, $mg \cdot kg^{-1}$	20
Zn, $mg \cdot kg^{-1}$	100
I, $mg \cdot kg^{-1}$	0.35
Se, $mg \cdot kg^{-1}$	0.3
Trivalent Cr, $mg \cdot kg^{-1}$	0.2
Vitamin A, $IU \cdot kg^{-1}$	8,000
Vitamin D_3, $IU \cdot kg^{-1}$	2,500[f]
Vitamin E, $mg \cdot kg^{-1}$	100[g]
Vitamin K, $mg \cdot kg^{-1}$	0.5[h]
Thiamin, $mg \cdot kg^{-1}$	3.0
Riboflavin, $mg \cdot kg^{-1}$	4.0
Pantothenic acid, $mg \cdot kg^{-1}$	12.0
Available niacin, $mg \cdot kg^{-1}$	25.0[i]
Vitamin B_6, $mg \cdot kg^{-1}$	4.0
Biotin, $mg \cdot kg^{-1}$	0.2
Folacin, $mg \cdot kg^{-1}$	4.0
Vitamin B_{12}, $mg \cdot kg^{-1}$	0.03
Vitamin C, $mg \cdot kg^{-1}$	200[j]
Choline, $mg \cdot kg^{-1}$	750

[a] Based upon primate research reported in previous chapters; nutrient requirements of other herbivorous, omnivorous, and carnivorous mammals published in the National Research Council nutrient requirement series; and composition of research and commercial primate diets that have successfully supported adult maintenance, reproduction, and growth of young after weaning. These nutrient concentrations have not been directly tested as a group with any primate, and may not be appropriate for all species or all post-weaning physiologic stages.

[b] Lactation and growth of young—particularly of smaller primates, such as callitrichids—can be more satisfactory when the higher protein concentrations in this range are used. Required concentrations are greatly affected by protein quality (amounts and proportions of essential amino acids), and this issue must be considered. Taurine appears to be a dietary essential for some primate species through the first postnatal year.

[c] Although not nutrients, neutral-detergent fiber (NDF) and acid-detergent fiber (ADF), when used at the concentrations shown in Table 11-1 for the indicated model species, were positively related to gastrointestinal health.

[d] Much of the phytate phosphorus found in soybean meal and some cereals appears to be of limited bioavailability.

[e] Because some primates appear to be susceptible to iron-storage disease, particularly in the absence of iron-binding polyphenols found in some plants and when large quantities of fruits are offered, it might be desirable to limit dietary iron concentrations to near or slightly below this concentration. However, this is difficult because of the iron associated with use of calcium phosphates (produced from rock phosphate) as a phosphorus source. Calcium phosphates produced from bone (as a byproduct of gelatin manufacture) are lower in iron. In either case, iron in the phosphate source is thought to be lower in bioavailability than iron in ferrous sulfate, as long as the intake of fruits and their associated citrate and ascorbate contents (which promote iron absorption) is limited.

[f] There are anecdotal reports of higher vitamin D_3 requirements in callitrichids under certain circumstances (see Chapter 7).

[g] As all-*rac*-α-tocopheryl acetate.

[h] As phylloquinone.

[i] Niacin in corn, grain sorghum, wheat, and barley is poorly available, as is niacin in byproducts of these grains unless they have undergone fermentation or wet-milling.

[j] Ascorbyl-2-polyphosphate is a source of vitamin C that is biologically active and relatively stable during diet extrusion and storage.

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in appropriate formulations, mixed, and are commonly extruded. Sometimes high-moisture fruits and vegetables, browse, or other supplements are fed along with dry extrusions for purposes of environmental enhancement, as described in Chapter 13. Foods used for environmental enhancement should not be used excessively and they should not dilute energy density, which can adversely limit dry matter consumption to below needs. Likewise, these foods should not distort the nutrient balance of a diet formulated to be nutritionally complete.

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12 Composition of Foods and Feed Ingredients

Information on the nutrient composition of foods and feed ingredients is essential for formulating feeds and diets to meet the nutrient requirements of nonhuman primates. Variability of nutrient composition of a specific feed ingredient is a function of several factors, including growing and harvest conditions, processing and storage influences and nutritional status of the organism. Selection of analytic methods can contribute to variability of published results (National Research Council, 1998).

Data presented in Table 12-1 include dry matter, gross energy, crude protein, linoleic acid, linolenic acid, ash, neutral detergent fiber, acid detergent fiber, total dietary fiber, cellulose, hemicellulose, and lignin. Gross energy (GE) is the only food energy value listed in Table 12-1 because other energy values, such as digestible energy (DE) or metabolizable energy (ME), are not constants but are functions of food composition, amount of food consumed per unit of time, and the ability of the consuming primate to digest or metabolize the food. Although ME concentrations of total diets have been determined for a few nonhuman primate species, ME concentrations in individual foods or feed ingredients consumed by nonhuman primates have not been reported. Because digestive tract morphology and physiology is so diverse, ME values of individual foods would be expected to vary appreciably among species within the Primate order. Although untested, ME values of low- to medium-fiber foods consumed by omnivorous primates, such as rhesus macaques, might be similar to ME values of those foods when consumed by humans. ME values of higher-fiber foods might be similar to ME values of those foods when consumed by small ruminants. Mineral and vitamin composition of foods and feed are presented in Tables 12-2 and 12-3, respectively. Amino acid composition is provided in Table 12-4. Mineral concentrations of macro mineral sources are presented in Table 12-5. Various sources of fats and oils are listed in Table 12-6 and their characteristics are described.

Although many common feed ingredients are used in the manufacture of commercial primate feeds, many food items included in nonhuman-primate diets are not typical of those used in livestock feeding programs. As a result, a wide variety of literature sources were used to develop the values in the following tables. When sufficient data are available, the nutrient concentrations expressed are averages, reflecting the most likely nutrient concentrations in commonly used feeds. The values in the tables are intended to be used as guides, and users are encouraged to have feed ingredients chemically analyzed before widespread application.

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TABLE 12-1 Composition of Important Feeds: Energy Values, Proximate Analyses, Plant Cell Wall Constituents, Data Expressed As-Fed and Dry (100% Dry Matter)[a]

Entry Number	Description	International Feed Number[b]	Dry Matter (%)	Gross Energy[c] (kcal/g)	Crude Protein (%)	Crude Fat (%)	Linoleic Acid (%)	Linolenic Acid (%)	Ash (%)	TDF (%)	Plant Cell Wall Constituents: NDF (%)	ADF (%)	Cellulose (%)	Hemicellulose (%)	Lignin (%)	Data Source
	Alder *Alnus* sp															
1	leaves, sun-cured	—	85.0	3.87	18.7	5.1	—	—	5.0	—	—	17.9	—	—	—	Bath et al., 1999
2			100.0	4.55	22.0	6.0	—	—	5.9	—	—	21.0	—	—	—	
	Alfalfa *Medicago sativa*															
3	meal dehy, 15% CP	1-00-022	90.0	—	15.6	2.2	—	—	9.1	—	46.0	37.0	26.0	—	11.0	NRC, 1982
4			100.0	4.10	17.3	2.4	—	—	10.1	—	51.1	41.1	28.9	—	12.2	
5	meal dehy, 17% CP	1-00-023	92.0	—	17.0	2.6	0.35	—	9.7	—	41.2	30.2	22.0	—	10.0	NRC, 1998; NRC, 1982
6			100.0	4.11	18.5	2.8	0.38	—	10.5	—	44.8	32.8	23.9	—	10.9	
7	meal dehy, 20% CP	1-00-024	92.0	—	19.6	3.3	0.44	—	10.4	—	38.8	26.4	20.0	—	7.0	NRC, 1998; NRC, 1982
8			100.0	4.17	21.3	3.6	0.48	—	11.3	—	42.2	28.7	21.7	—	7.6	
9	meal dehy, 22% CP	1-07-851	93.0	—	22.2	4.1	—	—	10.2	—	36.0	26.0	19.0	—	7.0	NRC, 1982
10			100.0	4.27	23.9	4.4	—	—	11.0	—	39.0	28.0	20.0	—	8.0	
	Almond *Prunus amygdalus*															
11	hulls	4-00-359	90.0	—	1.9	2.7	—	—	5.8	—	29.0	25.0	17.0	4.0	8.0	NRC, 1982
12			100.0	4.06	2.1	3.0	—	—	6.5	—	32.0	28.0	19.0	4.0	9.0	
	Apple *Malus sylvestris*															
13	fruit, raw, with peel	—	16.1	—	0.2	0.4	0.09	0.02	0.3	2.7	1.6	1.0	—	0.7	—	USDASR14; Schmidt et al., 1999
14			100.0	4.21	1.2	2.2	0.56	0.11	1.6	16.8	10.2	6.0	—	4.2	—	
15	pomace, dehy	—	89.0	—	4.4	4.5	—	—	2.0	—	—	23.1	—	—	—	Bath et al., 1999
16			100.0	4.41	4.9	5.1	—	—	2.2	—	—	26.0	—	—	—	
17	pomace, oat hulls added, dehy	4-28-096	89.0	—	4.6	4.7	—	—	3.1	—	—	40.0	—	—	12.0	NRC, 1982
18			100.0	4.36	5.2	5.3	—	—	3.5	—	—	44.9	—	—	13.5	
	Apricot *Prunus armeniaca*															
19	fruit, dried, sulfured	—	68.9	—	3.7	0.5	0.09	0.00	3.1	9.0	—	—	—	—	—	USDASR14
20			100.0	4.07	5.3	0.7	0.13	0.00	4.4	13.1	—	—	—	—	—	
21	fruit, raw, ep[d]	—	13.7	—	1.4	0.4	0.08	0.00	0.8	2.4	1.0	0.6	—	0.4	—	USDASR14; Schmidt et al., 1999
22			100.0	4.22	10.3	2.9	0.59	0.00	5.5	17.6	7.3	4.7	—	2.6	—	
	Ash *Fraxinus* spp.															
23	leaves, sun-cured	—	85.0	—	12.4	4.7	—	—	5.7	—	—	—	—	—	—	NRC, 1971
24			100.0	4.38	14.6	5.5	—	—	6.7	—	—	—	—	—	—	
	Asparagus *Asparagus officinalis*															
25	spear, raw	—	7.6	—	2.3	0.2	0.08	0.01	0.6	2.1	1.4	0.9	—	0.4	—	USDASR14; Schmidt et al., 1999
26			100.0	4.41	30.0	2.6	1.09	0.07	7.5	27.6	17.9	12.4	—	5.5	—	
	Aspen *Populus* spp															
27	leaves, sun-cured	—	85.0	—	14.6	4.6	—	—	7.7	—	—	26.4	—	—	—	Bath et al., 1999
28			100.0	4.30	17.2	5.4	—	—	9.1	—	—	31.0	—	—	—	
29	flower buds, spring	—	38.2	1.84	5.2	—	—	—	—	—	—	—	—	—	—	Guglielmo and Karasov, 1995
30			100.0	4.82	13.5	—	—	—	—	—	—	—	—	—	—	
	Avocado *Persea americana*															
31	fruit, raw, ep, all commerical varieties	—	25.7	—	2.0	15.3	1.84	0.11	1.0	5.0	—	—	—	—	—	USDASR14
32			100.0	7.41	7.7	59.5	7.15	0.43	4.0	19.4	—	—	—	—	—	
	Bamboo, arrow *Psuedosasa japonica*															
33	leaves	—	24.1	1.05	3.1	0.7	—	—	2.2	—	18.5	11.8	9.8	6.7	2.0	Warnell, 1988
34			100.0	4.35	12.7	2.7	—	—	9.1	—	76.8	48.9	40.5	27.9	8.4	
	Banyan, weeping Chinese *Ficus benjamina*															
35	leaves, mature, fresh	—	39.9	—	3.4	—	—	—	—	—	—	13.1	—	—	—	Janeke, 1995
36			100.0	—	8.5	—	—	—	—	—	—	32.8	—	—	—	
	Banyantree *Ficus benghalensis*															
37	leaves, fresh	2-27-208	32.0	—	3.1	—	—	—	—	—	—	—	—	—	—	NRC, 1981
38			100.0	—	9.6	—	—	—	—	—	—	—	—	—	—	

(continues)

723845CH12 12-27-02 05:33:19

TABLE 12-1 (*continued*)

Entry Number	Description	International Feed Number[b]	Dry Matter (%)	Gross Energy[c] (kcal/g)	Crude Protein (%)	Crude Fat (%)	Linoleic Acid (%)	Linolenic Acid (%)	Ash (%)	TDF (%)	Plant Cell Wall Constituents: NDF (%)	ADF (%)	Cellulose (%)	Hemicellulose (%)	Lignin (%)	Data Source
	Bakery waste															
39	dried bakery product	4-00-466	92.0	—	10.8	11.3	5.70	—	4.0	—	2.0	1.3	—	0.7	—	NRC, 1998
40			100.0	4.82	11.7	12.3	6.20	—	4.3	—	2.2	1.4	—	0.8	—	
	Banana *Musa sapientum*															
41	aerial part, fresh	2-00-483	16.0	—	1.0	0.1	—	—	2.1	—	—	—	—	—	—	NRC, 1971
42			100.0	3.71	6.4	0.8	—	—	13.1	—	—	—	—	—	—	
43	flower	—	8.7	—	1.4	—	—	—	1.0	—	3.6	2.0	—	1.6	—	Schmidt et al., 1999
44			100.0	—	15.8	—	—	—	11.1	—	41.2	22.6	—	18.6	—	
45	fruit, raw, ep	—	25.7	—	1.0	0.5	0.06	0.03	0.8	2.4	1.4	—	—	—	—	USDASR14
46			100.0	4.17	4.0	1.9	0.22	0.13	3.1	9.3	5.4	—	—	—	—	
47	fruit, raw, with peel	—	19.9	—	1.1	—	—	—	0.7	—	2.4	0.5	—	1.9	—	Schmidt et al., 1999
48			100.0	—	5.7	—	—	—	3.6	—	12.3	2.8	—	9.5	—	
49	leaves, fresh	2-09-902	19.0	—	2.9	—	—	—	—	—	—	—	—	—	—	NRC, 1981
50			100.0	—	15.7	—	—	—	—	—	—	—	—	—	—	
51	peel	—	16.2	—	1.0	1.4	—	—	1.9	—	—	—	—	—	—	NRC, 1971
52			100.0	4.21	6.1	8.7	—	—	11.7	—	—	—	—	—	—	
	Barley *Hordeum distichon*															
53	grain, two row	4-00-572	89.0	—	11.3	1.9	0.88	—	—	—	18.0	6.2	—	11.8	—	NRC, 1998
54			100.0	—	12.7	2.1	0.99	—	—	—	20.2	7.0	—	13.3	—	
	Barley *Hordeum vulgare*															
55	grain, six row	4-00-574	89.0	—	10.5	1.9	0.91	—	—	—	18.6	7.0	—	11.6	—	NRC, 1998
56			100.0	—	11.8	2.1	1.02	—	—	—	20.9	7.9	—	13.0	—	
57	grain, hulless	4-00-552	88.0	—	14.9	2.1	1.14	—	—	—	10.1	2.2	—	7.9	—	NRC, 1998
58			100.0	—	16.9	2.4	1.30	—	—	—	11.5	2.5	—	9.0	—	
	Bean, snap *Phaseolus* spp															
59	green, raw	—	9.7	—	1.8	0.1	0.02	0.04	0.7	3.4	2.1	1.8	—	0.3	—	USDASR14; Schmidt et al., 1999
60			100.0	4.19	18.7	1.2	0.24	0.37	6.8	34.9	21.9	18.3	—	3.6	—	
61	yellow, raw	—	9.7	—	1.8	0.1	0.02	0.04	0.7	3.4	2.1	—	—	—	—	USDASR14
62			100.0	4.19	18.7	1.2	0.24	0.37	6.8	34.9	21.6	—	—	—	—	
	Beech, American *Fagus grandifolia*															
63	leaves, sun-cured	1-00-628	86.0	—	10.5	2.2	—	—	4..1	—	55.6	40.9	21.3	14.7	14.4	NRC, 1971; Robbins and Moen, 1975
64			100.0	—	12.2	2.5	—	—	4..8	—	64.7	47.6	24.8	17.1	16.8	
	Beet, sugar *Beta vulgaris altissima*															
65	greens, raw	—	7.8	—	1.8	0.1	0.02	0.00	2.0	3.7	—	—	—	—	—	USDASR14
66			100.0	3.40	23.3	0.8	0.24	0.03	25.8	47.1	—	—	—	—	—	
67	pulp, dehy	4-00-669	91.0	—	8.6	0.8	—	—	—	—	42.4	24.3	—	18.1	—	NRC, 1998
68			100.0	—	9.5	0.9	—	—	—	—	46.6	26.7	—	19.9	—	
69	tops, fresh	—	17.0	—	2.6	0.2	—	—	3.9	—	—	2.4	—	—	—	Bath et al., 1999
70			100.0	3.42	15.1	1.1	—	—	22.9	—	—	14.0	—	—	—	
71	tubers, raw	—	12.4	—	1.6	0.2	0.06	0.01	1.1	2.8	—	—	—	—	—	USDASR14
72			100.0	4.03	13.0	1.4	0.45	0.04	8.7	22.5	—	—	—	—	—	
	Birch, paper *Betula papyrifera*															
73	leaves	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Robbins and Moen, 1975
74			100.0	—	—	—	—	—	—	—	44.7	30.8	13.5	13.8	10.9	
	Birch, sweet *Betula lenta*															
75	browse, immature, fresh	2-00-724	92.4	—	26.0	7.9	—	—	7.1	—	—	—	—	—	—	NRC, 1971
76			100.0	4.71	28.1	8.6	—	—	7.7	—	—	—	—	—	—	
77	browse, mid-bloom, fresh	2-00-725	93.7	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1971
78			100.0	—	—	—	—	—	—	—	—	—	—	—	—	
	Blackberry *Rubus ulmifolius*															
79	fruit, raw	—	14.4	—	0.7	0.4	0.15	0.08	0.5	5.3	3.7	2.6	—	1.1	—	USDASR14; Schmidt et al., 1999
80			100.0	4.22	5.0	2.7	1.03	0.52	3.3	36.9	25.4	18.0	—	7.5	—	

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	Blood															
81	meal, conventional	5-00-380	92.0	—	77.1	1.6	0.09	—	5.3	—	13.6	1.8	—	11.8	—	NRC, 1998
82			100.0	5.24	83.8	1.7	0.10	—	5.8	—	14.8	2.0	—	12.8	—	
83	meal, flash dried	5-26-006	92.0	—	87.6	1.6	—	—	—	—	—	—	—	—	—	NRC, 1998
84			100.0	—	95.2	1.7	—	—	—	—	—	—	—	—	—	
85	meal, spray or ring dried	5-00-381	93.0	—	88.8	1.3	0.17	—	6.6	—	—	—	—	—	—	NRC, 1998
86			100.0	5.34	95.5	1.4	0.18	—	7.1	—	—	—	—	—	—	
87	plasma, spray dried	—	91.0	—	78.0	2.0	—	—	—	—	—	—	—	—	—	NRC, 1998
88			100.0	—	85.7	2.2	—	—	—	—	—	—	—	—	—	
89	cells, spray dried	—	92.0	—	92.0	1.5	—	—	—	—	—	—	—	—	—	NRC, 1998
90			100.0	—	100.0	1.6	—	—	—	—	—	—	—	—	—	
	Blueberries *Vaccinium* spp.															
91	fruit, raw	—	15.4	—	0.7	0.4	0.10	0.07	0.2	2.7	2.0	1.1	—	0.9	—	USDASR14; Schmidt et al., 1999
92			100.0	4.29	4.4	2.5	0.64	0.44	1.4	17.5	13.2	7.1	—	6.2	—	
	Breadfruit *Artocarpus altilis*															
93	fruit, raw	—	29.4	—	1.1	0.2	0.05	0.02	0.9	4.9	—	—	—	—	—	USDASR14
94			100.0	4.10	3.7	0.8	0.16	0.06	3.2	16.7	—	—	—	—	—	
	Brewers' grain															
95	dried	5-02-141	92.0	—	26.5	7.3	3.14	—	3.6	—	48.7	21.9	—	26.8	—	NRC, 1998
96			100.0	4.85	28.8	7.9	3.41	—	3.9	—	52.9	23.8	—	29.1	—	
	Broccoli *Brassica oleracea* var. *italicca*															
97	raw	—	9.3	—	3.0	0.4	0.04	0.13	0.9	3.0	1.5	1.4	—	0.2	—	USDASR14; Schmidt et al., 1999
98			100.0	4.40	32.0	3.8	0.41	1.39	9.9	32.2	16.6	14.7	—	2.0	—	
	Brush cherry *Syzygium paniculata*															
99	leaves, mature, fresh	—	31.6	—	3.3	—	—	—	—	—	—	8.6	—	—	—	Janeke, 1995
100			100.0	—	10.3	—	—	—	—	—	—	27.2	—	—	—	
	Brussel sprouts *Brassica oleracea* var. *bullata gemmifera*															
101	raw	—	14.0	—	3.4	0.3	0.05	0.10	1.4	3.8	2.5	1.5	—	1.1	—	USDASR14; Schmidt et al., 1999
102			100.0	4.24	27.2	2.1	0.32	0.71	9.8	27.1	18.1	10.6	—	7.5	—	
	Buckwheat, common *Fagopyrum sagittatum*															
103	grain	4-00-994	88.0	—	11.1	2.4	0.53	—	2.1	—	17.8	14.3	—	3.5	—	NRC, 1998
104			100.0	4.38	12.6	2.7	0.60	—	2.4	—	20.2	16.3	—	4.0	—	
105	middlings	5-00-991	89.0	—	29.8	7.3	—	—	4.9	—	—	—	—	—	—	NRC, 1982
106			100.0	4.86	33.5	8.2	—	—	5.5	—	—	—	—	—	—	
	Cabbage *Brassica oleracea* var. *capitata*															
107	raw	—	7.8	—	1.4	0.3	0.05	0.07	0.7	2.3	1.4	0.8	—	0.5	—	USDASR14; Schmidt et al., 1999
108			100.0	4.21	18.3	3.4	0.66	0.87	9.0	29.3	17.2	10.4	—	6.8	—	
	Cabbage, bok choy															
109	raw	—	4.8	—	1.1	—	—	—	0.5	—	0.6	0.5	—	0.1	—	Schmidt et al., 1999
110			100.0	—	23.7	—	—	—	10.5	—	13.3	10.3	—	3.0	—	
	Cabbage, napa *Brassica pekinensis*															
111	raw	—	3.5	—	1.0	—	—	—	0.4	—	0.6	0.5	—	0.1	—	Schmidt et al., 1999
112			100.0	—	27.6	—	—	—	10.2	—	17.1	14.0	—	3.1	—	
	Carambola *Averrhoa carambola*															
113	fruit, raw	—	9.1	—	0.5	0.4	0.16	0.03	0.4	2.7	1.2	—	—	—	—	USDASR14
114			100.0	4.27	6.0	3.9	1.81	0.31	4.1	29.7	12.7	—	—	—	—	
	Carrot *Daucus carota*															
115	roots, fresh	—	12.2	—	1.0	0.2	0.07	0.01	0.9	—	1.2	1.1	—	0.1	—	USDASR14; Schmidt et al., 1999
116			100.0	4.04	8.4	1.6	0.55	0.08	7.1	—	9.7	8.9	—	0.8	—	
117	tops, fresh	—	16.0	—	2.1	0.6	—	—	2.4	—	—	3.7	—	—	—	Bath et al., 1999
118			100.0	3.89	13.1	3.8	—	—	15.0	—	—	23.0	—	—	—	
	Canola *Brassica napa*															
119	meal, sol. extr.	5-06-145	90.0	—	35.6	3.5	0.42	—	—	—	21.2	17.2	—	4.0	—	NRC, 1998
120			100.0	—	39.6	3.9	0.47	—	—	—	23.6	19.1	—	4.4	—	
121	oil	4-06-144	100.0	—	0.0	100.0	20.30	9.30	0.0	—	0.0	0.0	0.0	0.0	0.0	NRC, 1998
122			100.0	9.74	0.0	100.0	20.30	9.30	0.0	—	0.0	0.0	0.0	0.0	0.0	

(continues)

723845CH12 01-15-03 10:07:07

TABLE 12-1 (*continued*)

Entry Number	Description	International Feed Number[b]	Dry Matter (%)	Gross Energy[c] (kcal/g)	Crude Protein (%)	Crude Fat (%)	Linoleic Acid (%)	Linolenic Acid (%)	Ash (%)	TDF (%)	Plant Cell Wall Constituents: NDF (%)	ADF (%)	Cellulose (%)	Hemicellulose (%)	Lignin (%)	Data Source
	Casein (cattle)															
123	dehy	5-01-162	91.0	—	88.7	0.8	0.03	—	—	—	—	—	—	—	—	NRC, 1998
124			100.0	—	97.5	0.9	0.03	—	—	—	—	—	—	—	—	
	Cassava *Manihot esculenta*															
125	meal, dehydrated	4-01-152	88.0	—	3.3	0.5	—	—	—	—	7.7	4.6	—	3.1	—	NRC, 1998
126			100.0	—	3.8	0.6	—	—	—	—	8.8	5.2	—	3.5	—	
127	tubers, fresh	4-09-599	31.5	—	1.3	0.4	—	—	1.4	—	3.7	1.3	—	2.4	—	NRC, 1982; Schmidt et al., 1999
128			100.0	4.08	3.6	1.0	—	—	3.9	—	11.9	4.3	—	7.6	—	
	Cauliflower *Brassica oleracea* var. *botrytis*															
129	raw	—	8.1	—	2.0	0.2	0.02	0.08	0.7	2.5	1.5	1.4	—	0.2	—	USDASR14; Schmidt et al., 1999
130			100.0	4.27	24.5	2.6	0.28	0.94	8.8	30.9	19.1	17.2	—	1.9	—	
131	green, raw	—	10.2	—	3.0	0.3	0.03	0.10	0.9	3.2	—	—	—	—	—	USDASR14; Schmidt et al., 1999
132			100.0	4.36	28.9	2.9	0.28	1.02	8.6	31.3	—	—	—	—	—	
	Celery *Apium graveolens* var. *dulce*															
133	raw	—	5.4	—	0.8	0.1	0.07	0.00	0.8	1.7	0.8	0.7	—	0.2	—	USDASR14; Schmidt et al., 1999
134			100.0	3.83	14.0	2.6	1.29	0.00	15.3	31.7	15.7	12.6	—	3.1	—	
	Cereal															
135	screenings	4-02-156	90.0	—	12.1	3.7	—	—	5.4	—	—	—	—	—	—	NRC, 1982
136			100.0	4.31	13.4	4.1	—	—	6.0	—	—	—	—	—	—	
	Chalum *Inga* spp															
137	dehy, fruit	—	96.8	—	12.5	1.2	—	—	3.1	—	—	—	—	—	—	NRC, 1971
138			100.0	4.27	12.9	1.2	—	—	3.2	—	—	—	—	—	—	
139	dehy, pod	—	97.8	—	9.8	1.5	—	—	4.4	—	—	—	—	—	—	NRC, 1971
140			100.0	4.18	10.0	1.5	—	—	4.5	—	—	—	—	—	—	
141	dehy, seeds	—	93.5	—	20.2	1.0	—	—	2.0	—	—	—	—	—	—	NRC, 1971
142			100.0	4.43	21.6	1.1	—	—	2.1	—	—	—	—	—	—	
	Chayote *Cucurbita pepo*															
143	fruit, raw, with peel	—	5.8	—	0.8	0.1	0.05	0.08	0.3	1.7	1.2	0.8	—	0.3	—	USDASR14; Schmidt et al., 1999
144			100.0	4.32	12.9	4.3	0.67	5.7	29.5	16.6	12.1	—	4.5	—		
	Cherimoya *Annona cherimolia*															
145	fruit, raw	—	26.5	—	1.3	0.4	—	—	0.8	2.4	—	—	—	—	—	USDASR14
146			100.0	4.17	4.9	1.5	—	—	3.0	9.1	—	—	—	—	—	
	Cherry *Prunus* spp															
147	fruit, raw	—	13.9	—	1.0	0.3	0.05	0.04	0.4	1.6	—	—	—	—	—	USDASR14
148			100.0	4.25	7.2	2.2	0.33	0.32	2.9	11.5	—	—	—	—	—	
	Chicory *Cichorium intybus*															
149	greens, raw	—	8.0	—	1.7	0.3	0.11	0.02	1.3	4.0	—	—	—	—	—	USDASR14
150			100.0	3.96	21.3	3.8	1.40	0.24	16.3	50.0	—	—	—	—	—	
	Cockroach, American *Periplaneta americana*															
151	adult	—	33.3	1.84	21.1	—	—	—	1.9	—	—	4.2	—	—	—	Allen, 1989
152			100.0	5.52	63.5	—	—	—	5.6	—	—	12.6	—	—	—	
	Cockroach, Haitian *Blaberus discoidalus*															
153	adult	—	30.3	1.80	19.0	—	—	—	—	—	—	3.4	—	—	—	Allen, 1989
154			100.0	5.95	62.8	—	—	—	—	—	—	11.2	—	—	—	
	Coconut *Cocos nucifera*															
155	meal, sol. extr.	5-01-573	92.0	—	21.9	3.0	0.03	—	—	—	51.3	25.5	—	25.8	—	NRC, 1998
156			100.0	—	23.8	3.3	0.03	—	—	—	55.8	27.7	—	28.0	—	
157	oil	4-09-320	100.0	—	0.0	100.0	1.80	0.00	0.0	—	0.0	0.0	0.0	0.0	0.0	NRC, 1998
158			100.0	9.74	0.0	100.0	1.80	0.00	0.0	—	0.0	0.0	0.0	0.0	0.0	

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	Collard *Brassica oleracea* var.															
159	greens, raw	—	9.5	—	2.5	0.4	0.04	0.06	0.9	3.6	1.8	1.2	—	0.6	—	USDASR14; Schmidt et al., 1999
160			100.0	4.27	16.6	2.3	0.46	0.60	5.8	38.1	19.0	12.6	—	6.4	—	
	Corn, yellow *Zea mays indentata*															
161	bran	—	95.3	—	8.4	0.9	0.41	0.00	0.4	85.5	—	—	—	—	—	USDASR14
162			100.0	4.31	8.8	1.0	0.43	0.00	0.4	89.7	—	—	—	—	—	
163	cobs, ground	1-28-234	90.0	—	2.8	0.7	—	—	1.5	—	80.0	32.0	25.0	48.0	6.0	
164			100.0	4.16	3.2	0.7	—	—	1.7	—	89.0	35.0	28.0	54.0	7.0	
165	distillers' grain	5-02-842	94.0	—	24.8	7.9	4.46	—	—	—	40.4	17.5	—	22.9	—	NRC, 1998
166			100.0	—	26.4	8.4	4.74	—	—	—	43.0	18.6	—	24.4	—	
167	distillers' grain with solubles	5-02-843	93.0	—	27.7	8.4	2.15	—	—	—	34.6	16.3	—	18.3	—	NRC, 1998
168			100.0	—	29.8	9.0	2.31	—	—	—	37.2	17.5	—	19.7	—	
169	distillers' solubles	5-02-844	92.0	—	26.7	9.1	5.36	—	—	—	24.8	7.5	—	17.3	—	NRC, 1998
170			100.0	—	29.0	9.9	5.83	—	—	—	27.0	8.2	—	18.8	—	
171	flour, whole grain	—	89.1	—	6.9	3.9	1.71	0.05	1.5	13.4	—	—	—	—	—	USDASR14
172			100.0	4.43	7.8	4.3	1.92	0.06	1.6	15.0	—	—	—	—	—	
173	gluten feed	5-02-903	90.0	—	21.5	3.0	1.43	—	—	—	33.3	10.7	—	22.6	—	NRC, 1998
174			100.0	—	23.9	3.3	1.59	—	—	—	37.0	11.9	—	25.1	—	
175	gluten meal, 60% CP	5-28-242	90.0	—	60.2	2.9	1.17	—	—	—	8.7	4.6	—	4.1	—	NRC, 1998
176			100.0	—	66.9	3.2	1.30	—	—	—	9.7	5.1	—	4.6	—	
177	grain	4-02-935	89.0	—	8.3	3.9	1.92	—	—	—	9.6	2.8	—	6.8	—	NRC, 1998
178			100.0	—	9.3	4.4	2.16	—	—	—	10.8	3.1	—	7.6	—	
179	grits by-product (Hominy Feed)	4-03-011	90.0	—	10.3	6.7	2.97	—	—	—	28.5	8.1	—	20.4	—	NRC, 1998
180			100.0	—	11.4	7.4	3.30	—	—	—	31.7	9.0	—	22.7	—	
181	oil	4-07-882	100.0	9.30	0.0	100.0	59.00	0.70	0.0	—	0.0	0.0	0.0	0.0	0.0	NRC, 1998
182			100.0	9.30	0.0	100.0	59.00	0.70	0.0	—	0.0	0.0	0.0	0.0	0.0	
183	starch	4-02-889	91.7	—	0.3	0.1	0.03	—	0.1	0.9	—	—	—	—	—	USDASR14
184			100.0	4.15	0.3	0.1	0.03	—	0.1	1.0	—	—	—	—	—	
185	syrup, light	—	77.2	—	0.0	0.0	0.00	—	0.4	0.0	—	—	—	—	—	USDASR14
186			100.0	4.12	0.0	0.0	0.00	—	0.5	0.0	—	—	—	—	—	
	Corn, sweet *Zea mays saccharata*															
187	cobs, fresh	—	31.7	—	1.4	—	—	—	0.4	—	24.6	12.6	—	12.0	—	Schmidt et al., 1999
188			100.0	—	4.5	—	—	—	1.3	—	77.5	39.6	—	37.8	—	
189	ear, whole, with husk, fresh	—	20.8	—	2.3	—	—	—	0.6	—	9.2	4.0	—	5.2	—	Schmidt et al., 1999
190			100.0	—	10.9	—	—	—	3.0	—	44.2	19.0	—	25.2	—	
191	husk, fresh	—	26.1	—	2.9	—	—	—	0.9	—	16.6	7.7	—	8.9	—	Schmidt et al., 1999
192			100.0	—	11.1	—	—	—	3.5	—	63.7	29.6	—	34.1	—	
193	white, raw, ep	—	24.0	—	3.2	1.2	0.54	0.02	0.6	2.7	1.6	—	—	—	—	USDASR14
194			100.0	4.50	13.4	4.9	2.25	0.07	2.6	11.2	6.7	—	—	—	—	
195	yellow, raw, ep	—	24.0	—	3.2	1.2	0.54	0.02	0.6	2.7	1.6	—	—	—	—	USDASR14
196			100.0	4.51	13.4	4.9	2.25	0.07	2.6	11.2	6.7	—	—	—	—	
	Corn borer, European *Ostrinia nubilalis*															
197	larvae	—	27.3	1.55	16.5	4.7	—	—	0.8	—	—	3.6	—	—	—	Allen, 1989
198			100.0	5.69	60.4	17.2	—	—	2.9	—	—	13.1	—	—	—	
199	pupae	—	28.0	1.57	18.0	4.8	—	—	0.7	—	—	4.3	—	—	—	Allen, 1989
200			100.0	5.60	64.2	17.0	—	—	2.6	—	—	15.4	—	—	—	
	Cottonseed *Gossypium* spp															
201	meal, mech. extr., 41% CP	5-01-617	92.0	—	42.4	6.1	3.15	—	—	—	25.7	18.0	—	7.7	—	NRC, 1998
202			100.0	—	46.1	6.6	3.42	—	—	—	27.9	19.6	—	8.4	—	
203	meal, sol. extr. 41% CP	5-07-872	90.0	—	41.4	1.5	0.51	—	—	—	28.4	19.4	—	9.0	—	NRC, 1998
204			100.0	—	46.0	1.7	0.57	—	—	—	31.6	21.6	—	10.0	—	
	Crayfish, Mexico *Cambrus* sp., *Aegiale hesperiaris*															
205	adult	—	33.5	—	17.2	1.3	—	—	12.4	—	—	—	—	—	—	Massieu et al., 1951
206			100.0	3.51	51.3	4.0	—	—	36.9	—	—	—	—	—	—	
	Cricket, house *Acheta domesticus*															
207	adult	—	29.6	1.60	19.6	5.7	—	—	1.4	—	6.8	2.9	—	—	—	Allen, 1989; Finke, 2002
208			100.0	5.34	66.2	20.1	—	—	4.9	—	22.1	9.7	—	—	—	
209	juvenile	—	22.9	—	15.4	3.3	—	—	1.1	—	3.6	2.2	—	—	—	Finke, 2002
210			100.0	—	67.2	14.4	—	—	4.8	—	15.7	9.6	—	—	—	

(continues)

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TABLE 12-1 (*continued*)

Entry Number	Description	International Feed Number[b]	Dry Matter (%)	Gross Energy[c] (kcal/g)	Crude Protein (%)	Crude Fat (%)	Linoleic Acid (%)	Linolenic Acid (%)	Ash (%)	TDF (%)	Plant Cell Wall Constituents: NDF (%)	ADF (%)	Cellulose (%)	Hemicellulose (%)	Lignin (%)	Data Source
	Cricket, mormon *Anabrus simplex*															
211	adult, both sexes	—	29.7	—	17.2	4.5	—	—	2.1	—	—	—	—	—	—	DeFoliart et al., 1982
212			100.0	5.55	58.0	15.1	—	—	7.1	—	—	—	—	—	—	
	Cucumber *Cucumis sativus*															
213	raw, with peel	—	4.0	—	0.7	0.1	0.02	0.03	0.4	0.8	0.7	0.6	—	0.1	—	USDASR14; Schmidt et al., 1999
214			100.0	4.13	17.3	3.3	0.55	0.75	10.3	20.1	18.6	15.5	—	3.2	—	
	Custard apple *Annona* spp															
215	fruit, raw	—	28.5	—	1.7	0.6	—	—	1.0	2.4	—	—	—	—	—	USDASR14
216			100.0	4.20	6.0	2.1	—	—	3.5	8.4	—	—	—	—	—	
	Dandelion *Taraxacum officinale*															
217	greens, raw	2-01-748	14.4	0.45	2.7	0.7	0.26	0.04	1.8	3.5	—	—	—	—	—	USDASR14
218			100.0	3.13	18.8	4.9	1.81	0.31	12.5	24.3	—	—	—	—	—	
	Dock *Rumex* spp.															
219	greens, raw	—	7.0	—	2.0	0.7	—	—	1.1	2.9	—	—	—	—	—	USDASR14
220			100.0	4.44	28.6	10.0	—	—	15.7	41.4	—	—	—	—	—	
	Egg (Chicken)															
221	dehy, whole	—	96.9	—	47.4	41.0	4.61	0.11	3.7	0.0	—	—	—	—	—	USDASR14
222			100.0	7.08	48.9	42.3	4.76	0.11	3.8	0.0	—	—	—	—	—	
	Eggplant *Solanum melongena*															
223	fruit, raw	—	8.0	—	1.0	0.2	0.06	0.01	0.7	2.5	1.8	0.9	—	0.9	—	USDASR14; Schmidt et al., 1999
224			100.0	4.07	12.8	2.3	0.79	0.16	8.9	31.4	22.0	11.0	—	11.0	—	
	Fababean (Broadbean) *Phaseolus* spp															
225	seeds	5-09-262	87.0	—	25.4	1.4	0.62	—	—	—	13.7	9.7	—	4.0	—	NRC, 1998
226			100.0	—	29.2	1.6	0.71	—	—	—	15.7	11.1	—	4.6	—	
	Fat															
227	animal, hydrolyzed	4-00-376	100.0	9.50	0.0	100.0	3.10	0.60	0.0	0.0	0.0	0.0	0.0	0.0	0.0	USDASR11
228			100.0	9.50	0.0	100.0	3.10	0.60	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
229	animal, poultry	4-00-409	99.8	9.50	0.0	99.8	19.50	1.00	0.0	0.0	0.0	0.0	0.0	0.0	0.0	USDASR14
230			100.0	9.52	0.0	100.0	19.54	1.00	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
231	animal, swine (lard)	4-04-790	100.0	9.50	0.0	100.0	10.20	1.00	0.0	0.0	0.0	0.0	0.0	0.0	0.0	USDASR14
232			100.0	9.50	0.0	100.0	10.20	1.00	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
	Feather															
233	meal, hydrolyzed	5-03-795	93.0	—	84.5	4.6	0.83	—	—	—	—	—	—	—	—	NRC, 1981
234			100.0	—	90.9	4.9	0.89	—	—	—	—	—	—	—	—	
	Feijoa *Feijoa sellowiana*															
235	fruit, raw	—	13.4	—	1.2	0.8	—	—	0.7	0.0	—	—	—	—	—	USDASR14
236			100.0	4.37	9.3	5.8	—	—	5.5	0.0	—	—	—	—	—	
	Ficus nitida															
237	leaves, mature, fresh	—	35.3	—	3.1	—	—	—	—	—	—	13.1	—	—	—	Janeke, 1995
238			100.0	—	8.8	—	—	—	—	—	—	37.2	—	—	—	
	Ficus rumphii															
239	leaves, mature, fresh	—	29.6	—	4.3	—	—	—	—	—	—	7.9	—	—	—	Janeke, 1995
240			100.0	—	14.4	—	—	—	—	—	—	26.6	—	—	—	
	Ficus thonningii															
241	leaves, mature, fresh	—	27.7	—	4.2	—	—	—	—	—	—	9.4	—	—	—	Janeke, 1995
242			100.0	—	15.1	—	—	—	—	—	—	33.9	—	—	—	
	Fig *Ficus carica*															
243	fruit, raw	—	20.9	—	0.8	0.3	0.14	—	0.7	3.3	—	—	—	—	—	USDASR14
244			100.0	4.14	3.6	1.4	0.69	—	3.2	15.8	—	—	—	—	—	
245	fruit, dried	—	64.9	—	2.7	—	—	—	1.7	—	6.5	5.2	—	1.3	—	Schmidt et al., 1999
246			100.0	—	4.2	—	—	—	2.6	—	10.0	8.0	—	2.0	—	
247	leaves, mature, fresh	—	23.5	—	3.7	—	—	—	—	—	—	4.0	—	—	—	Janeke, 1995
248			100.0	—	15.8	—	—	—	—	—	—	16.9	—	—	—	

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	Fig, cluster *Ficus glomerata*															
249	leaves, fresh	2-27-209	30.0	—	3.4	—	—	—	—	—	—	—	—	—	—	NRC, 1981
250			100.0	—	11.2	—	—	—	—	—	—	—	—	—	—	
251	leaves, mature, fresh	—	32.8	—	3.7	—	—	—	—	—	—	9.3	—	—	—	Janeke, 1995
252			100.0	—	11.4	—	—	—	—	—	—	28.3	—	—	—	
	Fig, Indian laurel *Ficus retusa*															
253	leaves, mature, fresh	—	38.0	—	3.2	—	—	—	—	—	—	13.7	—	—	—	Janeke, 1995
254			100.0	—	8.5	—	—	—	—	—	—	36.1	—	—	—	
	Fig, Moreton bay *Ficus macrophylla*															
255	leaves, mature, fresh	—	37.0	—	3.2	—	—	—	—	—	—	10.1	—	—	—	Janeke, 1995
256			100.0	—	8.6	—	—	—	—	—	—	27.3	—	—	—	
	Fig, Roxburgh *Ficus roxburghii*															
257	leaves, fresh	2-30-177	33.0	—	4.5	—	—	—	—	—	—	—	—	—	—	NRC, 1981
258			100.0	—	13.4	—	—	—	—	—	—	—	—	—	—	
	Fig, rustyleaf *Ficus rubiginosa*															
259	leaves, mature, fresh	—	30.6	—	3.1	—	—	—	—	—	—	9.3	—	—	—	Janeke, 1995
260			100.0	—	10.1	—	—	—	—	—	—	30.3	—	—	—	
	Fig, spotted *Ficus virens*															
261	leaves, fresh	2-28-704	15.0	—	1.7	—	—	—	—	—	—	—	—	—	—	NRC, 1981
262			100.0	—	11.2	—	—	—	—	—	—	—	—	—	—	
	Fish															
263	solubles, condensed	5-01-969	51.0	—	32.7	6.5	0.20	—	—	—	—	—	—	—	—	NRC, 1998
264			100.0	—	64.1	12.7	0.39	—	—	—	—	—	—	—	—	
265	solubles, dried	5-01-971	92.0	—	64.2	7.4	0.12	—	—	—	—	—	—	—	—	NRC, 1998
266			100.0	—	69.8	8.0	0.13	—	—	—	—	—	—	—	—	
	Fish, anchovy *Engraulis ringen*															
267	meal, mech. extr.	5-01-985	92.0	—	64.6	7.9	0.27	—	—	—	—	—	—	—	—	NRC, 1998
268			100.0	—	70.2	8.6	0.29	—	—	—	—	—	—	—	—	
	Fish, herring *Clupea harengus*															
269	meal, mech. extr.	5-02-000	93.0	—	68.1	9.2	0.15	—	—	—	—	—	—	—	—	NRC, 1998
270			100.0	—	73.2	9.9	0.16	—	—	—	—	—	—	—	—	
	Fish, menhaden *Brevoortia tyrannus*															
271	meal, mech. extr.	5-02-009	92.0	—	62.3	9.4	0.11	—	—	—	—	—	—	—	—	NRC, 1998
272			100.0	—	67.7	10.2	0.12	—	—	—	—	—	—	—	—	
	Fish, white Gadidae (family); Lophiidae (family)															
273	meal, mech. extr.	5-02-025	91.0	—	63.3	4.8	0.08	—	—	—	—	—	—	—	—	NRC, 1998
274			100.0	—	69.6	5.3	0.09	—	—	—	—	—	—	—	—	
	Flax *Linum usitatissinum*															
275	meal, sol. extr.	5-02-048	90.0	—	33.6	1.7	0.37	—	—	—	23.9	15.0	—	8.9	—	NRC, 1998
276			100.0	—	37.3	1.9	0.41	—	—	—	26.6	16.7	—	9.9	—	
	Fructose															
277		—	99.5	3.96	0.0	0.0	0.00	—	—	—	—	—	—	—	—	IOM, 1996
278			100.0	3.98	0.0	0.0	0.00	—	—	—	—	—	—	—	—	
	Gelatin															
279		5-14-503	90.0	—	88.6	0.5	—	—	—	—	—	—	—	—	—	NRC, 1998
280			100.0	—	98.4	0.6	—	—	—	—	—	—	—	—	—	
	Glucose															
281	monohydrate	4-02-125	90.0	3.75	0.3	—	—	—	—	—	—	—	—	—	—	NRC, 1998
282			100.0	4.17	0.3	—	—	—	—	—	—	—	—	—	—	
	Granadilla, purple *Passiflora edulis*															
283	fruit, raw, ep	—	27.1	—	2.2	0.7	0.41	0.00	0.8	10.4	—	—	—	—	—	USDASR14
284			100.0	4.28	8.1	2.6	1.51	0.00	3.0	38.4	—	—	—	—	—	
	Grape, European type *Vitis* spp															
285	fruit, raw, ep	—	19.4	—	0.7	0.6	0.13	0.04	0.4	1.0	1.7	—	—	—	—	USDASR14
286			100.0	4.26	3.4	3.0	0.67	0.20	2.3	5.1	8.5	—	—	—	—	
	Grapefruit *Citrus paradisi*															
287	fruit, raw, ep	—	9.1	—	0.6	0.1	0.02	0.01	0.3	1.1	—	—	—	—	—	USDASR14
288			100.0	4.16	6.9	1.1	0.21	0.05	3.4	12.1	—	—	—	—	—	
289	peel	—	29.1	—	1.5	—	—	—	1.3	—	5.0	4.6	—	0.2	—	Schmidt et al., 1999
290			100.0	—	5.0	—	—	—	4.4	—	17.2	15.7	—	1.4	—	

(continues)

723845CH12 12-23-02 13:02:28

TABLE 12-1 (*continued*)

Entry Number	Description	International Feed Number[b]	Dry Matter (%)	Gross Energy[c] (kcal/g)	Crude Protein (%)	Crude Fat (%)	Linoleic Acid (%)	Linolenic Acid (%)	Ash (%)	TDF (%)	Plant Cell Wall Constituents: NDF (%)	ADF (%)	Cellulose (%)	Hemicellulose (%)	Lignin (%)	Data Source
	Grasshopper *Melanoplus femurrubrum*															
291	adult	—	30.5	1.60	24.2	1.9	—	—	1.5	—	—	—	—	—	—	Bird et al., 1982
292			100.0	5.25	79.2	6.3	—	—	5.0	—	—	—	—	—	—	
	Guava, common or lemon *Psidium guajava*															
293	fruit, raw, ep	—	13.9	—	0.8	0.6	0.18	0.07	0.6	5.4	—	—	—	—	—	USDASR14
294			100.0	4.28	5.9	4.3	1.31	0.51	4.3	38.8	—	—	—	—	—	
	Guava, strawberry *Psidium cattleianum*															
295	fruit, raw, ep	—	19.3	—	0.6	0.6	0.18	0.07	0.8	5.4	—	—	—	—	—	USDASR14
296			100.0	4.18	3.0	3.1	0.94	0.37	4.1	27.9	—	—	—	—	—	
	Hemicellulose extract															
297		4-08-030	76.0	—	0.6	0.3	—	—	3.1	—	—	—	—	—	—	NRC, 1982
298			100.0	4.00	0.7	0.4	—	—	4.1	—	—	—	—	—	—	
	Hibiscus, tropical *Hibiscus rosa-sinensis*															
299	leaves, mature, fresh	—	21.9	—	3.3	—	—	—	—	—	—	2.5	—	—	—	Janeke, 1995
300			100.0	—	15.1	—	—	—	—	—	—	11.3	—	—	—	
	Honeysuckle *Lonicera albiflora*															
301	leaves, fresh	2-29-875	33.0	—	3.3	—	—	—	—	—	6.0	—	—	—	—	NRC, 1981
302			100.0	—	10.0	—	—	—	—	—	20.0	—	—	—	—	
	Jack fruit *Artocarpus heterophyllus*															
303	fruit, raw, ep	—	26.8	—	1.5	0.3	0.06	0.02	1.0	1.6	—	—	—	—	—	USDASR14
304			100.0	4.12	5.5	1.1	0.24	0.09	3.7	6.0	—	—	—	—	—	
	Jujube *Zizyphus jujuba*															
305	browse, fresh	2-30-091	32.0	—	2.7	—	—	—	—	—	—	—	—	—	—	NRC, 1981
306			100.0	—	8.6	—	—	—	—	—	—	—	—	—	—	
307	fruit, raw, ep	—	22.1	—	1.2	0.2	—	—	0.5	0.0	—	—	—	—	—	USDASR14
308			100.0	4.17	5.4	0.9	—	—	2.3	0.0	—	—	—	—	—	
	Kale *Brassica oleracea* var. *acephala*															
309	leaves and stems, fresh	—	15.5	—	3.3	0.7	0.14	0.18	1.5	2.0	2.8	2.0	—	0.8	—	USDASR14; Schmidt et al., 1999
310			100.0	4.28	21.2	4.5	0.89	1.16	9.8	12.9	18.2	13.3	—	5.1	—	
	Kiwifruit *Actinidia chinensis*															
311	raw	—	17.0	—	1.0	0.4	0.21	0.04	0.6	—	2.7	2.1	—	0.6	—	USDASR14; Schmidt et al., 1999
312			100.0	4.21	5.8	2.6	1.22	0.21	3.8	—	16.2	12.6	—	3.5	—	
	Kohlrabi *Brassica oleracea* var. *gongylodes*															
313	tubers, fresh	—	9.0	—	1.7	0.1	0.02	0.03	1.0	3.6	1.1	—	—	—	—	USDASR14
314			100.0	4.00	18.9	1.1	0.22	0.29	11.1	40.0	12.2	—	—	—	—	
	Kudzu *Pueraria lobata*															
315	aerial part, fresh	2-02-482	26.4	—	4.6	0.7	—	—	2.0	—	—	—	—	—	—	NRC, 1971
316			100.0	4.22	17.6	2.7	—	—	7.6	—	—	—	—	—	—	
	Kumquat *Fortunella* spp															
317	fruit, raw, ep	—	18.3	—	0.9	0.1	0.02	0.01	0.9	6.6	—	—	—	—	—	USDASR14
318			100.0	4.04	4.9	0.6	0.10	0.03	4.8	36.1	—	—	—	—	—	
	Lactose															
319		07-881	96.0	—	0.3	—	—	—	—	—	—	—	—	—	—	NRC, 1998
320			100.0	—	0.3	—	—	—	—	—	—	—	—	—	—	
	Lentil *Len culinaris*															
321	seeds	5-02-506	89.0	—	24.4	1.3	0.41	—	—	—	10.1	5.4	—	4.7	—	NRC, 1998
322			100.0	—	27.4	1.5	0.46	—	—	—	11.3	6.1	—	5.3	—	
	Lettuce, endive *Cichorium endiva*															
323	leaves, fresh	—	6.2	—	1.3	0.2	0.08	0.01	1.4	3.1	—	—	—	—	—	USDASR14
324			100.0	3.64	20.9	3.2	1.21	0.21	22.7	49.9	—	—	—	—	—	

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	Lettuce, iceberg *Lactuca sativa*															
325	leaves, fresh	—	4.1	—	1.0	0.2	0.03	0.07	0.5	1.4	0.7	0.5	—	0.2	—	USDASR14; Schmidt et al., 1999
326			100.0	4.26	24.6	4.6	0.71	1.73	11.7	34.1	16.9	13.1	—	3.9	—	
	Lettuce, romaine															
327	leaves, fresh	—	5.1	—	1.6	0.2	0.04	0.08	0.9	1.7	1.1	1.0	—	0.2	—	USDASR14; Schmidt et al., 1999
328			100.0	4.06	31.8	3.9	0.61	1.07	17.7	33.4	16.3	14.1	—	2.2	—	
	Longan *Nephelium longana*															
329	fruit, raw, ep	—	17.3	—	1.3	0.1	—	—	0.7	1.1	—	—	—	—	—	USDASR14
330			100.0	4.11	7.6	0.6	—	—	4.1	6.4	—	—	—	—	—	
	Loquat *Eriobotrya japonica*															
331	fruit, raw, ep	—	13.3	—	0.4	0.2	0.08	0.01	0.5	1.7	—	—	—	—	—	USDASR14
332			100.0	4.11	3.2	1.5	0.58	0.10	3.8	12.8	—	—	—	—	—	
	Lupin (sweet white) *Lupinus albus*															
333	seeds	5-27-717	89.0	—	34.9	9.2	1.62	—	—	—	20.3	16.7	—	3.6	—	NRC, 1998
334			100.0	—	39.2	10.3	1.82	—	—	—	22.8	18.8	—	4.0	—	
	Lychee *Litchi chinensis*															
335	fruit, raw, ep	—	18.2	—	0.8	0.4	0.07	0.07	0.4	1.3	—	—	—	—	—	USDASR14
336			100.0	4.24	4.6	2.4	0.37	0.36	2.4	7.1	—	—	—	—	—	
	Mango *Mangifera indica*															
337	fruit, raw, ep	—	18.3	—	0.5	0.3	0.01	0.04	0.5	1.8	2.1	1.1	—	1.0	—	USDASR14; Schmidt et al., 1999
338			100.0	4.15	2.8	1.5	0.08	0.20	2.7	9.8	11.5	6.3	—	5.3	—	
	Maple, sugar *Acer saccharum*															
339	leaves	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Robbins and Moen, 1975
340			100.0	—	—	—	—	—	—	—	58.9	43.9	23.9	15.0	18.6	
	Mealworm *Tenebrio molitor*															
341	larvae	—	37.1	2.78	18.1	14.3	—	—	1.3	—	5.7	2.5	—	—	—	Allen, 1989; Finke, 2002
342			100.0	7.49	48.7	38.4	—	—	3.5	—	15.4	6.7	—	—	—	
343	larvae, gut loaded with high (8%) Ca diet	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
344			—	—	—	—	—	—	—	—	—	—	—			
345	oversized	—	39.0	—	18.4	16.8	—	—	1.2	—	2.9	2.5	—	—	—	Finke, 2002
346			100.0	—	47.2	43.1	—	—	3.1	—	7.4	6.4	—	—	—	
	Mealworm *Zophobas morio*															
347	larvae	—	42.1	—	19.7	17.7	—	—	1.0	—	3.9	2.7	—	—	—	Finke, 2002
348			100.0	—	46.8	42.0	—	—	2.4	—	9.3	6.4	—	—	—	
	Meat															
349	meal rendered	5-00-385	94.0	—	54.0	12.0	0.80	—	—	—	31.6	8.3	—	—	—	NRC, 1998
350			100.0	—	57.4	12.8	0.85	—	—	—	33.6	8.8	—	—	—	
351	meal rendered with bone	5-00-388	93.0	—	51.5	10.9	0.72	—	—	—	32.5	5.6	—	—	—	NRC, 1998
352			100.0	—	55.4	11.7	0.77	—	—	—	34.9	6.0	—	—	—	
	Melon, cantaloupe *Cucumis melo*															
353	fruit, raw, ep	—	10.2	—	0.9	0.3	0.05	0.06	0.7	0.8	1.6	1.5	—	0.1	—	USDASR14; Schmidt et al., 1999
354			100.0	4.12	8.6	2.7	0.46	0.62	7.0	7.8	15.9	14.5	—	1.3	—	
355	fruit, raw, with peel	—	7.5	—	1.0	—	—	—	0.6	—	1.6	1.5	—	0.1	—	Schmidt et al., 1999
356			100.0	—	13.1	—	—	—	8.1	—	22.0	20.4	—	1.7	—	
	Melon, casaba *Cucumis melo*															
357	fruit, raw, ep	—	8.0	—	0.9	0.1	0.02	0.22	0.8	0.8	—	—	—	—	—	USDASR14
358			100.0	3.94	11.3	1.3	0.21	0.28	10.0	10.0	—	—	—	—	—	
	Melon, honeydew *Cucumis melo*															
359	fruit, raw, ep	—	10.3	—	0.5	0.1	0.02	0.02	0.6	0.6	1.8	1.5	—	0.3	—	USDASR14; Schmidt et al., 1999
360			100.0	4.20	4.5	4.5	0.16	0.21	5.8	5.8	17.4	14.1	—	3.4	—	
361	fruit, raw, with peel	—	8.1	—	0.7	—	—	—	0.5	—	1.2	1.0	—	0.2	—	Schmidt et al., 1999
362			100.0	—	8.9	—	—	—	6.5	—	15.0	12.5	—	2.5	—	
	Milk, cattle *Bos taurus*															
363	dehy	5-01-167	96.0	—	25.4	26.6	—	—	5.4	—	—	—	—	—	—	NRC, 1982
364			100.0	5.85	26.5	27.8	—	—	5.7	—	—	—	—	—	—	
365	fresh	5-01-168	12.0	—	3.3	3.6	—	—	0.8	—	—	—	—	—	—	NRC, 1982
366			100.0	5.92	26.7	29.5	—	—	6.3	—	—	—	—	—	—	

(continues)

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TABLE 12-1 (*continued*)

Entry Number	Description	International Feed Number[b]	Dry Matter (%)	Gross Energy[c] (kcal/g)	Crude Protein (%)	Crude Fat (%)	Linoleic Acid (%)	Linolenic Acid (%)	Ash (%)	TDF (%)	Plant Cell Wall Constituents: NDF (%)	ADF (%)	Cellulose (%)	Hemicellulose (%)	Lignin (%)	Data Source
367	skimmed, dehy	5-01-175	94.0	—	33.7	0.9	0.01	—	7.9	—	—	—	—	—	—	NRC, 1998
368			100.0	4.36	35.9	1.0	0.01	—	8.4	—	—	—	—	—	—	
369	skimmed, fresh	5-01-170	10.0	—	3.0	0.1	—	—	0.7	—	—	—	—	—	—	NRC, 1982
370			100.0	4.36	31.2	1.0	—	—	6.9	—	—	—	—	—	—	
	Milk, human *Homo sapiens*															
371	fresh	—	12.5	—	1.0	3.8	—	—	0.2	—	—	—	—	—	—	Jensen, 1995
372			100.0	6.16	8.0	30.4	—	—	1.6	—	—	—	—	—	—	
	Milk, baboon *Papio*															
373	fresh, days 0-5	—	14.6	—	2.3	5.1	—	—	0.3	—	—	—	—	—	—	Hummer, 1970
374			100.0	6.25	15.8	34.9	—	—	2.1	—	—	—	—	—	—	
375	fresh, days 6-11	—	15.3	—	1.7	5.8	—	—	0.3	—	—	—	—	—	—	Hummer, 1970
376			100.0	6.35	11.1	37.9	—	—	2.0	—	—	—	—	—	—	
377	fresh, days 12-35	—	14.0	—	1.5	4.6	—	—	0.3	—	—	—	—	—	—	Hummer, 1970
378			100.0	6.05	10.7	32.9	—	—	2.1	—	—	—	—	—	—	
379	fresh, days 36-279	—	14.4	—	1.6	5.0	—	—	0.3	—	—	—	—	—	—	Hummer, 1970
380			100.0	6.16	11.1	34.7	—	—	2.1	—	—	—	—	—	—	
	Millet *Panicum miliaceum*															
381	grain	4-03-120	90.0	—	11.1	3.5	1.92	—	—	—	15.8	13.8	—	2.0	—	NRC, 1998
382			100.0	—	12.3	3.9	2.13	—	—	—	17.6	15.3	—	2.2	—	
	Mirror plant *Coprosma repens*															
383	leaves, mature, fresh	—	17.5	—	2.2	—	—	—	—	—	—	2.6	—	—	—	Janeke, 1995
384			100.0	—	12.6	—	—	—	—	—	—	14.9	—	—	—	
	Molasses and syrup															
385	beet, sugar, molasses	4-00-668	78.0	3.95	6.6	0.2	—	—	8.8	—	—	—	—	—	—	NRC, 1982
386			100.0	5.06	8.5	0.2	—	—	11.3	—	—	—	—	—	—	
387	citrus, syrup	4-01-241	68.0	—	5.5	0.2	—	—	5.3	—	—	—	—	—	—	NRC, 1982
388			100.0	3.94	8.2	0.3	—	—	7.9	—	—	—	—	—	—	
389	sugarcane, molasses, dehy	4-04-695	94.0	3.95	9.7	0.9	—	—	12.5	—	—	—	—	—	—	NRC, 1982
390			100.0	4.20	10.3	0.9	—	—	13.3	—	—	—	—	—	—	
391	sugarcane, molasses, more than 46%	4-04-696	75.0	—	4.4	0.1	—	—	9.8	—	—	—	—	—	—	NRC, 1982
392			100.0	3.66	5.8	0.1	—	—	13.1	—	—	—	—	—	—	
	Mulberry *Morus* spp.															
393	browse, fresh	2-03-150	40.0	—	7.3	2.3	—	—	6.0	—	—	—	—	—	—	NRC, 1981
394			100.0	4.07	18.1	5.7	—	—	15.0	—	—	—	—	—	—	
395	fruit, raw, ep	—	12.3	—	1.4	0.4	0.21	0.00	0.7	1.7	—	—	—	—	—	USDASR14
396			100.0	4.25	11.7	3.2	1.67	0.01	5.6	13.8	—	—	—	—	—	
	Mulberry, white *Morus alba*															
397	leaves, mature, fresh	—	31.1	—	6.4	—	—	—	—	—	—	3.5	—	—	—	Janeke, 1995
398			100.0	—	20.6	—	—	—	—	—	—	11.3	—	—	—	
	Mustard *Brassica oleracea* var.															
399	leaves and stems, fresh	—	9.2	—	2.7	0.2	0.02	0.02	1.4	3.3	1.8	1.5	—	0.3	—	USDASR14; Schmidt et al., 1999
400			100.0	4.04	29.3	2.2	0.22	0.20	15.2	35.9	19.7	16.8	—	2.9	—	
	Nectarine *Prunus persica*															
401	fruit, raw, ep	—	13.7	—	0.9	0.5	0.22	0.01	0.5	1.6	1.0	0.4	—	0.6	—	USDASR14; Schmidt et al., 1999
402			100.0	4.26	6.9	3.4	1.64	0.04	3.9	11.7	7.3	3.2	—	4.1	—	
	Oat *Avena sativa*															
403	grain	4-03-309	89.0	—	11.5	4.5	1.49	—	3.1	—	27.0	13.5	—	13.5	—	NRC, 1998
404			100.0	4.47	12.9	5.1	1.67	—	3.5	—	30.3	15.2	—	15.2	—	
405	grain, naked	4-25-101	86.0	—	17.1	6.5	2.52	—	—	—	9.9	3.7	—	6.2	—	NRC, 1998
406			100.0	—	19.9	7.6	2.93	—	—	—	11.5	4.3	—	7.2	—	
407	groat	4-03-331	90.0	—	13.9	6.2	2.40	—	—	—	—	—	—	—	—	NRC, 1998
408			100.0	—	15.4	6.9	2.67	—	—	—	—	—	—	—	—	
409	hulls	1-03-281	92.0	—	3.6	1.6	—	—	6.1	—	72.0	39.0	28.0	33.0	7.0	NRC, 1982
410			100.0	4.01	3.9	1.8	—	—	6.6	—	78.0	42.0	30.0	36.0	8.0	

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	Olive *Olea europaea*															
411	oil	—	100.0	9.30	0.0	100.0	7.90	0.60	0.0	—	—	—	—	—	—	NRC, 1998
412			100.0	9.30	0.0	100.0	7.90	0.60	0.0	—	—	—	—	—	—	
	Okra *Hibiscus esculentus*															
413		—	10.4	—	2.0	0.1	0.03	0.00	0.7	3.2	1.8	1.2	—	0.6	—	USDASR14; Schmidt et al., 1999
414			100.0	4.12	17.4	1.0	0.25	0.01	7.6	30.7	14.2	9.8	—	4.4	—	
	Onion *Allium cepa*															
415	green	—	9.1	—	1.9	—	—	—	0.8	—	1.3	0.6	—	0.6	—	Schmidt et al., 1999
416			100.0	—	20.7	—	—	—	8.7	—	13.8	7.0	—	6.8	—	
417	red	—	9.1	—	1.4	—	—	—	0.5	—	0.9	0.7	—	0.2	—	Schmidt et al., 1999
418			100.0	—	15.5	—	—	—	5.1	—	9.5	7.4	—	2.1	—	
419	yellow	—	10.3	—	0.9	—	—	—	0.4	—	1.1	0.8	—	0.3	—	Schmidt et al., 1999
420			100.0	—	9.1	—	—	—	4.3	—	10.3	7.4	—	2.8	—	
	Orange *Citrus* spp															
421	fruit, raw, ep	—	13.3	—	0.9	0.1	0.02	0.01	0.4	2.4	2.4	—	—	—	—	USDASR14
422			100.0	4.15	7.1	0.9	0.14	0.05	3.3	18.1	18.1	—	—	—	—	
423	fruit, raw, with peel	—	17.7	—	1.3	0.3	0.04	—	0.6	4.5	—	2.5	—	—	—	USDASR14; Bath et al., 1999
424			100.0	4.20	7.3	1.7	0.25	—	3.4	25.4	—	14.0	—	—	—	
425	peel	—	27.5	—	1.5	0.2	0.03	—	0.8	10.6	4.4	3.6	—	0.8	—	USDASR14; Schmidt et al., 1999
426			100.0	4.14	5.5	0.7	0.11	—	2.9	38.5	16.0	13.3	—	2.7	—	
	Papaya *Carica papaya*															
427	fruit, raw, ep	—	11.2	—	0.6	0.1	0.01	—	0.6	1.8	1.5	1.4	—	0.2	—	USDASR14; Schmidt et al., 1999
428			100.0	4.05	5.5	1.3	0.05	—	5.5	16.1	13.7	12.2	—	1.6	—	
	Parsley															
429	leaves and stems, fresh	—	12.3	—	3.0	0.8	0.11	0.01	2.2	3.3	2.5	2.1	—	0.4	—	USDASR14; Schmidt et al., 1999
430			100.0	—	24.1	6.4	0.94	0.07	12.2	26.9	21.1	17.8	—	3.3	—	
	Parsnip *Pastinaca sativa*															
431	roots, fresh	—	20.5	—	1.2	0.3	0.04	0.00	1.0	4.9	—	—	—	—	—	USDASR14
432			100.0	4.10	5.9	1.5	0.20	0.01	4.8	23.9	—	—	—	—	—	
	Pea *Pisum* spp															
433	seeds	5-03-600	89.0	—	22.8	1.2	0.47	—	—	—	12.7	7.2	—	5.5	—	NRC, 1998
434			100.0	—	25.6	1.3	0.53	—	—	—	14.3	8.1	—	6.2	—	
	Peach *Prunus persica*															
435	fruit, raw, ep	—	12.3	—	0.7	0.1	0.04	0.00	0.5	2.0	0.6	—	—	—	—	USDASR14
436			100.0	4.10	5.7	0.7	0.36	0.01	3.7	16.2	5.0	—	—	—	—	
	Pear *Pyrus communis*															
437	fruit, raw, ep	—	16.2	—	0.4	0.4	0.09	—	0.3	2.4	2.6	1.5	—	1.1	—	USDASR14; Schmidt et al., 1999
438			100.0	4.24	2.4	2.5	0.57	—	1.7	14.8	16.4	9.5	—	6.8	—	
	Peanut (Groundnut) *Arachis hypogaea*															
439	butter	—	98.8	—	25.2	51.0	13.71	0.08	3.3	5.9	—	—	—	—	—	USDASR14
440			100.0	7.27	25.5	51.6	13.88	0.08	3.3	6.0	—	—	—	—	—	
441	hulls	1-08-028	91.0	—	7.1	1.8	—	—	3.8	—	67.0	59.0	36.0	8.0	21.0	NRC, 1982
442			100.0	4.19	7.8	2.0	—	—	4.2	—	74.0	65.0	40.0	9.0	23.0	
443	kernels, meal mech extr	5-03-649	92.0	—	43.2	6.5	1.73	—	—	—	14.6	9.1	—	5.5	—	NRC, 1998
444			100.0	—	47.0	7.1	1.88	—	—	—	15.9	9.9	—	6.0	—	
445	kernels, meal solv extr	5-03-650	92.0	—	49.1	1.2	0.30	—	—	—	16.2	12.2	—	4.0	—	NRC, 1998
446			100.0	—	53.4	1.3	0.33	—	—	—	17.6	13.3	—	4.3	—	
	Peepultree *Ficus religiosa*															
447	leaves, fresh	2-27-207	17.0	—	3.4	—	—	—	—	—	—	—	—	—	—	NRC, 1981
448			100.0	—	11.2	—	—	—	—	—	—	—	—	—	—	
	Pepper, sweet, green *Capsicum annuum*															
449	fruit, raw, ep	—	7.8	—	0.9	0.2	0.06	0.01	0.3	1.8	1.0	0.9	—	0.1	—	USDASR14; Schmidt et al., 1999
450			100.0	4.21	17.7	2.4	1.19	0.12	7.5	23.0	19.7	17.0	—	2.6	—	
	Persimmon, American *Diospyros virginiana*															
451	fruit, raw, ep	—	35.6	—	0.8	0.4	—	—	0.9	0.0	—	—	—	—	—	USDASR14
452			100.0	4.13	2.3	1.1	—	—	2.5	0.0	—	—	—	—	—	
	Persimmon, Oriental (Kaki) *Diospyros kaki*															
453	fruit, raw, ep	—	19.7	—	0.6	0.2	0.04	0.00	0.3	3.6	—	—	—	—	—	USDASR14
454			100.0	4.17	3.0	1.0	0.20	0.02	1.7	18.3	—	—	—	—	—	

(continues)

723845CH12 12-23-02 13:02:28

TABLE 12-1 (*continued*)

Entry Number	Description	International Feed Number[b]	Dry Matter (%)	Gross Energy[c] (kcal/g)	Crude Protein (%)	Crude Fat (%)	Linoleic Acid (%)	Linolenic Acid (%)	Ash (%)	TDF (%)	Plant Cell Wall Constituents: NDF (%)	ADF (%)	Cellulose (%)	Hemicellulose (%)	Lignin (%)	Data Source
	Pineapple *Ananas comosus*															
455	fruit, raw, ep	—	13.5	—	0.4	0.4	0.08	0.06	0.3	1.2	2.1	0.8	—	1.3	—	USDASR14; Schmidt et al., 1999
456			100.0	4.27	2.9	3.2	0.62	0.46	2.2	8.9	15.3	5.8	—	9.6	—	
	Plantain *Musa sapientum*															
457	fruit, raw, ep	—	34.7	—	1.3	0.4	0.04	0.03	1.2	2.3	3.0	0.8	—	2.2	—	USDASR14; Schmidt et al., 1999
458			100.0	4.11	3.7	1.1	0.12	0.07	3.4	6.6	8.6	2.3	—	6.4	—	
	Plum *Prunus domestica*															
459	fruit, raw, ep	—	14.8	—	0.8	0.6	0.13	0.00	0.4	1.5	0.9	0.5	—	0.4	—	USDASR14; Schmidt et al., 1999
460			100.0	4.34	5.3	4.2	0.91	0.00	2.6	10.1	6.1	3.6	—	2.5	—	
	Pomegranate *Punica granatum*															
461	fruit, raw, ep	—	19.0	—	1.0	0.3	0.06	0.00	0.6	0.6	—	—	—	—	—	USDASR14
462			100.0	4.17	5.0	1.6	0.33	0.00	3.2	3.2	—	—	—	—	—	
	Poplar, black *Populus nigra*															
463	leaves, sun-cured	1-03-750	85.4	—	16.1	2.7	—	—	5.9	—	—	—	—	—	—	NRC, 1971
464			100.0	4.30	18.8	3.2	—	—	6.9	—	—	—	—	—	—	
	Potato *Solanum tuberosum*															
465	protein concentrate	5-25-392	91.0	—	73.8	1.7	—	—	—	—	1.8	—	—	—	—	NRC, 1998
466			100.0	—	81.1	1.9	—	—	—	—	2.0	—	—	—	—	
467	tubers, fresh	—	28.0	—	2.7	0.1	0.04	0.01	1.1	—	2.1	0.7	—	1.4	—	USDASR11; Schmidt et al., 1999
468			100.0	4.14	9.7	0.5	0.15	0.05	4.0	—	7.5	2.5	—	5.0	—	
	Poultry															
469	by-product, meal rendered	5-03-798	93.0	—	64.1	11.6	1.72	—	—	—	—	—	—	—	—	NRC, 1998
470			100.0	—	68.9	12.5	1.85	—	—	—	—	—	—	—	—	
	Prune															
471	with pits	—	82.0	—	4.3	2.4	—	—	—	—	—	13.1	—	—	—	Bath et al., 1999
472			100.0	—	5.3	2.9	—	—	—	—	—	16.0	—	—	—	
473	without pits	—	80.0	—	3.3	1.1	—	—	—	—	—	2.4	—	—	—	Bath et al., 1999
474			100.0	—	4.1	1.4	—	—	—	—	—	3.0	—	—	—	
	Pummelo *Citrus grandis*															
475	fruit, raw, ep	—	10.9	—	0.8	0.0	—	—	0.5	1.0	—	—	—	—	—	USDASR14
476			100.0	4.07	7.0	0.4	—	—	4.4	9.2	—	—	—	—	—	
	Pumpkin *Cucurbita pepo*															
477		—	20.0	—	1.5	—	—	—	0.9	—	4.4	1.5	—	2.9	—	Schmidt et al., 1999
478			100.0	—	7.3	—	—	—	4.6	—	22.0	7.7	—	14.3	—	
	Quince *Cydonia oblonga*															
479	fruit, raw, ep	—	16.2	—	0.4	0.1	0.05	0.00	0.4	1.9	—	—	—	—	—	USDASR14
480			100.0	4.11	2.5	0.6	0.30	0.00	2.5	11.7	—	—	—	—	—	
	Radicchio *Cichorium intybus* var. *foliosum*															
481	raw	—	6.9	—	1.4	0.3	0.09	0.02	0.7	0.9	—	—	—	—	—	USDASR14
482			100.0	4.21	20.9	3.6	1.36	0.23	10.2	13.1	—	—	—	—	—	
	Radish *Raphanus sativus*															
483	raw	—	5.2	—	0.6	0.5	0.02	0.03	0.5	1.6	0.8	0.7	—	0.1	—	USDASR14; Schmidt et al., 1999
484			100.0	4.44	11.6	10.5	0.37	0.56	10.5	31.0	15.5	14.1	—	1.4	—	
	Raisin, golden seedless *Vitis vinifera*															
485	fruit, raw, ep	—	85.0	—	3.4	0.5	0.10	0.03	1.7	4.0	—	—	—	—	—	USDASR14
486			100.0	4.15	4.0	0.5	0.12	0.04	2.0	4.7	—	—	—	—	—	
	Raisin, seeded *Vitis vinifera*															
487	fruit, raw, ep	—	83.4	—	2.5	0.5	0.12	0.04	1.9	6.8	—	—	—	—	—	USDASR14
488			100.0	4.12	3.0	0.7	0.15	0.04	2.3	8.2	—	—	—	—	—	
	Raisin, seedless *Vitis vinifera*															
489	fruit, raw, ep	—	84.6	—	3.2	0.5	0.10	0.03	1.8	4.0	—	—	—	—	—	USDASR14
490			100.0	4.14	3.8	0.5	0.12	0.04	2.1	4.7	—	—	—	—	—	

72384$CH12 12-27-02 05:33:19

	Raspberry *Rubus idaeus*															
491	fruit, raw, ep	—	13.4	—	0.9	0.6	0.21	0.11	0.4	6.8	3.6	3.0	—	0.6	—	USDASR14; Schmidt et al., 1999
492			100.0	4.41	6.8	4.1	1.55	0.78	1.6	50.6	26.8	22.0	—	4.8	—	
	Rice *Oryza sativa*															
493	bran	4-03-928	90.0	—	13.3	13.0	4.12	—	—	—	23.7	13.9	—	9.8	—	NRC, 1998
494			100.0	—	14.8	14.4	4.58	—	—	—	26.3	15.4	—	10.9	—	
495	flour	—	88.1	—	6.0	1.4	0.31	0.07	0.6	2.4	—	—	—	—	—	USDASR14
496			100.0	4.30	6.8	1.6	0.36	0.08	0.7	2.7	—	—	—	—	—	
497	grain, polished and broken	4-03-932	89.0	—	7.9	1.0	0.28	—	—	—	12.2	3.1	—	9.1	—	NRC, 1998
498	(Brewer's Rice)		100.0	—	8.9	1.1	0.31	—	—	—	13.7	3.5	—	10.2	—	
499	hulls	1-08-075	92.0	—	3.0	0.7	—	—	19.0	—	76.0	66.0	30.0	9.2	15.0	NRC, 1982
500			100.0	3.33	3.3	0.8	—	—	20.6	—	82.0	72.0	33.0	10.0	16.0	
501	polishings	4-03-943	90.0	—	13.0	13.7	3.58	—	—	—	—	4.0	—	—	—	NRC, 1998
502			100.0	—	14.4	15.2	3.98	—	—	—	—	4.4	—	—	—	
	Rocket *Eruca sativa*															
503	aerial part, fresh	2-03-949	15.8	—	1.8	0.3	—	—	1.5	—	—	—	—	—	—	NRC, 1971
504			100.0	4.03	11.4	2.2	—	—	9.3	—	—	—	—	—	—	
	Rutabaga *Brassica campestris* var. *rutabaga*															
505	raw	—	10.3	—	1.2	0.2	0.04	0.05	0.8	2.5	1.5	1.1	—	0.4	—	USDASR14; Schmidt et al., 1999
506			100.0	4.08	11.6	1.9	0.34	0.51	7.8	24.2	14.5	11.0	—	3.5	—	
507	tops, fresh	—	10.9	—	2.0	1.5	—	—	2.2	—	—	2.0	—	—	—	Bath et al., 1999
508			100.0	4.34	18.6	14.1	—	—	19.9	—	—	18.0	—	—	—	
	Rye *Secale cereale*															
509	grain	4-04-047	88.0	—	11.8	1.6	0.76	—	—	—	12.3	4.6	—	7.7	—	NRC, 1998
510			100.0	—	13.4	1.8	0.86	—	—	—	14.0	5.2	—	8.8	—	
	Safflower *Carthamus tinctorius*															
511	hulls	—	91.3	—	3.3	3.4	—	—	1.6	—	—	66.6	—	—	—	Bath et al., 1999
512			100.0	4.33	3.6	3.7	—	—	1.8	—	—	73.0	—	—	—	
513	meal, sol. extr.	5-04-110	92.0	—	23.4	1.4	0.84	—	—	—	55.9	38.8	—	17.1	—	NRC, 1998
514			100.0	—	25.4	1.5	0.91	—	—	—	60.8	42.2	—	18.6	—	
515	meal without hulls, sol. extr.	5-07-959	92.0	—	42.5	1.3	0.74	—	—	—	25.9	18.0	—	7.9	—	NRC, 1998
516			100.0	—	46.2	1.4	0.80	—	—	—	28.2	19.6	—	8.6	—	
517	oil	4-20-526	100.0	9.30	—	100.0	74.10	0.40	—	—	—	—	—	—	—	NRC, 1998
518			100.0	9.30	—	100.0	74.10	0.40	—	—	—	—	—	—	—	
519	seeds	—	94.0	—	16.4	33.0	—	—	2.9	—	—	37.6	—	—	—	Bath et al., 1999
520			100.0	6.23	17.4	35.1	—	—	3.1	—	—	40.0	—	—	—	
	Sapote *Achras sapotas*															
521	fruit, raw, ep	—	22.0	—	0.4	1.1	0.01	—	0.5	—	4.5	1.4	—	3.1	—	Schmidt et al., 1999
522			100.0	4.35	2.0	5.0	0.05	—	2.3	—	20.4	6.4	—	14.0	—	
	Sesame *Sesamum indicum*															
523	meal, mech. extr.	5-04-220	93.0	—	42.6	7.5	3.07	—	—	—	18.0	13.2	—	4.8	—	NRC, 1998
524			100.0	—	45.8	8.1	3.30	—	—	—	19.4	14.2	—	5.2	—	
525	seeds	—	92.0	—	22.3	42.9	—	—	5.6	—	—	12.9	—	—	—	Bath et al., 1999
526			100.0	6.85	24.2	46.6	—	—	6.1	—	—	14.0	—	—	—	
	Sorghum *Sorghum bicolor*															
527	grain	4-20-893	89.0	—	9.2	2.9	1.08	—	—	—	18.0	8.3	—	9.7	—	NRC, 1998
528			100.0	—	10.3	3.3	1.21	—	—	—	20.2	9.3	—	10.9	—	
	Soybean *Glycine max*															
529	flour, full-fat, raw	—	94.8	—	34.5	20.7	10.28	1.38	4.5	9.6	—	—	—	—	—	USDASR14
530			100.0	5.70	36.4	21.8	10.84	1.46	4.7	10.1	—	—	—	—	—	
531	hulls	1-4-560	91.0	—	11.0	1.9	—	—	—	—	61.0	45.0	—	16.0	—	NRC, 1982
532			100.0	—	12.1	2.1	—	—	—	—	67.0	50.0	—	17.0	—	
533	meal, sol. extr.	5-04-604	89.0	—	43.8	1.0	0.55	—	—	—	13.3	9.4	—	3.9	—	NRC, 1998
534			100.0	—	49.2	1.1	0.62	—	—	—	14.9	10.6	—	4.4	—	
535	meal without hulls, sol. extr.	5-04-612	90.0	—	47.5	0.8	0.35	—	—	—	8.9	5.4	—	3.5	—	NRC, 1998
536			100.0	—	52.8	0.9	0.39	—	—	—	9.9	6.0	—	3.9	—	
537	protein concentrate	—	90.0	—	64.0	3.0	—	—	—	—	—	—	—	—	—	NRC, 1998
538			100.0	—	71.1	3.3	—	—	—	—	—	—	—	—	—	
539	protein isolate	5-08-038	92.0	—	85.8	0.6	—	—	—	—	—	—	—	—	—	NRC, 1998
540			100.0	—	93.3	0.7	—	—	—	—	—	—	—	—	—	

(continues)

TABLE 12-1 (*continued*)

Entry Number	Description	International Feed Number[b]	Dry Matter (%)	Gross Energy[c] (kcal/g)	Crude Protein (%)	Crude Fat (%)	Linoleic Acid (%)	Linolenic Acid (%)	Ash (%)	TDF (%)	Plant Cell Wall Constituents: NDF (%)	ADF (%)	Cellulose (%)	Hemicellulose (%)	Lignin (%)	Data Source
541	seeds, heat processed	5-04-597	90.0	—	35.2	18.0	9.13	—	—	—	13.9	8.0	—	5.9	—	NRC, 1998
542			100.0	—	39.1	20.0	10.14	—	—	—	15.4	8.9	—	6.6	—	
	Spinach *Spinacia oleracea*															
543	raw	—	8.4	—	2.9	0.4	0.02	0.12	1.7	2.7	1.7	1.0	—	0.7	—	USDASR14; Schmidt et al., 1999
544			100.0	3.99	34.0	4.2	0.26	1.37	20.4	32.1	20.1	11.7	—	8.4	—	
	Squash, acorn *Cucurbita maxima*															
545	raw	—	12.2	—	0.8	0.1	0.02	0.03	0.9	1.5	2.4	2.0	—	0.4	—	USDASR14; Schmidt et al., 1999
546			100.0	3.96	6.6	0.8	0.13	0.21	7.4	12.3	19.7	16.6	—	3.1	—	
	Squash, butternut *Cucurbita maxima*															
547	raw	—	13.6	—	1.0	0.1	0.02	0.03	0.8	0.0	2.4	2.0	—	0.4	—	USDASR14; Schmidt et al., 1999
548			100.0	4.04	7.4	0.7	0.12	0.19	5.9	0.0	17.5	14.7	—	2.8	—	
	Squash, spaghetti *Cucurbita maxima*															
549	raw	—	8.4	—	0.6	0.6	0.09	0.15	0.3	0.0	2.6	2.0	—	0.6	—	USDASR14; Schmidt et al., 1999
550			100.0	4.49	7.6	6.8	1.07	1.77	3.3	0.0	30.9	24.2	—	6.8	—	
	Squash, zucchini *Cucurbita pepo*															
551	raw, with peel	—	4.7	—	1.2	0.1	0.02	0.04	0.5	1.2	0.7	0.5	—	0.2	—	USDASR14; Schmidt et al., 1999
552			100.0	4.20	24.6	3.0	0.47	0.79	11.0	25.4	15.1	10.2	—	4.9	—	
	Strawberry *Fragaria* spp															
553	fruit, raw, ep	—	8.4	—	0.6	0.4	0.11	0.08	0.4	2.3	1.0	0.6	—	0.3	—	USDASR14; Schmidt et al., 1999
554			100.0	4.27	7.2	4.4	1.28	0.93	5.1	27.3	11.4	7.5	—	3.9	—	
	Sucrose															
555		4-04-701	99.0	—	0.0	0.0	—	—	—	—	—	—	—	—	—	NRC, 1998
556			100.0	3.95	0.0	0.0	—	—	—	—	—	—	—	—	—	
	Sugarcane *Saccharum officinarum*															
557	stems, fresh	2-13-248	15.0	0.56	1.2	0.1	—	—	0.9	—	11.0	—	5.0	4.0	2.0	NRC, 1982
558			100.0	3.75	7.6	0.7	—	—	6.0	—	73.3	—	34.0	30.0	11.0	
559	sugar	4-04-701	100.0	3.75	—	—	—	—	0.1	—	—	—	—	—	—	NRC, 1982
560			100.0	3.75	—	—	—	—	0.1	—	—	—	—	—	—	
	Sunflower, common *Helianthus annuus*															
561	kernels	—	95.0	—	25.7	44.2	—	—	3.8	—	—	6.7	—	—	—	Bath et al., 1999
562			100.0	6.98	27.1	46.5	—	—	4.0	—	—	7.0	—	—	—	
563	meal, sol. extr.	5-09-340	90.0	—	26.8	1.3	0.98	—	—	—	42.4	30.3	—	12.1	—	NRC, 1998
564			100.0	—	29.8	1.4	1.09	—	—	—	47.1	33.7	—	13.4	—	
565	meal without hulls, sol. extr.	5-04-739	93.0	—	42.2	2.9	1.07	—	—	—	27.8	18.4	—	9.4	—	NRC, 1998
566			100.0	—	45.4	3.1	1.15	—	—	—	29.9	19.8	—	10.1	—	
567	seeds	—	94.0	—	16.8	26.0	—	—	3.1	—	—	36.7	—	—	—	Bath et al., 1999
568			100.0	5.82	17.9	27.7	—	—	3.3	—	—	39.0	—	—	—	
	Sweet potato *Ipomoea batatas*															
569	tubers, fresh	—	27.2	—	1.7	0.3	0.11	0.02	1.0	3.0	5.4	1.3	—	4.1	—	USDASR14; Schmidt et al., 1999
570			100.0	4.14	6.1	1.1	0.41	0.07	3.5	11.0	20.0	4.9	—	15.2	—	
	Tamarind *Tamarindus indica*															
571	pulp	—	68.6	—	2.8	0.6	0.06	0.00	2.7	5.1	—	—	—	—	—	USDASR14
572			100.0	4.08	4.1	0.9	0.09	0.00	3.9	7.4	—	—	—	—	—	
573	seed	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Glew et al., 1997
574			100.0	—	17.3	—	—	—	—	—	—	—	—	—	—	
	Tomatillo															
575	fruit, raw, ep	—	8.4	—	1.0	1.0	0.38	0.02	0.6	1.9	2.1	1.4	—	0.7	—	USDASR14; Schmidt et al., 1999
576			100.0	4.75	14.3	12.2	4.80	0.19	6.6	22.7	26.2	17.8	—	8.4	—	
	Tomato *Lycopersicon esculentum*															
577	pomace, dehy	—	92.0	—	21.6	9.5	—	—	6.9	—	50.0	46.0	36.0	4.0	10.0	NRC, 1982; Bath et al., 1999
578			100.0	4.74	23.5	10.3	—	—	7.5	—	55.0	50.0	39.0	5.0	11.0	
579	red, ripe, raw, year-round average	—	6.2	—	0.9	0.3	0.13	0.01	0.4	—	1.0	0.9	—	0.1	—	USDASR14; Schmidt et al., 1999
580			100.0	4.35	13.6	5.3	2.08	0.08	6.7	—	16.6	14.2	—	2.4	—	

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	Triticale *Triticale hexaploide*															
581	grain	4-20-362	90.0	—	12.5	1.8	0.71	—	—	—	12.7	3.8	—	8.9	—	NRC, 1998
582			100.0	—	13.9	2.0	0.79	—	—	—	14.1	4.2	—	9.9	—	
	Turnip *Brassica rapa rapa*															
583	greens, raw	—	8.9	—	1.5	0.3	0.04	0.08	1.4	3.2	1.8	1.6	—	0.2	—	USDASR14; Schmidt et al., 1999
584			100.0	3.89	16.8	3.4	0.40	0.94	15.7	35.8	20.1	17.5	—	2.6	—	
585	tubers, fresh	—	8.1	—	0.9	0.1	0.01	0.04	0.7	1.8	1.6	1.2	—	0.4	—	USDASR14; Schmidt et al., 1999
586			100.0	4.00	11.1	1.2	0.15	0.49	8.6	22.1	19.7	14.6	—	5.1	—	
	Walnut															
587	meats, ground	—	91.0	—	41.7	8.7	—	—	5.3	—	—	4.6	—	—	—	Bath et al., 1999
588			100.0	5.11	45.8	9.6	—	—	5.8	—	—	5.0	—	—	—	
	Watermelon *Citrullus vulgaris*															
589	fruit, raw, ep	—	8.5	—	0.6	0.4	0.15	—	0.3	—	0.5	0.4	—	0.1	—	Schmidt et al., 1999
590			100.0	4.40	7.3	5.1	1.72	—	3.1	—	6.1	5.1	—	1.0	—	
591	fruit, raw, with peel	—	6.7	—	0.5	—	—	—	0.3	—	0.8	0.7	—	0.1	—	Schmidt et al., 1999
592			100.0	—	7.8	—	—	—	4.8	—	11.7	9.9	—	1.8	—	
	Waxmoth *Galleria mellonella*															
593	larvae	—	42.7	—	13.8	25.9	—	—	0.7	—	8.3	3.5	—	—	—	Allen, 1989; Finke, 2002
594			100.0	7.73	32.4	60.8	—	—	1.6	—	19.5	8.2	—	—	—	
	Wheat *Triticum aestivum*															
595	bran	4-05-190	89.0	—	15.7	4.1	2.25	—	—	—	42.1	13.0	—	29.1	—	NRC, 1998
596			100.0	—	17.6	4.6	2.53	—	—	—	47.3	14.6	—	32.7	—	
597	flour, less than 2% fiber (feed flour)	4-28-221	88.0	—	11.0	1.8	—	—	0.4	—	—	—	—	—	—	NRC, 1982
598			100.0	4.42	12.5	2.0	—	—	0.5	—	—	—	—	—	—	
599	germs, ground	5-05-218	88.0	—	24.8	8.4	—	—	4.2	—	—	—	—	—	—	NRC, 1982
600			100.0	4.89	28.1	9.5	—	—	4.7	—	—	—	—	—	—	
601	grain	4-05-211	89.0	—	14.2	1.8	0.58	—	1.7	—	—	—	—	—	—	NRC, 1982
602			100.0	4.41	16.0	2.0	0.65	—	1.9	—	—	—	—	—	—	
603	grain, hard red spring	4-05-258	88.0	—	14.1	2.0	—	—	—	—	—	—	—	—	—	NRC, 1998
604			100.0	—	16.0	2.3	—	—	—	—	—	—	—	—	—	
605	grain, hard red winter	4-05-268	88.0	—	13.5	2.0	0.93	—	—	—	13.5	4.0	—	9.5	—	NRC, 1998
606			100.0	—	15.3	2.3	1.06	—	—	—	15.3	4.5	—	10.8	—	
607	grain, soft red winter	4-05-294	88.0	—	11.5	1.9	—	—	—	—	—	—	—	—	—	NRC, 1998
608			100.0	—	13.1	2.2	—	—	—	—	—	—	—	—	—	
609	grain, soft white winter	4-05-337	89.0	—	11.8	2.1	0.83	—	—	—	12.0	3.7	—	8.3	—	NRC, 1998
610			100.0	—	13.3	2.4	0.93	—	—	—	13.5	4.2	—	9.3	—	
611	middlings, < 9.5% fiber	4-05-205	89.0	—	15.9	4.6	2.48	—	—	—	35.6	10.7	—	24.9	—	NRC, 1998
612			100.0	—	17.9	5.2	2.79	—	—	—	40.0	12.0	—	28.0	—	
613	mill run, less than 9.5% fiber	4-05-206	90.0	—	15.4	4.1	—	—	5.3	—	—	—	—	—	—	NRC, 1982
614			100.0	4.40	17.2	4.6	—	—	5.9	—	—	—	—	—	—	
615	red dog, < 4% fiber	4-05-203	88.0	—	15.3	3.3	—	—	—	—	18.7	4.3	—	14.4	—	NRC, 1998
616			100.0	—	17.4	3.8	—	—	—	—	21.3	4.9	—	16.4	—	
617	shorts, < 7% fiber	4-05-201	88.0	—	16.0	4.6	1.90	—	—	—	28.4	8.6	—	19.8	—	NRC, 1998
618			100.0	—	18.2	5.2	2.16	—	—	—	32.3	9.8	—	22.5	—	
	Whey (cattle)															
619	dried	4-01-182	96.0	—	12.1	0.8	0.01	—	—	—	—	—	—	—	—	NRC, 1998
620			100.0	—	12.6	0.9	0.01	—	—	—	—	—	—	—	—	
621	low lactose, dried	4-01-186	96.0	—	17.6	1.1	0.04	—	—	—	—	—	—	—	—	NRC, 1998
622			100.0	—	18.3	1.2	0.04	—	—	—	—	—	—	—	—	
623	permeate, dried	—	96.0	—	3.8	0.2	—	—	—	—	—	—	—	—	—	NRC, 1998
624			100.0	—	4.0	0.2	—	—	—	—	—	—	—	—	—	
	Willow *Salix* spp.															
625	browse, fresh	2-05-472	41.0	—	4.0	2.0	—	—	3.0	—	—	—	—	—	—	NRC, 1971
626			100.0	4.24	9.8	4.9	—	—	7.4	—	—	—	—	—	—	
	Willow, yellow *Salix lutea*															
627	browse	2-05-475	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1971
628			100.0	—	14.4	2.9	—	—	6.8	—	—	—	—	—	—	
	Wood															
629	sawdust	1-07-714	90.0	—	2.8	0.0	—	—	—	—	80.0	32.0	—	48.0	—	NRC, 1971
630			100.0	—	3.2	0.0	—	—	—	—	89.0	35.0	—	54.0	—	

(continues)

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TABLE 12-1 (*continued*)

Entry Number	Description	International Feed Number[b]	Dry Matter (%)	Gross Energy[c] (kcal/g)	Crude Protein (%)	Crude Fat (%)	Linoleic Acid (%)	Linolenic Acid (%)	Ash (%)	TDF (%)	Plant Cell Wall Constituents: NDF (%)	ADF (%)	Cellulose (%)	Hemicellulose (%)	Lignin (%)	Data Source
	Yam *Dioscorea alata*															
631	tubers, fresh	—	30.4	—	1.5	0.2	0.06	0.01	0.8	4.1	—	—	—	—	—	USDASR14
632			100.0	4.13	5.0	0.6	0.21	0.04	2.7	13.5	—	—	—	—		
	Yeast, brewers' *Saccharomyces cerevisiae*															
633	dried	7-05-527	93.0	—	45.9	1.0	0.05	—	—	—	4.0	3.0	—	1.0	—	NRC, 1998
634			100.0	—	49.4	1.1	0.05	—	—	—	4.3	3.2	—	1.1	—	
	Yeast, torula *Torulopsis utilis*															
635	dried	7-05-534	93.0	—	46.4	2.4	0.05	—	—	—	—	—	—	—	—	NRC, 1998
636			100.0	—	49.9	2.6	0.05	—	—	—	—	—	—	—	—	

[a] Dash indicates that no data were available.

[b] First digit is class of feed: 1, dry forages and roughages; 2, pasture, range plants, and forages fed green; 3, silages; 4, energy feeds; 5, protein supplements; 6, minerals; 7, vitamins; 8, additives; the other five digits are the International Feed Number.

[c] Gross energy values listed only on a dry matter basis (i.e., dry matter equals 100%) are calculated using the equation from Ewan, 1989: GE = 4.143 + (56 × %EE) + (15 × %CP) − (44 × %Ash).

[d] Edible portion.

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TABLE 12-2 Composition of Important Feeds: Minerals, Data Expressed As-Fed and Dry (100% Dry Matter)[a]

Entry Number	Description	International Feed Number[b]	Dry Matter (%)	Calcium (%)	Phosphorus (%)	Sodium (%)	Chlorine (%)	Potassium (%)	Magnesium (%)	Sulfur (%)	Copper (mg/kg)	Iodine (mg/kg)	Iron (mg/kg)	Manganese (mg/kg)	Selenium[c] (mg/kg)	Zinc (mg/kg)	Data Source
	Alder *Alnus* sp																
1	leaves, sun-cured	—	85	—	—	—	—	—	—	—	—	—	—	—	—	—	Bath et al., 1999
2			100	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Alfalfa *Medicago sativa*																
3	meal dehy, 15% CP	1-00-022	90.0	1.24	0.22	0.07	0.44	2.24	0.28	0.22	9.00	0.12	280.00	28.00	0.28	19.00	NRC, 1982
4			100.0	1.37	0.24	0.08	0.48	2.48	0.31	0.24	10.00	0.13	309.00	31.00	0.31	21.00	
5	meal dehy, 17% CP	1-00-023	92.0	1.53	0.26	0.09	0.47	2.30	0.23	0.29	10.00	0.15	333.00	32.00	0.34	24.00	NRC, 1998; NRC, 1982
6			100.0	1.66	0.28	0.10	0.51	2.50	0.25	0.32	10.87	0.16	361.96	34.78	0.37	26.09	
7	meal dehy, 20% CP	1-00-024	92.0	1.61	0.28	0.09	0.47	2.40	0.36	0.26	11.00	0.14	346.00	42.00	0.29	21.00	NRC, 1998; NRC, 1982
8			100.0	1.75	0.30	0.10	0.51	2.61	0.39	0.28	11.96	0.15	376.09	45.65	0.32	22.83	
9	meal dehy, 22% CP	1-07-851	93.0	1.69	0.30	0.12	0.52	2.40	0.31	0.30	10.00	0.17	355.00	36.00	—	19.00	NRC, 1982
10			100.0	1.82	0.33	0.13	0.56	2.58	0.33	0.32	11.00	0.18	383.00	39.00	—	21.00	
	Almond *Prunus amygdalus*																
11	hulls	4-00-359	90.0	0.21	0.10	—	—	0.47	0.10	—	—	—	—	—	—	—	NRC, 1982
12			100.0	0.23	0.11	—	—	0.53	0.11	—	—	—	—	—	—	—	
	Apple *Malus sylvestris*																
13	fruit, raw, with peel	—	16.07	0.01	0.01	0.00	—	0.12	0.01	—	0.40	—	1.80	0.50	0.00	0.40	USDASR14; Schmidt et al., 1999
14			100.0	0.04	0.04	0.00	—	0.72	0.03	—	2.49	—	11.20	3.11	0.00	2.49	
15	pomace, dehy	—	89	0.12	0.11	—	—	0.43	0.06	—	—	—	—	—	—	—	Bath et al., 1999
16			100.0	0.13	0.12	—	—	0.48	0.07	—	—	—	—	—	—	—	
17	pomace, oat hulls added, dehy	4-28-096	89	0.11	0.10	0.12	—	0.43	0.06	0.02	—	—	266.00	7.00	—	—	NRC, 1982
18			100.0	0.13	0.12	0.14	—	0.49	0.07	0.02	—	—	299.00	8.00	—	—	
	Apricot *Prunus armeniaca*																
19	fruit, dried, sulfured	—	68.9	0.05	0.12	0.01	—	1.38	0.05	—	4.30	—	47.00	2.80	0.02	7.40	USDASR14
20			100.0	0.07	0.17	0.02	—	2.00	0.07	—	6.20	—	68.20	4.00	—	10.70	
21	fruit, raw, ep	—	13.7	0.01	0.02	0.00	—	0.30	0.01	—	0.90	—	5.40	0.80	0.00	2.60	USDASR14; Schmidt et al., 1999
22			100.0	0.10	0.14	0.01	—	2.17	0.06	—	6.50	—	39.60	5.80	—	19.00	
	Ash *Fraxinus* spp.																
23	leaves, sun-cured	—	85	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1971
24			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Asparagus *Asparagus officinalis*																
25	spear, raw	—	7.6	0.02	0.06	0.00	—	0.27	0.02	—	1.80	—	8.70	2.60	0.02	4.60	USDASR14; Schmidt et al., 1999
26			100.0	0.28	0.74	0.03	—	3.59	0.24	—	23.20	—	114.50	34.50	0.30	60.50	
	Aspen *Populus* spp																
27	leaves, sun-cured	—	85	—	—	—	—	—	—	—	—	—	—	—	—	—	Bath et al., 1999
28			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
29	flower buds, spring	—	38.2	—	—	—	—	—	—	—	—	—	—	—	—	—	Guglielmo and Karasov, 1995
30			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Avocado *Persea americana*																
31	fruit, raw, ep, all commerical varieties	—	25.7	0.01	0.04	0.01	—	0.60	0.04	—	2.60	—	10.20	2.30	0.00	4.20	USDASR14
32			100.0	0.04	0.16	0.04	—	2.33	0.15	—	10.20	—	39.60	8.80	0.02	16.30	
	Bamboo, arrow *Psuedosasa japonica*																
33	leaves	—	24.1	—	—	—	—	—	—	—	—	—	—	—	—	—	Warnell, 1988
34			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Banyan, weeping Chinese *Ficus benjamina*																
35	leaves, mature, fresh	—	39.9	1.38	0.04	—	—	—	—	—	—	—	—	—	—	—	Janeke, 1995
36			100.0	3.45	0.11	—	—	—	—	—	—	—	—	—	—	—	
	Banyantree *Ficus benghalensis*																
37	leaves, fresh	2-27-208	32	0.81	0.13	—	—	—	—	—	—	—	—	—	—	—	NRC, 1981
38			100.0	2.53	0.40	—	—	—	—	—	—	—	—	—	—	—	
	Bakery waste																
39	dried bakery product	4-00-466	92.0	0.13	0.25	1.14	1.48	0.39	0.24	0.02	5.00	—	28.00	65.00	—	15.00	NRC, 1998
40			100.0	0.14	0.27	1.24	1.61	0.42	0.26	0.02	5.43	—	30.43	70.65	—	16.30	

(continues)

TABLE 12-2 (*continued*)

Entry Number	Description	International Feed Number[b]	Dry Matter (%)	Calcium (%)	Phosphorus (%)	Sodium (%)	Chlorine (%)	Potassium (%)	Magnesium (%)	Sulfur (%)	Copper (mg/kg)	Iodine (mg/kg)	Iron (mg/kg)	Manganese (mg/kg)	Selenium[c] (mg/kg)	Zinc (mg/kg)	Data Source
	Banana *Musa sapientum*																
41	aerial part, fresh	2-00-483	16	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1971
42			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
43	flower	—	8.7	—	—	—	—	—	—	—	—	—	—	—	—	—	Schmidt et al., 1999
44			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
45	fruit, raw, ep	—	25.74	0.01	0.02	0.00	—	0.40	0.03	—	1.00	—	3.10	1.50	0.01	1.60	USDASR14
46			100.0	0.02	0.08	0.00	—	1.54	0.11	—	4.00	—	12.00	5.90	0.04	6.20	
47	fruit, raw, with peel	—	19.87	—	—	—	—	—	—	—	—	—	—	—	—	—	Schmidt et al., 1999
48			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
49	leaves, fresh	2-09-902	19	0.23	0.13	—	—	—	0.06	—	—	—	—	—	—	—	NRC, 1981
50			100.0	1.20	0.70	—	—	—	0.32	—	—	—	—	—	—	—	
51	peel	—	16.2	0.06	0.05	—	0.10	0.93	0.04	—	—	—	—	—	—	—	NRC, 1971
52			100.0	0.35	0.32	—	0.64	5.72	0.23	—	—	—	—	—	—	—	
	Barley *Hordeum distichon*																
53	grain, two row	4-00-572	89.0	0.06	0.35	0.04	0.12	0.45	0.14	0.15	7.00	—	78.00	18.00	0.19	25.00	NRC, 1998
54			100.0	0.07	0.39	0.04	0.13	0.51	0.16	0.17	7.87	—	87.64	20.22	0.21	28.09	
	Barley *Hordeum vulgare*																
55	grain, six row	4-00-574	89	0.06	0.35	0.02	0.15	0.47	0.12	0.15	8.00	—	88.00	16.00	0.10	15.00	NRC, 1998
56			100.0	0.07	0.39	0.02	0.17	0.53	0.13	0.17	8.99	—	98.88	17.98	0.11	16.85	
57	grain, hulless	4-00-552	88	0.04	0.45	0.02	0.10	0.44	0.12	0.12	5.00	—	56.00	16.00	—	27.00	NRC, 1998
58			100.0	0.05	0.51	0.02	0.11	0.50	0.14	0.14	5.68	—	63.64	18.18	—	30.68	
	Bean, snap *Phaseolus* spp																
59	green, raw	—	9.7	0.04	0.04	0.01	—	0.21	0.03	—	0.70	—	10.40	2.10	0.01	2.40	USDASR14; Schmidt et al., 1999
60			100.0	0.38	0.39	0.06	—	2.15	0.26	—	7.10	—	106.90	22.00	—	24.70	
61	yellow, raw	—	9.7	0.04	0.04	0.01	—	0.21	0.03	—	0.70	—	10.40	2.10	0.01	2.40	USDASR14
62			100.0	0.38	0.39	0.06	—	2.15	0.26	—	7.10	—	106.90	22.00	—	24.70	
	Beech, American *Fagus grandifolia*																
63	leaves, sun-cured	1-00-628	86	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1971; Robbins and Moen, 1975
64			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Beet, sugar *Beta vulgaris altissima*																
65	greens, raw	—	7.8	0.12	0.04	0.20	—	0.55	0.07	—	1.90	—	33.00	3.90	0.01	3.80	USDASR14
66			100.0	1.52	0.51	2.56	—	6.97	0.92	—	24.30	—	420.40	49.80	—	48.80	
67	pulp, dehy	4-00-669	91.0	0.70	0.10	0.20	0.10	0.61	0.22	0.31	11.00	—	411.00	46.00	0.09	12.00	NRC, 1998
68			100.0	0.77	0.11	0.22	0.11	0.67	0.24	0.34	12.09	—	451.65	50.55	0.10	13.19	
69	tops, fresh	—	17.0	0.17	0.04	—	—	0.98	0.19	—	—	—	—	—	—	—	Bath et al., 1999
70			100.0	1.01	0.22	—	—	5.79	1.12	—	—	—	—	—	—	—	
71	tubers, raw	—	12.4	0.02	0.04	0.08	—	0.33	0.02	—	0.80	—	8.00	3.30	0.01	3.50	USDASR14
72			100.0	0.13	0.32	0.63	—	2.62	0.19	—	6.00	—	64.00	26.50	—	28.20	
	Birch, paper *Betula papyrifera*																
73	leaves	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Robbins and Moen, 1975
74			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Birch, sweet *Betula lenta*																
75	browse, immature, fresh	2-00-724	92.4	1.12	0.30	—	—	—	—	—	—	—	—	135.50	—	—	NRC, 1971
76			100.0	1.21	0.32	—	—	—	—	—	—	—	—	146.80	—	—	
77	browse, mid-bloom, fresh	2-00-725	93.7	1.08	0.17	—	—	—	—	—	—	—	—	136.10	—	—	NRC, 1971
78			100.0	1.15	0.18	—	—	—	—	—	—	—	—	145.30	—	—	
	Blackberry *Robus ulmifolius*																
79	fruit, raw	—	14.36	0.03	0.02	0.00	—	0.20	0.02	—	1.40	—	5.70	12.90	0.01	2.70	USDASR14; Schmidt et al., 1999
80			100.0	0.22	0.15	0.00	—	1.37	0.14	—	9.70	—	39.70	89.90	—	18.80	
	Blood																
81	meal, conventional	5-00-380	92.0	0.37	0.27	0.50	0.30	0.11	0.11	0.48	11.00	—	1922.00	6.00	0.58	38.00	NRC, 1998
82			100.0	0.40	0.29	0.54	0.33	0.12	0.12	0.52	11.96	—	2089.13	6.52	0.63	41.30	
83	meal, flash dried	5-26-006	92.0	0.21	0.21	0.29	0.38	0.14	0.21	0.45	6.00	0.02	2341.00	10.00	—	16.00	NRC, 1998
84			100.0	0.23	0.23	0.32	0.41	0.15	0.23	0.49	6.52	0.02	2544.57	10.87	—	17.39	
85	meal, spray or ring dried	5-00-381	93.0	0.41	0.30	0.44	0.25	0.15	0.11	0.47	8.00	—	2919.00	6.00	—	30.00	NRC, 1998
86			100.0	0.44	0.32	0.47	0.27	0.16	0.12	0.51	8.60	—	3138.71	6.45	—	32.26	

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87	plasma, spray dried	—	91.0	0.15	1.71	3.02	1.50	0.20	0.34	—	—	—	55.00	—	—	—	NRC, 1998
88			100.0	0.16	1.88	3.32	1.65	0.22	0.37	—	—	—	60.44	—	—	—	
89	cells, spray dried	—	92.0	0.02	0.37	0.58	1.40	0.62	—	—	—	—	2700.00	—	—	—	NRC, 1998
90			100.0	0.02	0.40	0.63	1.52	0.67	—	—	—	—	2934.78	—	—	—	
	Blueberries *Vaccinium* spp.																
91	fruit, raw	—	15.39	0.01	0.01	0.01	—	0.09	0.01	—	0.60	—	1.70	2.80	0.01	1.10	USDASR14; Schmidt et al., 1999
92			100.0	0.04	0.07	0.04	—	0.58	0.03	—	4.00	—	11.00	18.30	—	7.10	
	Breadfruit *Artocarpus altilis*																
93	fruit, raw	—	29.4	0.02	0.03	0.00	—	0.49	0.03	—	0.80	—	5.40	0.60	0.01	1.20	USDASR14
94			100.0	0.06	0.10	0.01	—	1.67	0.09	—	2.90	—	18.40	2.00	—	4.10	
	Brewer's grain																
95	dried	5-02-141	92	0.32	0.56	0.26	0.15	0.08	0.16	0.31	21.00	0.07	250.00	38.00	0.70	62.00	NRC, 1998
96			100.0	0.35	0.61	0.28	0.16	0.09	0.17	0.34	23.00	0.07	266.00	40.00	0.76	30.00	
	Broccoli *Brassica oleracea* var. *italicca*																
97	raw	—	9.3	0.05	0.07	0.03	—	0.33	0.03	—	0.50	—	8.80	2.30	0.03	4.00	USDASR14; Schmidt et al., 1999
98			100.0	0.52	0.71	0.29	—	3.49	0.27	—	4.80	—	94.50	24.60	0.32	43.00	
	Brush cherry *Syzygium paniculata*																
99	leaves, mature, fresh	—	31.6	0.23	0.05	—	—	—	—	—	—	—	—	—	—	—	Janeke, 1995
100			100.0	0.74	0.16	—	—	—	—	—	—	—	—	—	—	—	
	Brussel sprouts *Brassica oleracea* var. *bullata gemmifera*																
101	raw	—	14.0	0.04	0.07	0.03	—	0.39	0.02	—	0.70	—	14.00	3.40	0.02	4.20	USDASR14; Schmidt et al., 1999
102			100.0	0.30	0.49	0.18	—	2.78	0.16	—	5.00	—	100.00	24.10	—	30.00	
	Buckwheat, common *Fagopyrum sagittatum*																
103	grain	4-00-994	88	0.09	0.31	0.05	0.05	0.41	0.09	0.14	1.00	—	44.00	34.00	0.18	9.00	NRC, 1998
104			100.0	0.10	0.35	0.06	0.06	0.47	0.10	0.16	1.14	—	50.00	38.64	0.20	10.23	
105	middlings	5-00-991	89	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1982
106			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Cabbage *Brassica oleracea* var. *capitata*																
107	raw	—	7.8	0.05	0.02	0.02	—	0.25	0.02	—	0.20	—	5.90	1.60	0.01	1.80	USDASR14; Schmidt et al., 1999
108			100.0	0.60	0.29	0.23	—	3.13	0.19	—	2.90	—	75.20	20.30	0.11	22.90	
	Cabbage, bok choy																
109	raw	—	4.78	—	—	—	—	—	—	—	—	—	—	—	—	—	Schmidt et al., 1999
110			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Cabbage, napa *Brassica pekinensis*																
111	raw	—	3.5	—	—	—	—	—	—	—	—	—	—	—	—	—	Schmidt et al., 1999
112			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Carambola *Averrhoa carambola*																
113	fruit, raw	—	9.1	0.00	0.02	0.00	—	0.16	0.01	—	1.20	—	2.60	0.80	0.01	1.10	USDASR14
114			100.0	0.04	0.18	0.02	—	1.80	0.10	—	13.20	—	28.60	9.00	—	12.10	
	Carrot *Daucus carota*																
115	roots, fresh	—	12.2	0.03	0.04	0.04	—	0.32	0.02	—	0.50	—	5.00	1.40	0.01	2.00	USDASR14; Schmidt et al., 1999
116			100.0	0.22	0.36	0.29	—	2.65	0.12	—	3.80	—	41.00	11.60	0.09	16.40	
117	tops, fresh	—	16.0	0.31	0.03	—	—	0.30	—	—	—	—	—	—	—	—	Bath et al., 1999
118			100.0	1.94	0.19	—	—	1.88	—	—	—	—	—	—	—	—	
	Canola *Brassica napa*																
119	meal, sol. extr.	5-06-145	90	0.63	1.01	0.07	0.11	1.22	0.51	0.85	6.00	—	142.00	49.00	1.10	69.00	NRC, 1998
120			100.0	0.70	1.12	0.08	0.12	1.36	0.57	0.94	6.67	—	157.78	54.44	1.22	76.67	
121	oil	4-06-144	100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1998
122			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Casein (cattle)																
123	dehy	5-01-162	91.0	0.61	0.82	0.01	0.04	0.01	0.01	0.60	4.00	—	14.00	4.00	0.16	30.00	NRC, 1998
124			100.0	0.67	0.90	0.01	0.04	0.01	0.01	0.66	4.40	—	15.38	4.40	0.18	32.97	
	Cassava *Manihot esculenta*																
125	meal, dehydrated	4-01-152	88	0.22	0.13	0.03	0.07	0.49	0.11	0.50	4.00	—	18.00	28.00	0.10	10.00	NRC, 1998
126			100.0	0.25	0.15	0.03	0.08	0.56	0.13	0.57	4.55	—	20.45	31.82	0.11	11.36	
127	tubers, fresh	4-09-599	31.49	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1982; Schmidt et al., 1999
128			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Cauliflower *Brassica oleracea* var. *botrytis*																
129	raw	—	8.1	0.02	0.04	0.03	—	0.30	0.02	—	0.40	—	4.40	1.60	0.01	2.80	USDASR14; Schmidt et al., 1999
130			100.0	0.27	0.54	0.37	—	3.75	0.19	—	5.20	—	54.40	19.30	0.07	34.60	
131	green, raw	—	10.2	0.03	0.06	0.02	—	0.30	0.02	—	0.40	—	7.30	2.50	0.01	6.40	USDASR14
132			100.0	0.32	0.61	0.23	—	2.94	0.20	—	4.00	—	71.50	24.20	—	62.70	

(continues)

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TABLE 12-2 (*continued*)

Entry Number	Description	International Feed Number[b]	Dry Matter (%)	Calcium (%)	Phosphorus (%)	Sodium (%)	Chlorine (%)	Potassium (%)	Magnesium (%)	Sulfur (%)	Copper (mg/kg)	Iodine (mg/kg)	Iron (mg/kg)	Manganese (mg/kg)	Selenium[c] (mg/kg)	Zinc (mg/kg)	Data Source
	Celery *Apium graveolens* var. *dulce*																
133	raw	—	5.36	0.04	0.03	0.09	—	0.29	0.01	—	0.30	—	4.00	1.00	0.01	1.30	USDASR14; Schmidt et al., 1999
134			100.0	0.75	0.47	1.16	—	5.35	0.21	—	6.30	—	74.60	19.00	0.17	24.30	
	Cereal																
135	screenings	4-02-156	90.0	0.33	0.35	0.40	—	0.30	0.12	—	—	—	—	44.00	—	—	NRC, 1982
136			100.0	0.37	0.39	0.44	—	0.33	0.13	—	—	—	—	48.89	—	—	
	Chalum *Inga* spp																
137	dehy, fruit	—	96.8	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1971
138			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
139	dehy, pod	—	97.8	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1971
140			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
141	dehy, seeds	—	93.5	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1971
142			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Chayote *Cucurbita pepo*																
143	fruit, raw, with peel	—	5.8	0.02	0.02	0.00	—	0.13	0.01	—	1.20	—	3.00	1.90	0.00	7.40	USDASR14; Schmidt et al., 1999
144			100.0	0.34	0.34	0.00	—	2.24	0.17	—	20.69	—	51.72	32.76	0.00	127.59	
	Cherimoya *Annona cherimolia*																
145	fruit, raw	—	26.5	0.02	0.04	—	—	—	—	—	—	—	5.00	—	—	—	USDASR14
146			100.0	0.08	0.15	—	—	—	—	—	—	—	18.87	—	—	—	
	Cherry *Prunus* spp																
147	fruit, raw	—	13.9	0.02	0.02	0.00	—	0.17	0.01	—	1.00	—	3.00	1.10	0.00	1.00	USDASR14
148			100.0	0.14	0.14	0.00	—	1.23	0.07	—	7.21	—	21.63	7.93	0.00	7.21	
	Chicory *Cichorium intybus*																
149	greens, raw	—	8	0.10	0.05	0.05	—	0.42	0.03	—	3.00	—	9.00	4.30	0.00	4.20	USDASR14
150			100.0	1.25	0.63	0.63	—	5.25	0.38	—	37.50	—	112.50	53.75	0.00	52.50	
	Cockroach, American *Periplaneta americana*																
151	adult	—	33.3	0.19	0.25	0.20	—	0.52	0.05	—	21.00	—	1692.00	10.50	0.18	75.00	Allen, 1989
152			100.0	0.57	0.74	0.61	—	1.57	0.15	—	62.00	—	5081.00	31.60	0.55	226.00	
	Cockroach, Haitian *Blaberus discoidalus*																
153	adult	—	30.3	—	—	—	—	—	—	—	—	—	—	—	—	—	Allen, 1989
154			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Coconut *Cocos nucifera*																
155	meal, sol. extr.	5-01-573	92.0	0.16	0.58	0.04	0.37	1.83	0.31	0.31	25.00	—	486.00	69.00	—	49.00	NRC, 1998
156			100.0	0.17	0.63	0.04	0.40	1.99	0.34	0.34	27.17		528.26	75.00		53.26	
157	oil	4-09-320	100.0														NRC, 1998
158			100.0														
	Collard *Brassica oleracea* var.																
159	greens, raw	—	9.45	0.15	0.01	0.02	—	0.17	0.01	—	0.40	—	2.00	2.80	0.01	1.30	USDASR14; Schmidt et al., 1999
160			100.0	1.59	0.11	0.21	—	1.80	0.11	—	4.23	—	21.16	29.63	0.11	13.76	
	Corn, yellow *Zea mays indentata*																
161	bran	—	95.3	0.04	0.07	0.01	—	0.04	0.06	—	2.48	—	27.90	1.40	0.17	15.60	USDASR14
162			100.0	0.04	0.08	0.01	—	0.05	0.07	—	2.60	—	29.28	1.47	0.18	16.37	
163	cobs, ground	1-28-234	90.0	0.11	0.79	0.42	—	0.79	0.04	0.42	7.00	—	208.00	6.00	—	—	
164			100.0	0.12	0.88	0.47	—	0.88	0.04	0.47	7.78	—	231.11	6.67	—	—	
165	distillers' grain	5-02-842	94.0	0.10	0.40	0.09	0.08	0.17	0.25	0.43	45.00	—	220.00	22.00	0.40	55.00	NRC, 1998
166			100.0	0.11	0.43	0.10	0.09	0.18	0.27	0.46	47.87	—	234.04	23.40	0.43	58.51	
167	distillers' grain with solubles	5-02-843	93.0	0.20	0.77	0.25	0.20	0.84	0.19	0.30	57.00	—	257.00	24.00	0.39	80.00	NRC, 1998
168			100.0	0.22	0.83	0.27	0.22	0.90	0.20	0.32	61.29	—	276.34	25.81	0.42	86.02	
169	distillers' solubles	5-02-844	92.0	0.29	1.03	0.26	0.25	1.50	0.64	0.37	83.00	—	560.00	74.00	0.33	85.00	NRC, 1998
170			100.0	0.32	1.12	0.28	0.27	1.63	0.70	0.40	90.22	—	608.70	80.43	0.36	92.39	
171	flour, whole grain	—	89.1	0.01	0.27	0.01	—	0.32	0.09	—	2.30	—	23.80	4.60	0.15	17.30	USDASR14
172			100.0	0.01	0.31	0.01	—	0.35	0.10	—	2.58	—	26.71	5.16	0.17	19.42	
173	gluten feed	5-02-903	90.0	0.22	0.83	0.15	0.22	0.98	0.33	0.22	48.00	—	460.00	24.00	0.27	70.00	NRC, 1998
174			100.0	0.24	0.92	0.17	0.24	1.09	0.37	0.24	53.33	—	511.11	26.67	0.30	77.78	
175	gluten meal, 60% CP	5-28-242	90.0	0.05	0.44	0.02	0.06	0.18	0.08	0.43	26.00	—	282.00	4.00	1.00	33.00	NRC, 1998
176			100.0	0.06	0.49	0.02	0.07	0.20	0.09	0.48	28.89	—	313.33	4.44	1.11	36.67	

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177	grain	4-02-935	89.0	0.03	0.28	0.02	0.05	0.33	0.12	0.13	3.00	—	29.00	7.00	0.07	18.00	NRC, 1998
178			100.0	0.03	0.31	0.02	0.06	0.37	0.13	0.15	3.37	—	32.58	7.87	0.08	20.22	
179	grits by-product (Hominy Feed)	4-03-011	90.0	0.05	0.43	0.08	0.07	0.61	0.24	0.03	13.00	—	67.00	15.00	0.10	30.00	NRC, 1998
180			100.0	0.06	0.48	0.09	0.08	0.68	0.27	0.03	14.44	—	74.44	16.67	0.11	33.33	
181	oil	4-07-882	100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1998
182			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
183	starch	4-02-889	91.7	0.00	0.01	0.01	—	0.00	0.00	—	0.50	—	4.70	0.53	0.03	0.60	USDASR14
184			100.0	0.00	0.01	0.01	—	0.00	0.00	—	0.55	—	5.13	0.58	0.03	0.65	
185	syrup, light	—	77.2	0.00	0.00	0.12	—	0.00	0.00	—	0.10	—	0.50	0.90	0.01	0.20	USDASR14
186			100.0	0.00	0.00	0.16	—	0.01	0.00	—	0.13	—	0.65	1.17	—	0.26	
	Corn, sweet *Zea mays saccharata*																
187	cobs, fresh	—	31.74														Schmidt et al., 1999
188			100														
189	ear, whole, with husk, fresh	—	20.8														Schmidt et al., 1999
190			100														
191	husk, fresh	—	26.06														Schmidt et al., 1999
192			100														
193	white, raw, ep	—	24.04	0.00	0.09	0.02	—	0.27	0.04	—	0.50	—	5.00	1.60	0.01	4.50	USDASR14
194			100.0	0.00	0.37	0.08	—	1.12	0.17	—	2.08	—	20.80	6.66	0.04	18.72	
195	yellow, raw, ep	—	24.04	0.00	0.09	0.02	—	0.27	0.04	—	0.50	—	5.00	1.60	0.01	4.50	USDASR14
196			100.0	0.00	0.37	0.08	—	1.12	0.17	—	2.08	—	20.80	6.66	0.04	18.72	
	Corn borer, European *Ostrinia nubilalis*																
197	larvae	—	27.3	0.06	0.17	—	—	—	0.03	—	6.55	—	78.89	4.90	0.08	24.57	Allen, 1989
198			100.0	0.22	0.64	—	—	—	0.12	—	24.00	—	289.00	18.00	0.31	90.00	
199	pupae	—	28.0	0.06	0.19	—	—	—	0.04	—	5.60	—	75.32	4.48	0.06	27.44	Allen, 1989
200			100.0	0.21	0.67	—	—	—	0.13	—	20.00	—	269.00	16.00	0.20	98.00	
	Cottonseed *Gossypium* spp																
201	meal, mech. extr., 41% CP	5-01-617	92	0.23	1.03	0.04	0.04	1.34	0.52	0.40	19.00		160.00	23.00	0.90	64.00	NRC, 1998
202			100.0	0.25	1.12	0.04	0.04	1.46	0.57	0.43	20.65	0.00	173.91	25.00	0.98	69.57	
203	meal, sol. extr. 41% CP	5-07-872	90	0.19	1.06	0.04	0.05	1.40	0.50	0.31	18.00		184.00	20.00	0.80	70.00	NRC, 1998
204			100.0	0.21	1.18	0.04	0.06	1.56	0.56	0.34	20.00	—	204.44	22.22	0.89	77.78	
	Crayfish, Mexico *Cambrus* sp., *Aegiale hesperiaris*																
205	adult	—	33.5	3.25	0.42	—	—	—	—	—	—	—	—	—	—	—	Massieu et al., 1951
206			100.0	9.70	1.26	—	—	—	—	—	—	—	—	—	—	—	
	Cricket, house *Acheta domesticus*																
207	adult	—	29.6	0.05	0.27	0.17	—	0.35	0.03	—	4.85	—	43.46	12.97	0.12	64.36	Allen, 1989; Finke, 2002
208			100.0	0.16	0.91	0.56	—	1.20	0.11	—	16.34	—	146.33	43.67	0.39	217.43	
209	juvenile	—	22.9	0.03	0.30	0.14	—	0.35	0.02	—	5.10	—	21.20	8.90	0.10	68.00	Finke, 2002
210			100.0	0.12	1.10	0.60	—	1.54	0.10	—	22.27	—	92.58	38.86	0.44	296.94	
	Cricket, mormon *Anabrus simplex*																
211	adult, both sexes	—	29.7	—	—	—	—	—	—	—	—	—	—	—	—	—	DeFoliart et al., 1982
212			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Cucumber *Cucumis sativus*																
213	raw, with peel	—	3.99	0.01	0.02	0.00	—	0.14	0.01	—	0.30	—	3.00	0.80	0.00	2.00	USDASR14; Schmidt et al., 1999
214			100.0	0.25	0.50	0.00	—	3.51	0.25	—	7.52	—	75.19	20.05	0.00	50.13	
	Custard apple *Annona* spp																
215	fruit, raw	—	28.5	0.03	0.02	0.00	—	0.38	0.02	—	—	—	7.00	—	—	—	USDASR14
216			100.0	0.11	0.07	0.00	—	1.33	0.07	—	—	—	24.56	—	—	—	
	Dandelion *Taraxacum officinale*																
217	greens, raw	2-01-748	14.4	0.19	0.07	0.08	—	0.40	0.04	—	1.70	—	31.00	3.40	0.01	4.10	USDASR14
218			100.0	1.32	0.49	0.56	—	2.78	0.28	—	11.81	—	215.28	23.61	0.07	28.47	
	Dock *Rumex* spp.																
219	greens, raw	—	7.0	0.04	0.06	0.00	—	0.39	0.10	—	1.30	—	24.00	3.50	0.01	2.00	USDASR14
220			100.0	0.57	0.86	0.00	—	5.57	1.43	—	18.57	—	342.86	50.00	0.14	28.57	
	Egg (Chicken)																
221	dehy, whole	—	96.9	0.23	0.83	0.52	—	0.49	0.04	—	2.00	—	68.00	1.30	1.20	52.80	USDASR14
222			100.0	0.24	0.86	0.54	—	0.51	0.04	—	2.06	—	70.18	1.34	1.24	54.49	
	Eggplant *Solanum melongena*																
223	fruit, raw	—	8.0	0.01	0.02	0.00	—	0.22	0.01	—	0.60	—	3.00	1.30	0.00	1.40	USDASR14; Schmidt et al., 1999
224			100.0	0.13	0.25	0.00	—	2.76	0.13	—	7.53	—	37.64	16.31	0.00	17.57	
	Fababean (Broadbean) *Phaseolus* spp																
225	seeds	5-09-262	87	0.11	0.48	0.03	0.07	1.20	0.15	0.29	11.00		75.00	15.00	0.02	42.00	NRC, 1998
226			100.0	0.13	0.55	0.03	0.08	1.38	0.17	0.33	12.64	—	86.21	17.24	0.02	48.28	

(continues)

TABLE 12-2 (*continued*)

Entry Number	Description	International Feed Number[b]	Dry Matter (%)	Calcium (%)	Phosphorus (%)	Sodium (%)	Chlorine (%)	Potassium (%)	Magnesium (%)	Sulfur (%)	Copper (mg/kg)	Iodine (mg/kg)	Iron (mg/kg)	Manganese (mg/kg)	Selenium[c] (mg/kg)	Zinc (mg/kg)	Data Source
	Fat																
227	animal, hydrolyzed	4-00-376	100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	USDASR11
228			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
229	animal, poultry	4-00-409	99.8	0.00	0.00	0.00	—	0.00	0.00	—	0.00	—	0.00	—	0.00	0.00	USDASR14
230			100.0	0.00	0.00	0.00	—	0.00	0.00	—	0.00	—	0.00	—	0.00	0.00	
231	animal, swine (lard)	4-04-790	100.0	0.00	0.00	0.00	—	0.00	0.00	—	0.00	—	0.00	0.00	0.00	1.10	USDASR14
232			100.0	0.00	0.00	0.00	—	0.00	0.00	—	0.00	—	0.00	0.00	0.00	1.10	
	Feather																
233	meal, hydrolyzed	5-03-795	93	0.33	0.50	0.34	0.26	0.19	0.20	1.39	10.00		76.00	10.00	0.69	111.00	NRC, 1981
234			100.0	0.35	0.54	0.37	0.28	0.20	0.22	1.49	10.75	—	81.72	10.75	0.74	119.35	
	Feijoa *Feijoa sellowiana*																
235	fruit, raw	—	13.4	0.02	0.02	0.00	—	0.16	0.01	—	.6	—	0.80	0.90	—	0.40	USDASR14
236			100.0	0.15	0.15	0.00	—	1.19	0.07	—	—	—	5.97	6.72	—	2.99	
	Ficus nitida																
237	leaves, mature, fresh	—	35.3	1.20	0.04	—	—	—	—	—	—	—	—	—	—	—	Janeke, 1995
238			100.0	3.39	0.12	—	—	—	—	—	—	—	—	—	—	—	
	Ficus rumphii																
239	leaves, mature, fresh	—	29.6	0.64	0.07	—	—	—	—	—	—	—	—	—	—	—	Janeke, 1995
240			100.0	2.17	0.22	—	—	—	—	—	—	—	—	—	—	—	
	Ficus thonningii																
241	leaves, mature, fresh	—	27.7	0.51	0.06	—	—	—	—	—	—	—	—	—	—	—	Janeke, 1995
242			100.0	1.84	0.23	—	—	—	—	—	—	—	—	—	—	—	
	Fig *Ficus carica*																
243	fruit, raw	—	20.9	0.04	0.01	0.00	—	0.23	0.02	—	0.70	—	4.00	1.30	0.01	1.50	USDASR14
244			100.0	0.19	0.05	0.00	—	1.10	0.10	—	3.35	—	19.15	6.22	0.05	7.18	
245	fruit, dried	—	64.9														Schmidt et al., 1999
246			100.0														
247	leaves, mature, fresh	—	23.5	0.36	0.04	—	—	—	—	—	—	—	—	—	—	—	Janeke, 1995
248			100.0	1.54	0.15	—	—	—	—	—	—	—	—	—	—	—	
	Fig, cluster *Ficus glomerata*																
249	leaves, fresh	2-27-209	30	1.13	0.21	—	—	—	—	—	—	—	—	—	—	—	NRC, 1981
250			100.0	3.77	0.71	—	—	—	—	—	—	—	—	—	—	—	
251	leaves, mature, fresh	—	32.8	0.74	0.08	—	—	—	—	—	—	—	—	—	—	—	Janeke, 1995
252			100.0	2.25	0.23	—	—	—	—	—	—	—	—	—	—	—	
	Fig, Indian laurel *Ficus retusa*																
253	leaves, mature, fresh	—	38.0	1.42	0.05	—	—	—	—	—	—	—	—	—	—	—	Janeke, 1995
254			100.0	3.73	0.12	—	—	—	—	—	—	—	—	—	—	—	
	Fig, Moreton Bay *Ficus macrophylla*																
255	leaves, mature, fresh	—	37	0.91	0.04	—	—	—	—	—	—	—	—	—	—	—	Janeke, 1995
256			100.0	2.45	0.11	—	—	—	—	—	—	—	—	—	—	—	
	Fig, Roxburgh *Ficus roxburghii*																
257	leaves, fresh	2-30-177	33.0	0.44	0.06	—	—	—	—	—	—	—	—	—	—	—	NRC, 1981
258			100.0	1.31	0.17	—	—	—	—	—	—	—	—	—	—	—	
	Fig, rustyleaf *Ficus rubiginosa*																
259	leaves, mature, fresh	—	30.6	0.57	0.04	—	—	—	—	—	—	—	—	—	—	—	Janeke, 1995
260			100.0	1.85	0.14	—	—	—	—	—	—	—	—	—	—	—	
	Fig, spotted *Ficus virens*																
261	leaves, fresh	2-28-704	15.0	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1981
262			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Fish																
263	solubles, condensed	5-01-969	51	0.22	0.59	0.21	2.70	1.61	0.02	0.12	45.00		160.00	14.00	2.00	38.00	NRC, 1998
264			100.0	0.43	1.16	0.41	5.29	3.16	0.04	0.24	88.24	—	313.73	27.45	3.92	74.51	
265	solubles, dried	5-01-971	92	0.55	1.25	0.37	6.29	2.03	0.30	0.40	35.00		300.00	50.00	2.20	76.00	NRC, 1998
266			100.0	0.60	1.36	0.40	6.84	2.21	0.33	0.43	38.04	—	326.09	54.35	2.39	82.61	

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	Fish, anchovy *Engraulis ringen*																
267	meal, mech. extr.	5-01-985	92.0	3.93	2.55	0.88	1.02	0.75	0.24	0.77	9.00		220.00	10.00	1.36	103.00	NRC, 1998
268			100.0	4.27	2.77	0.96	1.11	0.82	0.26	0.84	9.78	—	239.13	10.87	1.48	111.96	
	Fish, herring *Clupea harengus*																
269	meal, mech. extr.	5-02-000	93	2.40	1.76	0.61	1.12	1.01	0.18	0.69	6.00		181.00	8.00	1.93	132.00	NRC, 1998
270			100.0	2.58	1.89	0.66	1.20	1.09	0.19	0.74	6.45	—	194.62	8.60	2.08	141.94	
	Fish, menhaden *Brevoortia tyrannus*																
271	meal, mech. extr.	5-02-009	92.0	5.21	3.04	0.40	0.55	0.70	0.16	0.45	11.00		440.00	37.00	2.10	147.00	NRC, 1998
272			100.0	5.66	3.30	0.43	0.60	0.76	0.17	0.49	11.96	—	478.26	40.22	2.28	159.78	
	Fish, white Gadidae (family); Lophiidae (family)																
273	meal, mech. extr.	5-02-025	91	6.65	3.59	0.78	1.28	0.85	0.18	0.48	6.00		299.00	12.00	1.62	90.00	NRC, 1998
274			100.0	7.31	3.95	0.86	1.41	0.93	0.20	0.53	6.59	—	328.57	13.19	1.78	98.90	
	Flax *Linum usitatissinum*																
275	meal, sol. extr.	5-02-048	90.0	0.39	0.83	0.13	0.06	1.26	0.54	0.39	22.00		270.00	41.00	0.63	66.00	NRC, 1998
276			100.0	0.43	0.92	0.14	0.07	1.40	0.60	0.43	24.44	—	300.00	45.56	0.70	73.33	
	Fructose																
277		—	99.5														IOM, 1996
278			100														
	Gelatin																
279		5-14-503	90.0	0.49	—	—	—	—	0.05	—	—	—	—	—	—	—	NRC, 1998
280			100.0	0.54	—	—	—	—	0.05	—	—	—	—	—	—	—	
	Glucose																
281	monohydrate	4-02-125	90	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1998
282			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Granadilla, purple *Passiflora edulis*																
283	fruit, raw, ep	—	27.1	0.01	0.07	0.03	—	0.35	0.03	—	0.90	—	16.00	—	0.01	1.00	USDASR14
284			100.0	0.04	0.26	0.11	—	1.29	0.11	—	3.32	—	59.11	—	0.04	3.69	
	Grape, European type *Vitis* spp																
285	fruit, raw, ep	—	19.44	0.01	0.01	0.00	—	0.19	0.01	—	0.90	—	3.00	0.60	0.00	0.50	USDASR14
286			100.0	0.05	0.05	0.00	—	0.98	0.05	—	4.63	—	15.43	3.09	0.00	2.57	
	Grapefruit *Citrus paradisi*																
287	fruit, raw, ep	—	9.1	0.01	0.01	0.00	—	0.14	0.01	—	0.50	—	1.00	0.10	0.01	0.70	USDASR14
288			100.0	0.11	0.11	0.00	—	1.54	0.11	—	5.49	—	10.98	1.10	0.11	7.68	
289	peel	—	29.1														Schmidt et al., 1999
290			100.0														
	Grasshopper *Melanoplus femurrubrum*																
291	adult	—	30.5	0.09	0.22	0.13	—	—	—	—	—	—	—	—	—	—	Bird et al., 1982
292			100.0	0.31	0.72	0.43	—	—	—	—	—	—	—	—	—	—	
	Guava, common or lemon *Psidium guajava*																
293	fruit, raw, ep	—	13.9	0.02	0.03	0.00	—	0.28	0.01	—	1.00	—	3.00	1.40	0.01	2.30	USDASR14
294			100.0	0.14	0.22	0.00	—	2.01	0.07	—	7.19	—	21.58	10.07	0.07	16.55	
	Guava, strawberry *Psidium cattleianum*																
295	fruit, raw, ep	—	19.34	0.02	0.03	0.04	—	0.29	0.02	—	1.00	0.00	2.00	—	—	—	USDASR14
296			100.0	0.10	0.16	0.21	—	1.50	0.10	—	5.17	0.00	10.34	—	—	—	
	Hemicellulose extract																
297		4-08-030	76.0	0.79	0.07	—	—	—	—	—	—	—	—	—	—	—	NRC, 1982
298			100.0	1.04	0.09	—	—	—	—	—	—	—	—	—	—	—	
	Hibiscus, tropical *Hibiscus rosa-sinensis*																
299	leaves, mature, fresh	—	21.9	0.61	0.09	—	—	—	—	—	—	—	—	—	—	—	Janeke, 1995
300			100.0	2.79	0.40	—	—	—	—	—	—	—	—	—	—	—	
	Honeysuckle *Lonicera albiflora*																
301	leaves, fresh	2-29-875	33.0	—	0.04	—	—	—	—	—	—	—	—	—	—	—	NRC, 1981
302			100.0	—	0.11	—	—	—	—	—	—	—	—	—	—	—	
	Jack fruit *Artocarpus heterophyllus*																
303	fruit, raw, ep	—	26.77	0.03	0.04	0.00	—	0.30	0.04	—	1.90	—	6.00	2.00	0.01	4.20	USDASR14
304			100.0	0.11	0.15	0.00	-	1.12	0.15	—	7.10	—	22.41	7.47	0.04	15.69	
	Jujube *Zizyphus jujuba*																
305	browse, fresh	2-30-091	32.0	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1981
306			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
307	fruit, raw, ep	—	22.1	0.02	0.02	0.00	—	0.25	0.01	—	0.70	—	5.00	0.80	—	0.50	USDASR14
308			100.0	0.09	0.09	0.00	—	1.13	0.05	—	3.16	—	22.58	3.61	—	2.26	

(continues)

TABLE 12-2 (*continued*)

Entry Number	Description	International Feed Number[b]	Dry Matter (%)	Calcium (%)	Phosphorus (%)	Sodium (%)	Chlorine (%)	Potassium (%)	Magnesium (%)	Sulfur (%)	Copper (mg/kg)	Iodine (mg/kg)	Iron (mg/kg)	Manganese (mg/kg)	Selenium[c] (mg/kg)	Zinc (mg/kg)	Data Source
	Kale *Brassica oleracea* var. *acephala*																
309	leaves and stems, fresh	—	15.54	0.14	0.06	0.04	—	0.45	0.03	—	2.90	—	17.00	7.70	0.01	4.40	USDASR14; Schmidt et al., 1999
310			100.0	0.90	0.39	0.26	—	2.90	0.19	—	18.66	—	109.40	49.55	0.06	28.31	
	Kiwifruit *Actinidia chinensis*																
311	raw	—	17.0	0.03	0.04	0.01	—	0.33	0.03	—	1.60	—	4.00	—	0.01	1.70	USDASR14; Schmidt et al., 1999
312			100.0	0.18	0.24	0.06	—	1.95	0.18	—	9.44	—	23.60	—	0.06	10.03	
	Kohlrabi *Brassica oleracea* var. *gongylodes*																
313	tubers, fresh	—	9	0.00	0.05	0.02	—	0.35	0.02	—	1.30	—	4.00	1.40	0.01	0.30	USDASR14
314			100.0	0.00	0.56	0.22	—	3.89	0.22	—	14.44	—	44.44	15.56	0.11	3.33	
	Kudzu *Pueraria lobata*																
315	aerial part, fresh	2-02-482	26.4	0.83	0.06	—	—	—	—	—	—	—	—	—	—	—	NRC, 1971
316			100.0	3.14	0.23	—	—	—	—	—	—	—	—	—	—	—	
	Kumquat *Fortunella* spp																
317	fruit, raw, ep	—	18.3	0.04	0.02	0.01	—	0.20	0.01	—	1.10	—	4.00	0.90	0.01	0.80	USDASR14
318			100.0	0.22	0.11	0.05	—	1.09	0.05	—	6.01	—	21.86	4.92	0.05	4.37	
	Lactose																
319		4-07-881	96.0														NRC, 1998
320			100.0														
	Lentil *Len culinaris*																
321	seeds	5-02-506	89	0.10	0.38	0.02	0.03	0.89	0.12	0.20	10.00		85.00	13.00	0.10	25.00	NRC, 1998
322			100.0	0.11	0.43	0.02	0.03	1.00	0.13	0.22	11.24	—	95.51	14.61	0.11	28.09	
	Lettuce, endive *Cichorium endiva*																
323	leaves, fresh	—	6.2	0.05	0.03	0.02	—	0.31	0.02	—	1.00	—	8.00	4.20	0.00	7.90	USDASR14
324			100.0	0.81	0.48	0.32	—	4.99	0.32	—	16.10	—	128.82	67.63	0.00	127.21	
	Lettuce, iceberg *Lactuca sativa*																
325	leaves, fresh	—	4.11	0.02	0.02	0.01	—	0.16	0.01	—	0.30	—	5.00	1.50	0.00	2.20	USDASR14; Schmidt et al., 1999
326			100.0	0.49	0.49	0.24	—	3.89	0.24	—	7.30	—	121.65	36.50	0.00	53.53	
	Lettuce, romaine																
327	leaves, fresh	—	7.0	0.04	0.05	0.01	—	0.29	0.01	—	0.40	—	11.00	6.40	0.00	2.20	USDASR14; Schmidt et al., 1999
328			100.0	0.71	0.88	0.16	—	5.70	0.12	—	7.30	—	216.10	125.00	—	49.10	
	Longan *Nephelium longana*																
329	fruit, raw, ep	—	17.25	0.00	0.02	0.00	—	0.27	0.01	—	1.70	—	1.00	0.50	—	0.50	USDASR14
330			100.0	0.00	0.12	0.00	—	1.57	0.06	—	9.86	—	5.80	2.90	—	2.90	
	Loquat *Eriobotrya japonica*																
331	fruit, raw, ep	—	13.3	0.02	0.03	0.00	—	0.27	0.01	—	0.40	—	3.00	1.50	0.01	0.50	USDASR14
332			100.0	0.15	0.23	0.00	—	2.03	0.08	—	3.01	—	22.61	11.30	0.08	3.77	
	Lupin (sweet white) *Lupinus albus*																
333	seeds	5-27-717	89	0.22	0.51	0.02	0.03	1.10	0.19	0.24	6.00		54.00	1390.00	0.07	32.00	NRC, 1998
334			100.0	0.25	0.57	0.02	0.03	1.24	0.21	0.27	6.74	—	60.67	1561.80	0.08	35.96	
	Lychee *Litchi chinensis*																
335	fruit, raw, ep	—	18.2	0.01	0.03	0.00	—	0.17	0.01	—	1.50	—	3.00	0.60	0.01	0.70	USDASR14
336			100.0														
	Mango *Mangifera indica*																
337	fruit, raw, ep	—	18.29	0.01	0.01	0.00	—	0.16	0.01	—	1.10	—	1.00	0.30	0.01	0.40	USDASR14; Schmidt et al., 1999
338			100.0	0.05	0.05	0.00	—	0.87	0.05	—	6.01	—	5.47	1.64	0.05	2.19	
	Maple, sugar *Acer saccharum*																
339	leaves	—	—														Robbins and Moen, 1975
340			100.0														
	Mealworm *Tenebrio molitor*																
341	larvae	—	37.1	0.02	0.25	0.04	—	0.30	0.06	—	5.38	—	31.36	3.90	0.22	61.12	Allen, 1989; Finke, 2002
342			100.0	0.06	0.67	0.10	—	0.80	0.16	—	14.51	—	84.53	10.52	0.60	164.74	
343	larvae, gut loaded with high (8%) Ca diet	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
344			—	1.01	0.76	—	—	—	—	—	—	—	—	—	—	—	
345	oversized	—	39.0	0.02	0.27	0.05	—	0.30	0.09	—	6.40	—	21.50	3.60	0.13	44.50	Finke, 2002
346			100.0	0.05	0.70	0.13	—	0.76	0.22	—	16.41	—	55.13	9.23	0.33	114.10	

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	Mealworm *Zophobas morio*																	
347	larvae	—	42.1	0.02	0.24	0.05	—	0.32	0.05	—	3.60	—	16.50	4.30	0.14	30.70	Finke, 2002
348			100.0	0.04	0.56	0.11	—	0.75	0.12	—	8.55	—	39.19	10.21	0.33	72.92	
	Meat																	
349	meal rendered	5-00-385	94	9.00	3.88	0.80	0.97	0.57	0.35	0.45	10.00		440.00	10.00	0.37	94.00	NRC, 1998
350			100.0	9.57	4.13	0.85	1.03	0.61	0.37	0.48	10.64	—	468.09	10.64	0.39	100.00	
351	meal rendered with bone	5-00-388	93	9.99	4.98	0.63	0.69	0.65	0.41	0.38	11.00		606.00	17.00	0.31	96.00	NRC, 1998
352			100.0	10.74	5.35	0.68	0.74	0.70	0.44	0.41	11.83	—	651.61	18.28	0.33	103.23	
	Melon, cantaloupe *Cucumis melo*																
353	fruit, raw, ep	—	10.2	0.01	0.02	0.01	—	0.31	0.01	—	0.40	—	2.00	0.50	0.00	1.60	USDASR14; Schmidt et al., 1999
354			100.0	0.10	0.20	0.10	—	3.03	0.10	—	3.91	—	19.57	4.89	0.00	15.66	
355	fruit, raw, with peel	—	7.5														Schmidt et al., 1999
356			100.0														
	Melon, casaba *Cucumis melo*																
357	fruit, raw, ep	—	8	0.01	0.01	0.01	—	0.21	0.01	—	0.40	—	4.00	—	0.00	1.60	USDASR14
358			100.0	0.13	0.13	0.13	—	2.63	0.13	—	5.00	—	50.00	—	0.00	20.00	
	Melon, honeydew *Cucumis melo*																
359	fruit, raw, ep	—	10.3	0.01	0.01	0.01	—	0.27	0.01	—	0.40	—	0.70	0.20	0.00	0.70	USDASR14; Schmidt et al., 1999
360			100.0	0.10	0.10	0.10	—	2.61	0.10	—	3.87	—	6.77	1.93	0.00	6.77	
361	fruit, raw, with peel	—	8.1														Schmidt et al., 1999
362			100.0														
	Milk, cattle *Bos taurus*																
363	dehy	5-01-167	96	0.91	0.71	0.37	0.88	1.04	0.71	0.31	1.00	—	10.00	0.00	—	22.00	NRC, 1982
364			100.0	0.95	0.74	0.38	0.92	1.08	0.74	0.32	1.00	—	10.00	0.00	—	23.00	
365	fresh	5-01-168	12	0.12	0.09	0.05	0.11	0.14	0.09	0.04	0.00	—	1.00	—	—	3.00	NRC, 1982
366			100.0	0.95	0.76	0.38	0.92	1.12	0.76	0.32	1.00	—	10.00	—	—	23.00	
367	skimmed, dehy	5-01-175	94	1.31	1.00	0.48	1.00	1.60	0.12	0.32	5.00	—	8.00	2.00	0.12	42.00	NRC, 1998
368			100.0	1.39	1.06	0.51	1.06	1.70	0.13	0.34	5.32	—	8.51	2.13	0.13	44.68	
369	skimmed, fresh	5-01-170	10	0.13	0.10	0.04	0.09	0.18	0.01	0.03	—	—	1.00	0.00	—	5.00	NRC, 1982
370			100.0	1.31	1.04	0.05	0.96	1.90	0.12	0.32	—	—	10.00	2.00	—	51.00	
	Milk, human *Homo sapiens*																
371	fresh	—	12.5	—	—	—	—	—	—	—	—	—	—	—	—	—	Jensen, 1995
372			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Milk, baboon *Papio*																
373	fresh, days 0-5	—	14.6	—	—	—	—	—	—	—	—	—	—	—	—	—	Hummer, 1970
374			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
375	fresh, days 6-11	—	15.3	—	—	—	—	—	—	—	—	—	—	—	—	—	Hummer, 1970
376			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
377	fresh, days 12-35	—	14	—	—	—	—	—	—	—	—	—	—	—	—	—	Hummer, 1970
378			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
379	fresh, days 36-279	—	14.4	—	—	—	—	—	—	—	—	—	—	—	—	—	Hummer, 1970
380			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Millet *Panicum miliaceum*																
381	grain	4-03-120	90.0	0.03	0.31	0.04	0.03	0.43	0.16	0.14	26.00	—	71.00	30.00	0.70	18.00	NRC, 1998
382			100.0	0.03	0.34	0.04	0.03	0.48	0.18	0.16	28.89	—	78.89	33.33	0.78	20.00	
	Mirror plant *Coprosma repens*																
383	leaves, mature, fresh	—	17.5	0.28	0.06												Janeke, 1995
384			100.0	1.61	0.33												
	Molasses and syrup																
385	beet, sugar, molasses	4-00-668	78.0	0.13	0.03	1.15	1.28	4.72	0.23	0.46	17.00	—	68.00	4.00	—	14.00	NRC, 1982
386			100.0	0.17	0.03	1.48	1.64	6.07	2.90	0.60	22.00	—	87.00	6.00	—	18.00	
387	citrus, syrup	4-01-241	68.0	1.16	0.09	0.28	0.07	0.09	0.14	0.16	73.00	—	344.00	26.00	—	93.00	NRC, 1982
388			100.0	1.72	0.13	0.41	0.11	0.14	0.21	0.23	108.00	—	508.00	38.00	—	137.00	
389	sugarcane, molasses, dehy	4-04-695	94.0	1.04	0.14	0.19	—	0.14	0.44	0.43	75.00	1.98	236.00	54.00	—	31.00	NRC, 1982
390			100.0	1.10	0.15	0.20	—	0.15	0.47	0.46	79.00	2.10	250.00	57.00	—	33.00	
391	sugarcane, molasses, more than 46%	4-04-696	75.0	0.75	0.08	0.16	2.31	0.08	0.32	0.35	59.00	1.57	186.00	42.00	—	22.00	NRC, 1982
392			100.0	1.00	0.11	0.22	3.10	0.11	0.43	0.47	79.00	2.10	250.00	56.00	—	30.00	
	Mulberry *Morus* spp.																
393	browse, fresh	2-03-150	40	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1981
394			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
395	fruit, raw, ep	—	12.32	0.04	0.04	0.01	—	0.19	0.02	—	0.60	—	19.00	—	0.01	1.20	USDASR14
396			100	0.32	0.32	0.08	—	1.54	0.16	—	4.87	—	154.22	—	0.08	9.74	

(continues)

TABLE 12-2 (*continued*)

Entry Number	Description	International Feed Number[b]	Dry Matter (%)	Calcium (%)	Phosphorus (%)	Sodium (%)	Chlorine (%)	Potassium (%)	Magnesium (%)	Sulfur (%)	Copper (mg/kg)	Iodine (mg/kg)	Iron (mg/kg)	Manganese (mg/kg)	Selenium[c] (mg/kg)	Zinc (mg/kg)	Data Source
	Mulberry, white *Morus alba*																
397	leaves, mature, fresh	—	31.1	0.77	0.08												Janeke, 1995
398			100.0	2.49	0.25												
	Mustard *Brassica oleracea* var.																
399	leaves and stems, fresh	—	9.2	0.10	0.04	0.03	—	0.35	0.03	—	1.50	—	15.00	4.80	0.01	2.00	USDASR14; Schmidt et al., 1999
400			100	1.09	0.43	0.33	—	3.80	0.33	—	16.30	—	163.04	52.17	0.11	21.74	
	Nectarine *Prunus persica*																
401	fruit, raw, ep	—	13.7	0.01	0.02	0.00	—	0.21	0.01	—	0.70	—	2.00	0.40	0.00	0.90	USDASR14; Schmidt et al., 1999
402			100.0	0.07	0.15	0.00	—	1.53	0.07	—	5.10	—	14.58	2.92	0.00	6.56	
	Oat *Avena sativa*																
403	grain	4-03-309	89	0.07	0.31	0.08	0.10	0.42	0.16	0.21	6.00		85.00	43.00	0.30	38.00	NRC, 1998
404			100	0.08	0.35	0.09	0.11	0.47	0.18	0.24	6.74	—	95.51	48.31	0.34	42.70	
405	grain, naked	4-25-101	86	0.08	0.38	0.02	0.11	0.36	0.12	0.14	4.00		58.00	37.00	0.09	34.00	NRC, 1998
406			100	0.09	0.44	0.02	0.13	0.42	0.14	0.16	4.65	—	67.44	43.02	0.10	39.53	
407	groat	4-03-331	90	0.08	0.41	0.05	0.09	0.38	0.11	0.20	6.00		49.00	32.00	—	—	NRC, 1998
408			100	0.09	0.46	0.06	0.10	0.42	0.12	0.22	6.67	—	54.44	35.56			
409	hulls	1-03-281	92	0.14	0.14	0.04	0.08	0.57	0.08	0.14	4.00	—	102.00	19.00	—	—	NRC, 1982
410			100	0.15	0.15	0.04	0.09	0.62	0.09	0.15	4.00	—	111.00	20.00	—	—	
	Olive *Olea europaea*																
411	oil	—	100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1998
412			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Okra *Hibiscus esculentus*																
413		—	12.56	0.08	0.06	0.01	—	0.30	0.06	—	0.90	—	8.00	9.90	0.01	6.00	USDASR14; Schmidt et al., 1999
414			100	0.64	0.48	0.08	—	2.39	0.48	—	7.17	—	63.69	78.82	0.08	47.77	
	Onion *Allium cepa*																
415	green	—	9.1	—	—	—	—	—	—	—	—	—	—	—	—	—	Schmidt et al., 1999
416			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
417	red	—	9.1	—	—	—	—	—	—	—	—	—	—	—	—	—	Schmidt et al., 1999
418			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
419	yellow	—	10.3	—	—	—	—	—	—	—	—	—	—	—	—	—	Schmidt et al., 1999
420			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Orange *Citrus* spp																
421	fruit, raw, ep	—	13.25	0.04	0.01	0.00	—	0.18	0.01	—	0.50	—	1.00	0.30	0.01	0.70	USDASR14
422			100	0.30	0.08	0.00	—	1.36	0.08	—	3.77	—	7.55	2.26	0.08	5.28	
423	fruit, raw, with peel	—	17.7	0.07	0.02	0.00	—	0.20	0.01	—	0.60	—	8.00	—	0.01	1.10	USDASR14; Bath et al., 1999
424			100	0.40	0.11	0.00	—	1.13	0.06	—	3.39	—	45.20	—	0.06	6.21	
425	peel	—	27.5	0.16	0.02	0.00	—	0.21	0.02	—	0.90	—	8.00	—	0.01	2.50	USDASR14; Schmidt et al., 1999
426			100	0.58	0.07	0.00	—	0.76	0.07	—	3.27	—	29.09	—	0.04	9.09	
	Papaya *Carica papaya*																
427	fruit, raw, ep	—	11.2	0.02	0.01	0.00	—	0.26	0.01	—	0.20	—	1.00	0.10	0.01	0.70	USDASR14; Schmidt et al., 1999
428			100.0	0.18	0.09	0.00	—	2.33	0.09	—	1.79	—	8.95	0.90	0.09	6.27	
	Parsley																
429	leaves and stems, fresh	—	12.03	0.14	0.06	0.06	—	0.55	0.05	—	1.50	—	62.00	1.60	0.00	10.70	USDASR14; Schmidt et al., 1999
430			100	1.16	0.50	0.50	—	4.57	0.42	—	12.47	—	515.38	13.30	0.00	88.94	
	Parsnip *Pastinaca sativa*																
431	roots, fresh	—	20.5	0.04	0.07	0.01	—	0.38	0.03	—	1.20	—	5.90	5.60	0.02	5.90	USDASR14
432			100.0	0.20	0.34	0.05	—	1.86	0.15	—	5.86	—	28.82	27.36	0.10	28.82	
	Pea *Pisum* spp																
433	seeds	5-03-600	89	0.11	0.39	0.04	0.05	1.02	0.12	0.20	9.00		65.00	23.00	0.38	23.00	NRC, 1998
434			100	0.12	0.44	0.04	0.06	1.15	0.13	0.22	10.11	—	73.03	25.84	0.43	25.84	
	Peach *Prunus persica*																
435	fruit, raw, ep	—	12.3	0.01	0.01	0.00	—	0.20	0.01	—	0.70	—	1.00	0.50	0.00	1.40	USDASR14
436			100.0	0.08	0.08	0.00	—	1.62	0.08	—	5.67	—	8.10	4.05	0.00	11.35	
	Pear *Pyrus communis*																
437	fruit, raw, ep	—	16.19	0.01	0.01	0.00	—	0.13	0.01	—	1.10	—	2.50	0.80	0.01	1.20	USDASR14; Schmidt et al., 1999
438			100	0.06	0.06	0.00	—	0.80	0.06	—	6.79	—	15.44	4.94	0.06	7.41	

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	Peanut (Groundnut) *Arachis hypogaea*																
439	butter	—	98.8	0.04	0.37	0.47	—	0.67	0.16	—	1.40	—	18.40	4.50	0.08	29.20	USDASR14
440			100.0	0.04	0.37	0.48	—	0.68	0.16	—	1.42	—	18.63	4.56	0.08	29.56	
441	hulls	1-08-028	91.0														NRC, 1982
442			100.0														
443	kernels, meal mech extr	5-03-649	92.0	0.17	0.59	0.06	0.03	1.20	0.33	0.29	15.00		285.00	39.00	0.28	47.00	NRC, 1998
444			100.0	0.18	0.64	0.07	0.03	1.30	0.36	0.32	16.30	—	309.78	42.39	0.30	51.09	
445	kernels, meal solv extr	5-03-650	92.0	0.22	0.65	0.07	0.04	1.25	0.31	0.30	15.00		260.00	40.00	0.21	41.00	NRC, 1998
446			100.0	0.24	0.71	0.08	0.04	1.36	0.34	0.33	16.30	—	282.61	43.48	0.23	44.57	
	Peepultree *Ficus religiosa*																
447	leaves, fresh	2-27-207	17	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1981
448			100	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Pepper, sweet, green *Capsicum annuum*																
449	fruit, raw, ep	—	5.3	0.01	0.02	0.00	—	0.18	0.01	—	0.70	—	5.00	1.20	0.00	1.20	USDASR14; Schmidt et al., 1999
450			100.0	0.19	0.38	0.00	—	3.43	0.19	—	13.33	—	95.24	22.86	0.00	22.86	
	Persimmon, American *Diospyros virginiana*																
451	fruit, raw, ep	—	35.6	0.03	0.03	0.00	—	0.31	—	—	—	—	25.00	—	—	—	USDASR14
452			100	0.08	0.08	0.00	—	0.87	—	—	—	—	70.22	—	—	—	
	Persimmon, Oriental (Kaki) *Diospyros kaki*																
453	fruit, raw, ep	—	19.7	0.01	0.02	0.00	—	0.16	—	—	1.10	—	1.50	3.60	0.01	1.10	USDASR14
454			100.0	0.05	0.10	0.00	—	0.81	—	—	5.59	—	7.62	18.29	0.05	5.59	
	Pineapple *Ananas comosus*																
455	fruit, raw, ep	—	13.5	0.01	0.01	0.00	—	0.11	0.01	—	1.10	—	3.70	16.50	0.01	0.80	USDASR14; Schmidt et al., 1999
456			100	0.07	0.07	0.00	—	0.81	0.07	—	8.15	—	27.41	122.22	0.07	5.93	
	Plantain *Musa sapientum*																
457	fruit, raw, ep	—	34.7	0.00	0.03	0.00		0.50	0.04		0.80		6.00	—	0.02	1.40	USDASR14; Schmidt et al., 1999
458			100.0	0.00	0.09	0.00	0.00	1.44	0.12	0.00	2.30	0.00	17.28	—	0.06	4.03	
	Plum *Prunus domestica*																
459	fruit, raw, ep	—	14.8	0.00	0.01	0.00	—	0.17	0.01	—	0.40	—	3.00	0.50	0.01	1.00	USDASR14; Schmidt et al., 1999
460			100	0.00	0.07	0.00	—	1.15	0.07	—	2.70	—	20.27	3.38	0.07	6.76	
	Pomegranate *Punica granatum*																
461	fruit, raw, ep	—	19.0	0.00	0.01	0.00	—	0.26	0.00	—	0.70	—	3.00	—	0.01	1.20	USDASR14
462			100.0	0.00	0.05	0.00	—	1.37	0.00	—	3.68	—	15.76	—	0.05	6.31	
	Poplar, black *Populus nigra*																
463	leaves, sun-cured	1-03-750	85.4	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1971
464			100	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Potato *Solanum tuberosum*																
465	protein concentrate	5-25-392	91.0	0.17	0.19	0.03	0.20	0.80	0.05	0.23	13.00		40.00	5.00	1.00	25.00	NRC, 1998
466			100.0	0.19	0.21	0.03	0.22	0.88	0.05	0.25	14.29	—	43.96	5.49	1.10	27.47	
467	tubers, fresh	—	28.0	0.01	0.06	0.02	—	0.53	0.04	0.06	—	—	22.00	—	—	—	USDASR11; Schmidt et al., 1999
468			100.0	0.04	0.23	0.09	—	2.13	0.14	0.23	—	—	90.00	—	—	—	
	Poultry																
469	by-product, meal rendered	5-03-798	93	4.46	2.41	0.49	0.49	0.53	0.18	0.52	10.00	—	442.00	9.00	0.88	94.00	NRC, 1998
470			100	4.80	2.59	0.53	0.53	0.57	0.19	0.56	10.75	—	475.27	9.68	0.95	101.08	
	Prune																
471	with pits	—	82.0	0.10	0.09	—	—	—	—	—	—	—	—	—	—	—	Bath et al., 1999
472			100.0	0.13	0.11	—	—	—	—	—	—	—	—	—	—	—	
473	without pits	—	80.0	0.03	0.10	—	—	—	—	—	—	—	—	—	—	—	Bath et al., 1999
474			100.0	0.04	0.12	—	—	—	—	—	—	—	—	—	—	—	
	Pummelo *Citrus grandis*																
475	fruit, raw, ep	—	10.9	0.00	0.02	0.00	—	0.22	0.01	—	0.50	—	1.00	0.20	—	0.80	USDASR14
476			100	0.00	0.18	0.00	—	2.02	0.09	—	4.59	—	9.17	1.83	—	7.34	
	Pumpkin *Cucurbita pepo*																
477		—	20.0														Schmidt et al., 1999
478			100.0														
	Quince *Cydonia oblonga*																
479	fruit, raw, ep	—	16.2	0.01	0.02	0.00	—	0.20	0.01	—	1.30	—	7.00	—	0.01	0.40	USDASR14
480			100	0.06	0.12	0.00	—	1.23	0.06	—	8.02	—	43.21	—	0.06	2.47	
	Radicchio *Cichorium intybus* var. *foliosum*																
481	raw	—	6.9	0.02	0.04	0.02	—	0.30	0.01	—	3.40	—	6.00	1.40	0.01	6.20	USDASR14
482			100.0	0.29	0.58	0.29	—	4.37	0.15	—	49.56	—	87.46	20.41	0.15	90.38	

(continues)

TABLE 12-2 (*continued*)

Entry Number	Description	International Feed Number[b]	Dry Matter (%)	Calcium (%)	Phosphorus (%)	Sodium (%)	Chlorine (%)	Potassium (%)	Magnesium (%)	Sulfur (%)	Copper (mg/kg)	Iodine (mg/kg)	Iron (mg/kg)	Manganese (mg/kg)	Selenium[c] (mg/kg)	Zinc (mg/kg)	Data Source
	Radish *Raphanus sativus*																
483	raw	—	5.2	0.02	0.02	0.02	—	0.30	0.01	—	0.40	—	3.00	0.70	0.01	3.00	USDASR14; Schmidt et al., 1999
484			100.0	0.39	0.39	0.39	—	5.81	0.19	—	7.75	—	58.14	13.57	0.19	58.14	
	Raisin, golden seedless *Vitis vinifera*																
485	fruit, raw, ep	—	85.0	0.05	0.12	0.01	—	0.75	0.04	—	3.60	—	18.00	3.10	0.01	3.20	USDASR14
486			100.0	0.06	0.14	0.01	—	0.88	0.05	—	4.23	—	21.17	3.65	0.01	3.76	
	Raisin, seeded *Vitis vinifera*																
487	fruit, raw, ep	—	83.43	0.03	0.08	0.03	—	0.83	0.03	—	3.00	—	26.00	2.70	0.01	1.80	USDASR14
488			100.0	0.04	0.10	0.04	—	0.99	0.04	—	3.60	—	31.16	3.24	0.01	2.16	
	Raisin, seedless *Vitis vinifera*																
489	fruit, raw, ep	—	84.6	0.05	0.10	0.01	—	0.75	0.03	—	3.10	—	21.00	3.10	0.01	2.70	USDASR14
490			100.0	0.06	0.12	0.01	—	0.89	0.04	—	3.67	—	24.83	3.67	0.01	3.19	
	Raspberry *Rubus idaeus*																
491	fruit, raw, ep	—	13.4	0.02	0.01	0.00	—	0.15	0.02	—	0.70	—	5.70	10.10	0.01	4.60	USDASR14; Schmidt et al., 1999
492			100.0	0.15	0.07	0.00	—	1.12	0.15	—	5.21	—	42.44	75.20	0.07	34.25	
	Rice *Oryza sativa*																
493	bran	4-03-928	90.0	0.07	1.61	0.03	0.07	1.56	0.90	0.18	9.00		190.00	228.00	0.40	30.00	NRC, 1998
494			100.0	0.08	1.79	0.03	0.08	1.73	1.00	0.20	10.00	—	211.11	253.33	0.44	33.33	
495	flour	—	88.1	0.01	0.10	0.00	—	0.08	0.04	—	1.30	—	4.00	12.00	0.15	8.00	USDASR14
496			100.0	0.01	0.11	0.00	—	0.09	0.05	—	1.48	—	4.54	13.62	0.17	9.08	
497	grain, polished and broken	4-03-932	89.0	0.04	0.18	0.04	0.07	0.13	0.11	0.06	21.00		18.00	12.00	0.27	17.00	NRC, 1998
498	(Brewer's Rice)		100.0	0.04	0.20	0.04	0.08	0.15	0.12	0.07	23.60	—	20.22	13.48	0.30	19.10	
499	hulls	1-08-075	92.0	0.04	0.20	0.04	0.08	0.15	0.12	0.07	23.60	—	20.22	13.48	0.30	19.10	NRC, 1982
500			100.0	0.05	0.22	0.05	0.09	0.16	0.13	0.07	25.65	—	21.98	14.66	0.33	20.76	
501	polishings	4-03-943	90.0	0.09	1.18	0.06	0.11	1.11	0.65	0.17	6.00		160.00	12.00	—	26.00	NRC, 1998
502			100.0	0.10	1.31	0.07	0.12	1.23	0.72	0.19	6.67	—	177.78	13.33	—	28.89	
	Rocket *Eruca sativa*																
503	aerial part, fresh	2-03-949	15.8														NRC, 1971
504			100.0														
	Rutabaga *Brassica campestris* var. *rutabaga*																
505	raw	—	10.3	0.05	0.06	0.02	—	0.34	0.02	—	0.40	—	5.00	1.70	0.01	3.40	USDASR14; Schmidt et al., 1999
506			100.0	0.48	0.58	0.19	—	3.29	0.19	—	3.87	—	48.36	16.44	0.10	32.88	
507	tops, fresh	—	10.9	—	—	—	—	—	—	—	—	—	—	—	—	—	Bath et al., 1999
508			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Rye *Secale cereale*																
509	grain	4-04-047	88.0	0.06	0.33	0.02	0.03	0.48	0.12	0.15	7.00		60.00	58.00	0.38	31.00	NRC, 1998
510			100.0	0.07	0.38	0.02	0.03	0.55	0.14	0.17	7.95	—	68.18	65.91	0.43	35.23	
	Safflower *Carthamus tinctorius*																
511	hulls	—	91.3	0.34	0.75	0.05	0.08	0.76	0.35	0.13	10.00	—	495.00	18.00	—	41.00	Bath et al., 1999
512			100.0	0.37	0.82	0.05	0.09	0.83	0.38	0.14	10.95	—	542.17	19.72	—	44.91	
513	meal, sol. extr.	5-04-110	92.0	0.37	1.31	0.04	0.16	1.00	1.02	0.20	9.00	—	484.00	39.00	—	33.00	NRC, 1998
514			100.0	0.40	1.42	0.04	0.17	1.09	1.11	0.22	9.78	—	526.09	42.39	—	35.87	
515	meal without hulls, sol. extr.	5-07-959	92.0														NRC, 1998
516			100.0														
517	oil	4-20-526	100.0	0.24	0.63	0.06	0.34	0.74	0.34	—	10.00	—	468.00	19.00	—	—	NRC, 1998
518			100.0	0.24	0.63	0.06	0.34	0.74	0.34	—	10.00	—	468.00	19.00	—	—	
519	seeds	—	94.0	2.44	0.63	0.06	0.34	0.74	0.34	—	10.34	—	470.00	18.80	—	41.36	Bath et al., 1999
520			100.0	2.60	0.67	0.06	0.36	0.79	0.36	—	11.00	—	500.00	20.00	—	44.00	
	Sapote *Achras sapotas*																
521	fruit, raw, ep	—	22.0	—	—	—	—	—	—	—	—	—	—	—	—	—	Schmidt et al., 1999
522			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Sesame *Sesamum indicum*																
523	meal, mech. extr.	5-04-220	93.0	1.90	1.22	0.04	0.07	1.10	0.54	0.56	34.00	—	93.00	53.00	0.21	100.00	NRC, 1998
524			100.0	2.04	1.31	0.04	0.08	1.18	0.58	0.60	36.56	—	100.00	56.99	0.23	107.53	
525	seeds	—	92.0	0.94	0.70	—	—	—	—	—	—	—	—	—	—	—	Bath et al., 1999
526			100.0	1.02	0.76	—	—	—	—	—	—	—	—	—	—	—	

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	Sorghum *Sorghum bicolor*																
527	grain	4-20-893	89	0.03	0.29	0.01	0.09	0.35	0.15	0.08	5.00	—	45.00	15.00	0.20	15.00	NRC, 1998
528			100	0.03	0.33	0.01	0.10	0.39	0.17	0.09	5.62	—	50.56	16.85	0.22	16.85	
	Soybean *Glycine max*																
529	flour, full-fat, raw	—	94.8	0.21	0.49	0.01	—	2.52	0.43	—	29.20	—	64.00	22.80	0.08	39.20	USDASR14
530			100.0	0.22	0.52	0.01	—	2.66	0.45	—	30.79	—	67.48	24.04	0.08	41.33	
531	hulls	1-4-560	91.0	0.45	1.16	0.01	—	1.16	0.19	0.08	16.00	—	295.00	10.00	—	22.00	NRC, 1982
532			100.0	0.49	1.27	0.01	—	1.27	0.21	0.09	18.00	—	324.00	11.00	—	24.00	
533	meal, sol. extr.	5-04-604	89.0	0.32	0.65	0.01	0.05	1.96	0.27	0.43	20.00	—	202.00	29.00	0.32	50.00	NRC, 1998
534			100.0	0.36	0.73	0.01	0.06	2.20	0.30	0.48	22.47	—	226.97	32.58	0.36	56.18	
535	meal without hulls, sol. extr.	5-04-612	90.0	0.34	0.69	0.02	0.05	2.14	0.30	0.44	20.00	—	176.00	36.00	0.27	55.00	NRC, 1998
536			100.0	0.38	0.77	0.02	0.06	2.38	0.33	0.49	22.22	—	195.56	40.00	0.30	61.11	
537	protein concentrate	—	90.0	0.35	0.81	0.05	—	2.20	0.32	—	13.00	—	110.00	—	—	30.00	NRC, 1998
538			100.0	0.39	0.90	0.06	—	2.44	0.36	—	14.44	—	122.22	—	—	33.33	
539	protein isolate	5-08-038	92.0	0.15	0.65	0.07	0.02	0.27	0.08	0.71	14.00	—	137.00	5.00	0.14	34.00	NRC, 1998
540			100.0	0.16	0.71	0.08	0.02	0.29	0.09	0.77	15.22	—	148.91	5.43	0.15	36.96	
541	seeds, heat processed	5-04-597	90.0	0.25	0.59	0.03	0.03	1.70	0.28	0.30	16.00	—	80.00	30.00	0.11	39.00	NRC, 1998
542			100.0	0.28	0.66	0.03	0.03	1.89	0.31	0.33	17.78	—	88.89	33.33	0.12	43.33	
	Spinach *Spinacia oleracea*																
543	raw	—	8.4	0.10	0.05	0.08	—	0.56	0.08	—	1.30	—	27.00	9.00	0.01	5.30	USDASR14; Schmidt et al., 1999
544			100.0	1.19	0.59	0.95	—	6.65	0.95	—	15.44	—	320.67	106.89	0.12	62.95	
	Squash, acorn *Cucurbita maxima*																
545	raw	—	12.2	0.03	0.04	0.00	—	0.35	0.03	—	0.70	—	7.00	1.70	0.01	1.30	USDASR14; Schmidt et al., 1999
546			100.0	0.25	0.33	0.00	—	2.86	0.25	—	5.73	—	57.28	13.91	0.08	10.64	
	Squash, butternut *Cucurbita maxima*																
547	raw	—	13.59	0.05	0.03	0.00	—	0.35	0.03	—	0.70	—	7.00	1.70	0.01	1.50	USDASR14; Schmidt et al., 1999
548			100.0	0.37	0.22	0.00	—	2.58	0.22	—	5.15	—	51.51	12.51	0.07	11.04	
	Squash, spaghetti *Cucurbita maxima*																
549	raw	—	8.4	0.02	0.01	0.02	—	0.11	0.01	—	0.40	—	3.00	1.30	0.00	1.90	USDASR14; Schmidt et al., 1999
550			100.0	0.24	0.12	0.24	—	1.31	0.12	—	4.76	—	35.71	15.48	0.00	22.62	
	Squash, zucchini *Cucurbita pepo*																
551	raw, with peel	—	4.7	0.02	0.03	0.00	0.25	1.30	0.02	—	0.60	—	4.00	1.30	0.00	2.00	USDASR14; Schmidt et al., 1999
552			100.0	0.42	0.64	0.00	5.30	27.54	0.42	—	12.71	—	84.75	27.54	0.00	42.37	
	Strawberry *Fragaria* spp																
553	fruit, raw, ep	—	8.4	0.01	0.02	0.00	—	0.25	0.01	—	0.50	—	4.00	2.90	0.01	1.30	USDASR14; Schmidt et al., 1999
554			100.0	0.12	0.24	0.00	—	2.97	0.12	—	5.93	—	47.45	34.40	0.12	15.42	
	Sucrose																
555		4-04-701	99.0	0.04	0.01												NRC, 1998
556			100.0	0.04	0.01	0.00	0.00	0.00	0.00	0.00	0.00	—	0.00	0.00	0.00	0.00	
	Sugarcane *Saccharum officinarum*																
557	stems, fresh	2-13-248	15.0	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1982
558			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
559	sugar	4-04-701	100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1982
560			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Sunflower, common *Helianthus annuus*																
561	kernels	—	95.0	0.36	0.86	0.02	0.10	1.07	0.68	0.30	26.00		254.00	41.00	0.50	66.00	Bath et al., 1999
562			100.0	0.38	0.91	0.02	0.11	1.13	0.72	0.32	27.37	—	267.37	43.16	0.53	69.47	
563	meal, sol. extr.	5-09-340	90.0	0.37	1.01	0.04	0.13	1.27	0.75	0.38	25.00		200.00	35.00	0.32	98.00	NRC, 1998
564			100.0	0.41	1.12	0.04	0.14	1.41	0.83	0.42	27.78	—	222.22	38.89	0.36	108.89	
565	meal without hulls, sol. extr.	5-04-739	93.0														NRC, 1998
566			100.0														
567	seeds	—	94.0	0.17	0.53	—	—	0.67	—	—	—	—	—	—	—	—	Bath et al., 1999
568			100.0	0.18	0.56	—	—	0.71	—	—	—	—	—	—	—	—	
	Sweet potato *Ipomoea batatas*																
569	tubers, fresh	—	27.2	0.02	0.03	0.01	—	0.20	0.01	—	1.70	—	6.00	3.60	0.01	2.80	USDASR14; Schmidt et al., 1999
570			100.0	0.07	0.11	0.04	—	0.74	0.04	—	6.26	—	22.09	13.25	0.04	10.31	
	Tamarind *Tamarindus indica*																
571	pulp	—	68.6	0.07	0.11	0.03	—	0.63	0.09	—	0.90	—	28.00	—	0.01	1.00	USDASR14
572			100.0	0.10	0.16	0.04	—	0.92	0.13	—	1.31	—	40.82	—	0.01	1.45	
573	seed	—	—			—	—	—		—	—	—	—	—	—		Glew et al., 1997
574			100.0	0.19	0.23	—	—	—	0.20	—	11.60	—	26.70	—	—	26.30	

(continues)

TABLE 12-2 (*continued*)

Entry Number	Description	International Feed Number[b]	Dry Matter (%)	Calcium (%)	Phosphorus (%)	Sodium (%)	Chlorine (%)	Potassium (%)	Magnesium (%)	Sulfur (%)	Copper (mg/kg)	Iodine (mg/kg)	Iron (mg/kg)	Manganese (mg/kg)	Selenium[c] (mg/kg)	Zinc (mg/kg)	Data Source
	Tomatillo																
575	fruit, raw, ep	—	8.0	0.01	0.04	0.00	—	0.27	0.02	—	0.80	—	6.00	1.50	0.01	2.20	USDASR14; Schmidt et al., 1999
576			100.0	0.13	0.50	0.00	—	3.40	0.25	—	10.06	—	75.47	18.87	0.13	27.67	
	Tomato *Lycopersicon esculentum*																
577	pomace, dehy	—	92.0	0.40	0.55	—	—	3.34	0.18	—	—	—	—	—	—	—	NRC, 1982; Bath et al., 1999
578			100.0	0.43	0.60	—	—	3.63	0.20	—	—	—	—	—	—	—	
579	red, ripe, raw, year-round average	—	6.2	0.01	0.02	0.01	—	0.22	0.01	—	0.70	—	5.00	1.10	0.00	0.90	USDASR14; Schmidt et al., 1999
580			100.0	0.16	0.32	0.16	—	3.53	0.16	—	11.22	—	80.13	17.63	0.00	14.42	
	Triticale *Triticale hexaploide*																
581	grain	4-20-362	90.0	0.05	0.33	0.03	0.03	0.46	0.10	0.15	8.00		31.00	43.00		32.00	NRC, 1998
582			100.0	0.06	0.37	0.03	0.03	0.51	0.11	0.17	8.89	—	34.44	47.78	0.00	35.56	
	Turnip *Brassica rapa rapa*																
583	greens, raw	—	8.9	0.19	0.04	0.04	—	0.30	0.03	—	3.50	—	11.00	4.70	0.01	1.90	USDASR14; Schmidt et al., 1999
584			100.0	2.13	0.45	0.45	—	3.36	0.34	—	39.19	—	123.18	52.63	0.11	21.28	
585	tubers, fresh	—	8.1	0.03	0.03	0.07	—	0.19	0.01	—	0.90	—	3.00	1.30	0.01	2.70	USDASR14; Schmidt et al., 1999
586			100.0	0.37	0.37	0.86	—	2.34	0.12	—	11.07	—	36.90	15.99	0.12	33.21	
	Walnut																
587	meats, ground	—	91.0	—	—	—	—	—	—	—							Bath et al., 1999
588			100.0	—	—	—	—	—	—	—							
	Watermelon *Citrullus vulgaris*																
589	fruit, raw, ep	—	8.5	—	—	—	—	—	—	—	—	—	—	—	—	—	Schmidt et al., 1999
590			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
591	fruit, raw, with peel	—	6.7	—	—	—	—	—	—	—	—	—	—	—	—	—	Schmidt et al., 1999
592			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Waxmoth *Galleria mellonella*																
593	larvae	—	42.7	0.02	0.18	0.02	—	0.22	0.04	—	3.24	—	20.15	1.20	0.20	21.94	Allen, 1989; Finke, 2002
594			100.0	0.04	0.43	0.04	—	0.53	0.10	—	7.58	—	47.18	2.82	0.46	51.38	
	Wheat *Triticum aestivum*																
595	bran	4-05-190	89.0	0.16	1.20	0.04	0.07	1.26	0.52	0.22	14.00		170.00	113.00	0.51	100.00	NRC, 1998
596			100.0	0.18	1.35	0.04	0.08	1.42	0.58	0.25	15.73	—	191.01	126.97	0.57	112.36	
597	flour, less than 2% fiber (feed flour)	4-28-221	88.0	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1982
598			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
599	germs, ground	5-05-218	88.0	0.05	0.92	0.03	0.07	0.97	0.25	0.25	10.00	—	51.00	134.00	0.36	119.00	NRC, 1982
600			100.0	0.06	1.05	0.03	0.08	1.09	0.28	0.28	11.00	—	58.00	151.00	0.40	135.00	
601	grain	4-05-211	89.0	0.04	0.37	0.04	0.07	0.38	0.15	0.16	6.00	0.09	54.00	37.00	0.26	44.00	NRC, 1982
602			100.0	0.04	0.42	0.05	0.08	0.42	0.16	0.18	7.00	0.10	61.00	42.00	0.30	50.00	
603	grain, hard red spring	4-05-258	88.0	0.05	0.36	0.02	0.09	0.41	0.16	0.17	7.00	—	64.00	42.00	0.30	43.00	NRC, 1998
604			100.0	0.06	0.41	0.02	0.10	0.47	0.18	0.19	7.95	—	72.73	47.73	0.34	48.86	
605	grain, hard red winter	4-05-268	88.0	0.06	0.37	0.01	0.06	0.49	0.13	0.15	6.00	—	39.00	34.00	0.33	40.00	NRC, 1998
606			100.0	0.07	0.42	0.01	0.07	0.56	0.15	0.17	6.82	—	44.32	38.64	0.38	45.45	
607	grain, soft red winter	4-05-294	88.0	0.04	0.39	0.01	0.08	0.46	0.10	0.16	8.00	—	32.00	38.00	0.28	47.00	NRC, 1998
608			100.0	0.05	0.44	0.01	0.09	0.52	0.11	0.18	9.09	—	36.36	43.18	0.32	53.41	
609	grain, soft white winter	4-05-337	89.0	0.05	0.35	0.01	0.07	0.44	0.15	0.18	7.00	—	60.00	37.00	0.26	28.00	NRC, 1998
610			100.0	0.06	0.39	0.01	0.08	0.49	0.17	0.20	7.87	—	67.42	41.57	0.29	31.46	
611	middlings, < 9.5% fiber	4-05-205	89.0	0.12	0.93	0.05	0.04	1.06	0.41	0.17	10.00	—	84.00	100.00	0.72	92.00	NRC, 1998
612			100.0	0.13	1.04	0.06	0.04	1.19	0.46	0.19	11.24	—	94.38	112.36	0.81	103.37	
613	mill run, less than 9.5% fiber	4-05-206	90.0	0.10	1.02	0.22	—	1.19	0.47	0.30	18.00	—	95.00	104.00	—	—	NRC, 1982
614			100.0	0.11	1.13	2.40	—	1.33	0.52	0.34	21.00	—	105.00	116.00	—	—	
615	red dog, < 4% fiber	4-05-203	88.0	0.07	0.57	0.04	0.10	0.63	0.16	0.24	6.00	—	46.00	55.00	0.30	65.00	NRC, 1998
616			100.0	0.08	0.65	0.05	0.11	0.72	0.18	0.27	6.82	—	52.27	62.50	0.34	73.86	
617	shorts, < 7% fiber	4-05-201	88.0	0.09	0.84	0.02	0.04	1.06	0.25	0.20	12.00	—	100.00	89.00	0.75	100.00	NRC, 1998
618			100.0	0.10	0.95	0.02	0.05	1.20	0.28	0.23	13.64	—	113.64	101.14	0.85	113.64	
	Whey (cattle)																
619	dried	4-01-182	96.0	0.75	0.72	0.94	1.40	1.96	0.13	0.72	13.00	—	130.00	3.00	0.12	10.00	NRC, 1998
620			100.0	0.78	0.75	0.98	1.46	2.04	0.14	0.75	13.54	—	135.42	3.13	0.13	10.42	

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621	low lactose, dried	4-01-186	96.0	2.00	1.37	1.85	3.43	4.68	0.25	1.59	3.00	—	85.00	8.00	0.06	11.00	NRC, 1998
622			100.0	2.08	1.43	1.93	3.57	4.88	0.26	1.66	3.13	—	88.54	8.33	0.06	11.46	
623	permeate, dried	—	96.0	0.86	0.66	1.00	2.23	2.10	—	—	—	—	—	—	—	—	NRC, 1998
624			100.0	0.90	0.69	1.04	2.32	2.19	—	—	—	—	—	—	—	—	
	Willow *Salix* spp.																
625	browse, fresh	2-05-472	41.0	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1971
626			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Willow, yellow *Salix lutea*																
627	browse	2-05-475	—	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1971
628			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Wood																
629	sawdust	1-07-714	90.0	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1971
630			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Yam *Dioscorea alata*																
631	tubers, fresh	—	30.4	0.02	0.06	0.01	—	0.82	0.02	—	1.80	—	5.00	4.00	0.01	2.40	USDASR14
632			100.0	0.07	0.20	0.03		2.70	0.07	—	5.92	—	16.45	13.16	0.03	7.89	
	Yeast, brewer's *Saccharomyces cerevisiae*																
633	dried	7-05-527	93.0	0.16	1.44	0.10	0.12	1.80	0.23	0.40	33.00	—	215.00	8.00	1.00	49.00	NRC, 1998
634			100.0	0.17	1.55	0.11	0.13	1.94	0.25	0.43	35.48	—	231.18	8.60	1.08	52.69	
	Yeast, torula *Torulopsis utilis*																
635	dried	7-05-534	93.0	0.58	1.52	0.07	0.12	1.94	0.20	0.55	17.00	—	222.00	13.00	0.02	99.00	NRC, 1998
636			100.0	0.62	1.63	0.08	0.13	2.09	0.22	0.59	18.28	—	238.71	13.98	0.02	106.45	

[a] Dash indicates that no data were available.

[b] First digit is class of feed: 1, dry forages and roughages; 2, pasture, range plants, and forages fed green; 3, silages; 4, energy feeds; 5, protein supplements; 6, minerals; 7, vitamins; 8, additives; the other five digits are the International Feed Number.

[c] Selenium values are extremely dependent on soil conditions and some values may differ substantially from those presented here.

TABLE 12-3 Composition of Important Feeds: Vitamins, Data Expressed As-Fed and Dry (100% Dry Matter)[a]

Entry Number	Description	International Feed Number[b]	Dry Matter (%)	Biotin (mg/kg)	Choline (mg/kg)	Folacin (mg/kg)	Niacin[c] (mg/kg)	Pantothenic Acid (mg/kg)	Thiamin (mg/kg)	Riboflavin (mg/kg)	Vitamin B6 (mg/kg)	Vitamin B12 (mg/kg)	Vitamin C (mg/kg)	Vitamin A (IU/kg)	Beta-Carotene (mg/kg)	Vitamin D2 (IU/kg)	Vitamin D3 (IU/kg)	Vitamin E (mg/kg)	Vitamin K (mg/kg)	Data Source
	Alder *Alnus* sp																			
1	leaves, sun-cured	—	85.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Bath et al., 1999
2			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Alfalfa *Medicago sativa*																			
3	meal dehy, 15% CP	1-00-022	90.0	0.25	1573	1.6	42.0	20.7	3.0	10.6	6.3	0.0	—	0.0	74.0	—	—	82.0	9.6	NRC, 1982
4			100.0	0.28	1739	1.7	46.0	22.9	3.3	11.7	6.9	0.0	—	0.0	82.0	—	—	91.0	10.6	
5	meal dehy, 17% CP	1-00-023	92.0	0.54	1401	4.4	38.0	29.0	3.4	13.6	6.5	0.0	—	0.0	94.6	—	—	49.8	8.2	NRC, 1998; NRC, 1982
6			100.0	0.59	1494	4.8	40.0	32.4	3.7	14.1	7.7	0.0	—	0.0	131.0	—	—	121.0	9.0	
7	meal dehy, 20% CP	1-00-024	92.0	0.54	1419	4.4	45.0	34.0	5.8	15.2	8.0	0.0	—	0.0	94.6	—	—	49.8	14.2	NRC, 1998; NRC, 1982
8			100.0	0.59	1547	3.2	52.0	38.8	5.9	16.6	9.6	0.0	—	0.0	174.0	—	—	165.0	15.5	
9	meal dehy, 22% CP	1-07-851	93.0	0.33	1605	5.1	50.0	39.0	5.9	17.6	8.3	0.0	—	0.0	235.0	—	—	221.0	11.6	NRC, 1982
10			100.0	0.36	1729	5.5	54.0	42.0	6.3	19.0	8.9	0.0	—	0.0	253.0	—	—	238.0	12.6	
	Almond *Prunus amygdalus*																			
11	hulls	4-00-359	90.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1982
12			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Apple *Malus sylvestris*																			
13	fruit, raw, with peel	—	16.1	—	—	0.0	1.0	1.0	0.2	0.1	0.5	0.0	57.0	0.0	0.3	—	—	3.2	—	USDASR14; Schmidt et al., 1999
14			100.0	—	—	0.2	5.0	4.0	1.1	0.9	3.1	0.0	354.7	0.0	1.6	—	—	19.9	—	
15	pomace, dehy	—	89.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Bath et al., 1999
16			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
17	pomace, oat hulls added, dehy	4-28-096	89.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1982
18			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Apricot *Prunus armeniaca*																			
19	fruit, dried, sulfured	—	68.9	—	—	0.1	30.0	8.0	0.1	1.5	1.6	0.0	24.0	0.0	176.0	—	—	15.0	—	USDASR14
20			100.0	—	—	0.1	44.0	11.0	0.1	2.2	2.3	0.0	34.8	0.0	255.4	—	—	21.8	—	
21	fruit, raw, ep	—	13.7	—	—	0.1	6.0	2.0	0.3	0.4	0.5	0.0	100.0	0.0	35.2	—	—	8.9	—	USDASR14; Schmidt et al., 1999
22			100.0	—	—	0.6	44.0	18.0	2.2	2.9	3.7	0.0	732.6	0.0	258.2	—	—	65.2	—	
	Ash *Fraxinus* spp.																			
23	leaves, sun-cured	—	85.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1971
24			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Asparagus *Asparagus officinalis*																			
25	spear, raw	—	7.6	—	—	1.3	12.0	2.0	1.4	1.3	1.3	0.0	132.0	0.0	4.5	—	—	20.0	0.4	USDASR14; Schmidt et al., 1999
26			100.0	—	—	16.8	154.0	23.0	18.4	16.8	17.1	0.0	1736.8	0.0	59.1	—	—	236.2	5.3	
	Aspen *Populus* spp																			
27	leaves, sun-cured	—	85.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Bath et al., 1999
28			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
29	flower buds, spring	—	38.2	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Guglielmo and Karasov, 1995
30			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Avocado *Persea americana*																			
31	fruit, raw, ep, all commerical varieties	—	25.7	—	—	0.6	19.0	10.0	1.1	1.2	2.8	0.0	79.0	0.0	0.3	—	—	13.4	—	USDASR14
32			100.0	—	—	2.4	75.0	38.0	4.2	4.7	10.9	0.0	307.0	0.0	1.3	—	—	52.1	—	
	Bamboo, arrow *Psuedosasa japonica*																			
33	leaves	—	24.1	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Warnell, 1988
34			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Banyan, weeping Chinese *Ficus benjamina*																			
35	leaves, mature, fresh	—	39.9	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Janeke, 1995
36			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Banyantree *Ficus benghalensis*																			
37	leaves, fresh	2-27-208	32.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1981
38			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Bakery waste																			
39	dried bakery product	4-00-466	92.0	0.07	923	0.2	26.0	8.3	2.9	1.4	4.3	—	—	6.5	4.0	—	—	41.0	—	NRC, 1998
40			100.0	0.08	1005	0.2	28.0	9.0	3.2	1.5	4.7	—	—	7.0	5.0	—	—	45.0	—	
	Banana *Musa sapientum*																			
41	aerial part, fresh	2-00-483	16.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1971
42			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
43	flower	—	8.7	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Schmidt et al., 1999
44			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	

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45	fruit, raw, ep	—	25.7	—	—	0.2	5.0	3.0	0.5	1.0	5.8	0.0	91.0	0.0	0.0	—	—	2.7	0.0	USDASR14
46			100.0	—	—	0.7	21.0	10.0	1.7	3.9	22.5	0.0	353.5	0.0	0.0	—	—	10.5	0.0	
47	fruit, raw, with peel	—	19.9	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Schmidt et al., 1999
48			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
49	leaves, fresh	2-09-902	19.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1981
50			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
51	peel	—	16.2	—	—	—	—	—	—	—	—	0.0	—	0.0	9.7	—	—	—	—	NRC, 1971
52			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	60.0	—	—	—	—	
	Barley *Hordeum distichon*																			
53	grain, two row	4-00-572	89.0	0.14	1034	0.3	55.0	8.0	4.5	1.8	5.0	0.0	—	0.0	4.1	—	—	7.4	—	NRC, 1998
54			100.0	0.16	1162	0.3	61.8	9.0	5.1	2.0	5.6	0.0	—	0.0	4.6	—	—	8.3	—	
	Barley *Hordeum vulgare*																			
55	grain, six row	4-00-574	89.0	0.15	1034	0.4	48.0	7.0	4.0	1.6	2.9	0.0	—	0.0	4.1	—	—	7.4	—	NRC, 1998
56			100.0	0.17	1162	0.4	53.9	7.9	4.5	1.8	3.3	0.0	—	0.0	4.6	—	—	8.3	—	
57	grain, hulless	4-00-552	88.0	0.07	—	0.6	48.0	6.8	4.3	1.8	5.6	0.0	—	0.0	—	—	—	6.0	—	NRC, 1998
58			100.0	0.08	—	0.7	54.5	7.7	4.9	2.0	6.4	0.0	—	0.0	—	—	—	6.8	—	
	Bean, snap *Phaseolus* spp																			
59	green, raw	—	9.7	—	—	0.4	8.0	1.0	0.8	1.0	0.7	0.0	163.0	0.0	6.3	—	—	4.1	0.5	USDASR14; Schmidt et al., 1999
60			100.0	—	—	3.8	77.0	10.0	8.6	10.8	7.2	0.0	1675.2	0.0	64.7	—	—	42.1	4.8	
61	yellow, raw	—	9.7	—	—	0.4	8.0	1.0	0.8	1.0	0.7	0.0	163.0	0.0	—	—	—	0.0	0.5	USDASR14
62			100.0	—	—	3.8	77.0	10.0	8.6	10.8	7.2	0.0	1675.2	0.0	—	—	—	0.0	4.8	
	Beech, American *Fagus grandifolia*																			
63	leaves, sun-cured	1-00-628	86.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1971; Robbins and Moen, 1975
64			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Beet, sugar *Beta vulgaris altissima*																			
65	greens, raw	—	7.9	—	—	0.2	4.0	3.0	1.0	2.2	1.1	0.0	300.0	0.0	25.6	—	—	15.0	—	USDASR14
66			100.0	—	—	1.9	51.0	32.0	12.7	28.0	14.0	0.0	3821.7	0.0	326.1	—	—	191.1	—	
67	pulp, dehy	4-00-669	91.0	—	818	—	18.0	1.3	0.4	0.7	1.9	0.0	—	0.0	10.6	577.0	—	13.2	—	NRC, 1998
68			100.0	—	899	—	18.0	1.5	0.4	0.8	2.4	0.0	—	0.0	0.0	637.0	—	14.5	—	
69	tops, fresh	—	17.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Bath et al., 1999
70			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
71	tubers, raw	—	12.4	—	—	1.1	3.0	2.0	0.3	0.4	0.7	0.0	49.0	0.0	—	—	—	3.0	0.0	USDASR14
72			100.0	—	—	8.8	27.0	12.0	2.5	3.2	5.6	0.0	394.5	0.0	—	—	—	24.2	0.2	
	Birch, paper *Betula papyrifera*																			
73	leaves	—	—	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Robbins and Moen, 1975
74			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Birch, sweet *Betula lenta*																			
75	browse, immature, fresh	2-00-724	92.4	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1971
76			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
77	browse, mid-bloom, fresh	2-00-725	93.7	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1971
78			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Blackberry *Rubus ulmifolius*																			
79	fruit, raw	—	14.4	—	—	0.3	4.0	2.0	0.3	0.4	0.6	0.0	210.0	0.0	—	—	—	7.1	—	USDASR14; Schmidt et al., 1999
80			100.0	—	—	2.4	28.0	17.0	2.1	2.8	4.2	0.0	1464.4	0.0	—	—	—	49.4	—	
	Blood																			
81	meal, conventional	5-00-380	92.0	0.03	852	0.1	31.0	2.0	0.4	2.4	4.4	44.0	—	—	0.0	—	—	1.0	—	NRC, 1998
82			100.0	0.03	926	0.1	33.7	2.2	0.4	2.6	4.8	47.8	—	—	0.0	—	—	1.1	—	
83	meal, flash dried	5-26-006	92.0	0.08	781	0.1	23.0	1.0	1.0	1.4	4.4	44.0	—	—	0.0	—	—	1.0	—	NRC, 1998
84			100.0	0.09	849	0.1	25.0	1.1	1.1	1.5	4.8	47.8	—	—	0.0	—	—	1.1	—	
85	meal, spray or ring dried	5-00-381	93.0	0.28	485	0.4	23.0	3.7	3.2	0.3	4.4	0.0	—	—	0.0	—	—	1.0	—	NRC, 1998
86			100.0	0.30	522	0.4	24.7	4.0	3.4	0.3	4.7	0.0	—	—	0.0	—	—	1.1	—	
87	plasma, spray dried	—	91.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1998
88			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
89	cells, spray dried	—	92.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1998
90			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Blueberries *Vaccinium* spp.																			
91	fruit, raw	—	15.4	—	—	0.1	4.0	1.0	0.5	0.5	0.4	0.0	130.0	0.0	0.1	—	—	10.0	—	USDASR14; Schmidt et al., 1999
92			100.0	—	—	0.4	23.0	6.0	3.1	3.2	2.6	0.0	844.7	0.0	0.7	—	—	65.0	—	
	Breadfruit *Artocarpus altilis*																			
93	fruit, raw	—	29.4	—	—	0.1	9.0	5.0	1.1	0.3	1.0	0.0	290.0	0.0	—	—	—	11.2	—	USDASR14
94			100.0	—	—	0.5	31.0	16.0	3.7	1.0	3.4	0.0	988.1	0.0	—	—	—	38.2	—	
	Brewer's grain																			
95	dried	5-02-141	92.0	0.24	1723	7.1	43.0	8.0	0.6	1.4	0.7	—	—	—	0.2	—	—	0.0	—	NRC, 1998
96			100.0	0.26	1873	7.7	46.7	8.7	0.7	1.5	0.8	—	—	—	0.2	—	—	0.0	—	
	Broccoli *Brassica oleracea* var. *italicca*																			
97	raw	—	9.3	—	—	0.7	6.0	5.0	0.7	1.2	1.6	0.0	932.0	0.0	7.0	—	—	16.6	2.1	USDASR14; Schmidt et al., 1999
98			100.0	—	—	7.6	69.0	57.0	7.0	12.8	17.2	0.0	1010.7	0.0	75.2	—	—	178.3	22.0	

(continues)

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TABLE 12-3 (*continued*)

Entry Number	Description	International Feed Number[b]	Dry Matter (%)	Biotin (mg/kg)	Choline (mg/kg)	Folacin (mg/kg)	Niacin[c] (mg/kg)	Pantothenic Acid (mg/kg)	Thiamin (mg/kg)	Riboflavin (mg/kg)	Vitamin B6 (mg/kg)	Vitamin B12 (mg/kg)	Vitamin C (mg/kg)	Vitamin A (IU/kg)	Beta-Carotene (mg/kg)	Vitamin D2 (IU/kg)	Vitamin D3 (IU/kg)	Vitamin E (mg/kg)	Vitamin K (mg/kg)	Data Source
	Brush cherry *Syzygium paniculata*																			
99	leaves, mature, fresh	—	31.6	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Janeke, 1995
100			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Brussel sprouts *Brassica oleracea* var. *bullata gemmifera*																			
101	raw	—	14.0	—	—	0.6	7.0	3.0	1.4	0.9	2.2	0.0	850.0	0.0	4.8	—	—	8.8	—	USDASR14; Schmidt et al., 1999
102			100.0	—	—	4.4	53.0	22.0	9.9	6.4	15.7	0.0	6071.0	0.0	34.3	—	—	62.9	—	
	Buckwheat, common *Fagopyrum sagittatum*																			
103	grain	4-00-994	88.0	0.06	440	0.6	19.0	12.0	4.0	5.5	3.0	0.0	—	0.0	—	—	—	—	—	NRC, 1998
104			100.0	0.07	501	0.7	21.0	13.1	4.2	5.4	3.4	0.0	—	0.0	—	—	—	—	—	
105	middlings	5-00-991	89.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1982
106			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Cabbage *Brassica oleracea* var. *capitata*																			
107	raw	—	7.9	—	—	0.4	3.0	1.0	0.5	0.4	1.0	0.0	322.0	0.0	0.8	—	—	1.1	—	USDASR14; Schmidt et al., 1999
108			100.0	—	—	5.5	38.0	18.0	6.4	5.1	12.7	0.0	4102.0	0.0	10.2	—	—	13.4	—	
	Cabbage, bok choy																			
109	raw	—	4.8	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Schmidt et al., 1999
110			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Cabbage, napa *Brassica pekinensis*																			
111	raw	—	3.5	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Schmidt et al., 1999
112			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Carambola *Averrhoa carambola*																			
113	fruit, raw	—	9.1	—	—	0.1	4.0	—	0.3	0.3	1.0	0.0	212.0	0.0	—	—	—	3.7	—	USDASR14
114			100.0	—	—	1.5	45.0	—	3.1	3.0	11.0	0.0	2334.0	0.0	—	—	—	40.8	—	
	Carrot *Daucus carota*																			
115	roots, fresh	—	12.2	—	—	0.1	9.0	2.0	1.0	0.6	1.5	0.0	93.0	0.0	79.0	—	—	4.6	—	USDASR14; Schmidt et al., 1999
116			100.0	—	—	1.1	76.0	16.0	7.9	4.8	12.3	0.0	761.7	0.0	647.0	—	—	37.7	—	
117	tops, fresh	—	16.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Bath et al., 1999
118			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Canola *Brassica napa*																			
119	meal, sol. extr.	5-06-145	90.0	0.98	6700	0.8	160.0	9.5	5.2	5.8	7.2	0.0	—	0.0	—	—	—	13.4	—	NRC, 1998
120			100.0	1.09	7444	0.9	177.8	10.6	5.8	6.4	8.0	0.0	—	0.0	—	—	—	14.9	—	
121	oil	4-06-144	100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1998
122			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Casein (cattle)																			
123	dehy	5-01-162	91.0	0.04	205	0.5	1.0	2.7	0.4	1.5	0.4	—	—	—	0.0	—	—	0.0	—	NRC, 1998
124			100.0	0.04	225	0.6	1.1	3.0	0.4	1.6	0.4	—	—	—	0.0	—	—	0.0	—	
	Cassava *Manihot esculentaed*																			
125	meal, dehydrated	4-01-152	88.0	0.05	0	0.0	3.0	0.3	1.6	0.8	0.7	0.0	—	0.0	0.0	—	—	0.2	—	NRC, 1998
126			100.0	0.06	0	0.0	3.4	0.3	1.8	0.9	0.8	0.0	—	0.0	0.0	—	—	0.2	—	
127	tubers, fresh	4-09-599	31.5	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1982; Schmidt et al., 1999
128			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Cauliflower *Brassica oleracea* var. *botrytis*																			
129	raw	—	8.1	—	—	0.6	5.0	7.0	0.6	0.6	2.2	0.0	464.0	0.0	0.1	—	—	0.4	—	USDASR14; Schmidt et al., 1999
130			100.0	—	—	0.7	65.0	81.0	7.0	7.8	27.2	0.0	5735.5	0.0	1.0	—	—	4.9	—	
131	green, raw	—	10.2	—	—	0.6	7.0	7.0	0.8	1.0	2.2	0.0	881.0	0.0	—	—	—	0.4	—	USDASR14
132			100.0	—	—	0.6	72.0	68.0	7.8	10.0	21.5	0.0	8628.8	0.0	—	—	—	3.9	—	
	Celery *Apium graveolens* var. *dulce*																			
133	raw	—	5.4	—	—	0.3	3.0	2.0	0.5	0.4	0.9	0.0	70.0	0.0	7.1	—	—	3.6	—	USDASR14; Schmidt et al., 1999
134			100.0	—	—	0.5	60.0	35.0	8.6	8.4	16.8	0.0	1306.0	0.0	132.5	—	—	67.2	—	
	Cereal																			
135	screenings	4-02-156	90.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1982
136			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Chalum *Inga* spp																			
137	dehy, fruit	—	96.8	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1971
138			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	

139	dehy, pod	—	97.8	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1971
140			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
141	dehy, seeds	—	93.5	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1971
142			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Chayote *Cucurbita pepo*																			
143	fruit, raw, with peel	—	7.0	—	—	0.9	4.7	2.5	0.3	0.3	0.8	0.0	77.0	0.0	—	—	—	1.2	—	USDASR14; Schmidt et al., 1999
144			100.0	—	—	12.9	67.1	35.7	4.3	4.3	11.4	0.0	1100.0	0.0	—	—	—	17.1	—	
	Cherimoya *Annona cherimolia*																			
145	fruit, raw	—	26.5	—	—	—	13.0	—	1.0	1.1	0.0	0.0	90.0	0.0	—	—	—	—	—	USDASR14
146			100.0	—	—	—	49.1	—	3.8	4.2	0.0	0.0	339.6	0.0	—	—	—	—	—	
	Cherry *Prunus* spp																			
147	fruit, raw	—	13.9	—	—	0.1	4.0	1.0	0.3	0.4	0.4	0.0	100.0	0.0	—	—	—	1.3	—	USDASR14
148			100.0	—	—	0.7	28.8	7.2	2.2	2.9	2.9	0.0	721.0	0.0	—	—	—	9.4	—	
	Chicory *Cichorium intybus*																			
149	greens, raw	—	8.0	—	—	1.1	5.0	12.0	0.6	1.0	1.1	0.0	240.0	0.0	—	—	—	22.6	—	USDASR14
150			100.0	—	—	13.8	62.5	150.0	7.5	12.5	13.8	0.0	3000.0	0.0	—	—	—	282.5	—	
	Cockroach, American *Periplaneta americana*																			
151	adult	—	33.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Allen, 1989
152			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Cockroach, Haitian *Blaberus discoidalus*																			
153	adult	—	30.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Allen, 1989
154			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Coconut *Cocos nucifera*																			
155	meal, sol. extr.	5-01-573	92.0	0.25	1089	0.3	28.0	6.5	0.7	3.5	4.4	0.0	—	0.0	0.0	—	—	7.7	—	NRC, 1998
156			100.0	0.27	1184	0.3	30.4	7.1	0.8	3.8	4.8	0.0	—	0.0	0.0	—	—	8.4	—	
157	oil	4-09-320	100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1998
158			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Collard *Brassica oleracea* var.																			
159	greens, raw	—	9.5	—	—	1.7	7.0	3.0	0.5	1.3	1.7	0.0	353.0	0.0	—	—	—	22.6	—	USDASR14; Schmidt et al., 1999
160			100.0	—	—	18.0	74.1	31.7	5.3	13.8	18.0	0.0	3735.4	0.0	—	—	—	239.2	—	
	Corn, yellow *Zea mays indentata*																			
161	bran	—	95.3	—	—	0.0	27.4	6.4	0.1	1.0	1.5	0.0	0.0	—	—	—	—	23.2	—	USDASR14
162			100.0	—	—	0.0	28.7	6.7	0.1	1.0	1.6	0.0	0.0	—	—	—	—	24.3	—	
163	cobs, ground	1-28-234	90.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
164			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
165	distillers' grain	5-02-842	94.0	0.49	1180	0.9	37.0	11.7	1.7	5.2	4.4	0.0	—	—	3.0	—	—	12.9	—	NRC, 1998
166			100.0	0.52	1255	1.0	39.4	12.4	1.8	5.5	4.7	0.0	—	—	3.2	—	—	13.7	—	
167	distillers' grain with solubles	5-02-843	93.0	0.78	2637	0.9	75.0	14.0	2.8	8.6	8.0	0.0	—	—	3.5	—	—	0.0	—	NRC, 1998
168			100.0	0.84	2835	1.0	80.6	15.1	3.0	9.2	8.6	0.0	—	—	3.8	—	—	0.0	—	
169	distillers' solubles	5-02-844	92.0	1.66	4842	1.1	116.0	21.0	6.9	17.0	8.8	3.0	—	—	0.0	—	—	0.0	—	NRC, 1998
170			100.0	1.80	5263	1.2	126.1	22.8	7.5	18.5	9.6	3.3	—	—	0.0	—	—	0.0	—	
171	flour, whole grain	—	89.1	19.00	—	0.3	19.0	7.0	2.5	0.8	3.7	0.0	0.0	—	—	—	—	2.5	—	USDASR14
172			100.0	21.33	—	0.3	21.3	7.9	2.8	0.9	4.2	0.0	0.0	—	—	—	—	2.8	—	
173	gluten feed	5-02-903	90.0	0.14	1518	0.3	66.0	17.0	2.4	2.0	13.0	0.0	—	0.0	1.0	—	—	8.5	—	NRC, 1998
174			100.0	0.16	1687	0.3	73.3	18.9	2.7	2.2	14.4	0.0	—	0.0	1.1	—	—	9.4	—	
175	gluten meal, 60% CP	5-28-242	90.0	0.15	330	0.1	55.0	3.5	2.2	0.3	6.9	0.0	—	0.0	0.0	—	—	6.7	—	NRC, 1998
176			100.0	0.17	367	0.1	61.1	3.9	2.4	0.3	7.7	0.0	—	0.0	0.0	—	—	7.4	—	
177	grain	4-02-935	89.0	0.06	620	0.2	24.0	6.0	1.2	3.5	5.0	0.0	—	0.0	0.8	—	—	8.3	—	NRC, 1998
178			100.0	0.07	697	0.2	27.0	6.7	1.3	3.9	5.6	0.0	—	0.0	0.9	—	—	9.3	—	
179	grits by-product (Hominy Feed)	4-03-011	90.0	0.13	1155	0.2	47.0	8.2	2.1	8.1	11.0	0.0	—	0.0	9.0	—	—	6.5	—	NRC, 1998
180			100.0	0.14	1283	0.2	52.2	9.1	2.3	9.0	12.2	0.0	—	0.0	10.0	—	—	7.2	—	
181	oil	4-07-882	100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1998
182			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
183	starch	4-02-889	99.0	—	—	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	—	—	—	0.0	—	USDASR14
184			100.0	—	—	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	—	—	—	0.0	—	
185	syrup, light	—	77.2	—	—	0.0	0.2	0.2	0.1	0.1	0.1	0.0	0.0	0.0	—	—	—	0.0	—	USDASR14
186			100.0	—	—	0.0	0.3	0.3	0.1	0.1	0.1	0.0	0.0	0.0	—	—	—	0.0	—	
	Corn, sweet *Zea mays saccharata*																			
187	cobs, fresh	—	31.7	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Schmidt et al., 1999
188			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
189	ear, whole, with husk, fresh	—	20.8	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Schmidt et al., 1999
190			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
191	husk, fresh	—	26.1	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Schmidt et al., 1999
192			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
193	white, raw, ep	—	24.0	—	—	0.5	17.0	8.0	2.0	0.6	0.6	0.0	68.0	0.0	—	—	—	0.9	—	USDASR14
194			100.0	—	—	2.1	70.7	33.3	8.3	2.5	2.5	0.0	282.9	0.0	—	—	—	3.7	—	
195	yellow, raw, ep	—	24.0	—	—	0.5	17.0	8.0	2.0	0.6	0.6	0.0	68.0	0.0	—	—	—	0.9	—	USDASR14
196			100.0	—	—	2.1	70.7	33.3	8.3	2.5	2.5	0.0	282.9	0.0	—	—	—	3.7	—	

(continues)

TABLE 12-3 (*Continued*)

Entry Number	Description	International Feed Number[b]	Dry Matter (%)	Biotin (mg/kg)	Choline (mg/kg)	Folacin (mg/kg)	Niacin[c] (mg/kg)	Pantothenic Acid (mg/kg)	Thiamin (mg/kg)	Riboflavin (mg/kg)	Vitamin B6 (mg/kg)	Vitamin B12 (mg/kg)	Vitamin C (mg/kg)	Vitamin A (IU/kg)	Beta-Carotene (mg/kg)	Vitamin D2 (IU/kg)	Vitamin D3 (IU/kg)	Vitamin E (mg/kg)	Vitamin K (mg/kg)	Data Source
	Corn borer, European *Ostrinia nubilalis*																			
197	larvae	—	27.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Allen, 1989
198			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
199	pupae	—	28.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Allen, 1989
200			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Cottonseed *Gossypium* spp																			
201	meal, mech. extr., 41% CP	5-01-617	92.0	0.30	2753	1.7	38.0	10.0	6.4	5.1	5.3	0.0	—	0.0	0.2	—	—	35.0	—	NRC, 1998
202			100.0	0.33	2992	1.8	41.3	10.9	7.0	5.5	5.8	0.0	—	0.0	0.2	—	—	38.0	—	
203	meal, sol. extr. 41% CP	5-07-872	90.0	0.30	2933	1.7	40.0	12.0	5.9	7.0	5.1	0.0	—	0.0	0.2	—	—	14.0	—	NRC, 1998
204			100.0	0.33	3259	1.8	44.4	13.3	6.6	7.8	5.7	0.0	—	0.0	0.2	—	—	15.6	—	
	Crayfish, Mexico *Cambrus* sp., *Aegiale hesperiaris*																			
205	adult	—	33.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Massieu et al., 1951
206			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Cricket, house *Acheta domesticus*																			
207	adult	—	30.8	0.17	1519	1.5	38.4	23.0	0.4	34.1	2.3	0.05	30.0	<1000	<0.02	—	<256	19.7	—	Finke, 2002
208			100.0	0.55	4932	4.9	124.7	74.7	1.3	110.7	7.5	0.16	97.4	—	—	—	—	64.0	—	
209	juvenile	—	22.9	0.05	1094	1.4	32.8	26.3	0.2	9.5	1.7	0.09	18.0	<1000	<0.02	—	<256	9.6	—	Finke, 2002
210			100.0	0.22	4777	6.4	143.2	114.8	0.9	41.5	7.4	0.39	78.6	—	—	—	—	41.9	—	
	Cricket, mormon *Anabrus simplex*																			
211	adult, both sexes	—	29.7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	DeFoliart et al., 1982
212			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Cucumber *Cucumis sativus*																			
213	raw, with peel	—	4.0	—	—	0.1	2.0	2.0	0.2	0.2	0.4	0.0	53.0	0.0	—	—	—	0.8	—	USDASR14; Schmidt et al., 1999
214			100.0	—	—	2.5	50.1	50.1	5.0	5.0	10.0	0.0	1328.3	0.0	—	—	—	20.1	—	
	Custard apple *Annona* spp																			
215	fruit, raw	—	28.5	—	—	—	5.0	1.0	0.8	1.0	2.2	0.0	192.0	0.0	—	—	—	—	—	USDASR14
216			100.0	—	—	—	17.5	3.5	2.8	3.5	7.7	0.0	673.7	0.0	—	—	—	—	—	
	Dandelion *Taraxacum officinale*																			
217	greens, raw	2-01-748	14.4	—	—	0.3	8.0	1.0	1.9	2.6	2.5	0.0	350.0	0.0	—	—	—	25.0	—	USDASR14
218			100.0	—	—	2.1	55.6	6.9	13.2	18.1	17.4	0.0	2430.6	0.0	—	—	—	173.6	—	
	Dock *Rumex* spp.																			
219	greens, raw	—	7.0	—	—	0.1	5.0	0.4	0.4	1.0	1.2	0.0	480.0	0.0	—	—	—	—	—	USDASR14
220			100.0	—	—	1.4	71.4	5.7	5.7	14.3	17.1	0.0	6857.1	0.0	—	—	—	—	—	
	Egg (Chicken)																			
221	dehy, whole	—	96.9	—	—	1.7	3.0	59.0	2.0	15.4	3.9	0.0	0.0	0.0	—	—	—	43.8	—	USDASR14
222			100.0	—	—	1.8	3.1	60.9	2.1	15.9	4.0	0.0	0.0	0.0	—	—	—	45.2	—	
	Eggplant *Solanum melongena*																			
223	fruit, raw	—	8.0	—	—	0.2	6.0	3.0	0.5	0.3	0.8	0.0	17.0	0.0	—	—	—	0.3	—	USDASR14; Schmidt et al., 1999
224			100.0	—	—	2.5	75.3	37.6	6.3	3.8	10.0	0.0	213.3	0.0	—	—	—	3.8	—	
	Fababean (Broadbean) *Phaseolus* spp																			
225	seeds	5-09-262	87.0	0.09	1670	0.0	26.0	3.0	5.5	2.9	0.0	0.0	—	0.0	0.0	—	—	0.8	—	NRC, 1998
226			100.0	0.10	1920	0.0	29.9	3.4	6.3	3.3	0.0	0.0	—	0.0	0.0	—	—	0.9	—	
	Fat																			
227	animal, hydrolyzed	4-00-376	100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	USDASR11
228			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
229	animal, poultry	4-00-409	99.8	—	—	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	—	—	—	—	27.0	—	USDASR14
230			100.0	—	—	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	—	—	—	—	27.1	—	
231	animal, swine (lard)	4-04-790	100.0	—	—	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	—	—	—	—	12.0	—	USDASR14
232			100.0	—	—	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	—	—	—	—	12.0	—	
	Feather																			
233	meal, hydrolyzed	5-03-795	93.0	0.13	891	0.2	21.0	10.0	0.1	2.1	3.0	7.8	—	—	0.0	—	—	7.3	—	NRC, 1981
234			100.0	0.14	958	0.2	22.6	10.8	0.1	2.3	3.2	8.4	—	—	0.0	—	—	7.8	—	
	Feijoa *Feijoa sellowiana*																			
235	fruit, raw	—	13.4	—	—	0.4	3.0	2.0	0.1	0.3	0.5	0.0	203.0	0.0	—	—	—	—	—	USDASR14
236			100.0	—	—	3.0	22.4	14.9	0.7	2.2	3.7	0.0	1514.9	0.0	—	—	—	—	—	
	Ficus nitida																			
237	leaves, mature, fresh	—	35.3	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Janeke, 1995
238			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	

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	Ficus rumphii																			
239	leaves, mature, fresh	—	29.6	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Janeke, 1995
240			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Ficus thonningii																			
241	leaves, mature, fresh	—	27.7	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Janeke, 1995
242			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Fig *Ficus carica*																			
243	fruit, raw	—	20.9	—	—	31.0	4.0	3.0	0.6	0.5	1.1	0.0	20.0	0.0	—	—	—	8.9	—	USDASR14
244			100.0	—	—	148.4	19.1	14.4	2.9	2.4	5.3	0.0	95.7	0.0	—	—	—	42.6	—	
245	fruit, dried	—	64.9	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Schmidt et al., 1999
246			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
247	leaves, mature, fresh	—	23.5	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Janeke, 1995
248			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Fig, cluster *Ficus glomerata*																			
249	leaves, fresh	2-27-209	30.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1981
250			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
251	leaves, mature, fresh	—	32.8	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Janeke, 1995
252			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Fig, Indian laurel *Ficus retusa*																			
253	leaves, mature, fresh	—	38.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Janeke, 1995
254			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Fig, Moreton Bay *Ficus macrophylla*																			
255	leaves, mature, fresh	—	37.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Janeke, 1995
256			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Fig, Roxburgh *Ficus roxburghii*																			
257	leaves, fresh	2-30-177	33.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1981
258			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Fig, rustyleaf *Ficus rubiginosa*																			
259	leaves, mature, fresh	—	30.6	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Janeke, 1995
260			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Fig, spotted *Ficus virens*																			
261	leaves, fresh	2-28-704	15.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1981
262			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Fish																			
263	solubles, condensed	5-01-969	51.0	0.18	3519	0.0	169.0	35.0	14.6	5.5	12.2	347.0	—	—	0.0	—	—	0.0	—	NRC, 1998
264			100.0	0.35	6900	0.0	331.4	68.6	28.6	10.8	23.9	680.4	—	—	0.0	—	—	0.0	—	
265	solubles, dried	5-01-971	92.0	0.26	5507	0.6	271.0	55.0	15.6	7.4	23.8	401.0	—	—	0.0	—	—	0.0	—	NRC, 1998
266			100.0	0.28	5986	0.7	294.6	59.8	17.0	8.0	25.9	435.9	—	—	0.0	—	—	0.0	—	
	Fish, anchovy *Engraulis ringen*																			
267	meal, mech. extr.	5-01-985	92.0	0.13	4408	0.4	100.0	15.0	0.3	7.1	4.0	280.0	—	—	0.0	—	—	5.0	—	NRC, 1998
268			100.0	0.14	4791	0.4	108.7	16.3	0.3	7.7	4.3	304.3	—	—	0.0	—	—	5.4	—	
	Fish, herring *Clupea harengus*																			
269	meal, mech. extr.	5-02-000	93.0	0.13	5306	0.4	93.0	17.0	0.4	9.9	4.8	403.0	—	—	0.0	—	—	15.0	—	NRC, 1998
270			100.0	0.14	5705	0.4	100.0	18.3	0.4	10.6	5.2	433.3	—	—	0.0	—	—	16.1	—	
	Fish, menhaden *Brevoortia tyrannus*																			
271	meal, mech. extr.	5-02-009	92.0	0.13	3056	0.4	55.0	9.0	0.5	4.9	4.0	143.0	—	—	0.0	—	—	5.0	—	NRC, 1998
272			100.0	0.14	3322	0.4	59.8	9.8	0.5	5.3	4.3	155.4	—	—	0.0	—	—	5.4	—	
	Fish, white Gadidae (family); Lophiidae (family)																			
273	meal, mech. extr.	5-02-025	91.0	0.13	3099	0.4	59.0	9.9	1.7	9.1	5.9	90.0	—	—	0.0	—	—	5.0	—	NRC, 1998
274			100.0	0.14	3405	0.4	64.8	10.9	1.9	10.0	6.5	98.9	—	—	0.0	—	—	5.5	—	
	Flax *Linum usitatissinum*																			
275	meal, sol. extr.	5-02-048	90.0	0.41	1512	1.3	33.0	14.7	7.5	2.9	6.0	0.0	—	0.0	0.2	—	—	2.0	—	NRC, 1998
276			100.0	0.46	1680	1.4	36.7	16.3	8.3	3.2	6.7	0.0	—	0.0	0.2	—	—	2.2	—	
	Fructose																			
277		—	99.5	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	IOM, 1996
278			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Gelatin																			
279		5-14-503	90.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1998
280			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Glucose																			
281	monohydrate	4-02-125	90.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1998
282			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Granadilla, purple *Passiflora edulis*																			
283	fruit, raw, ep	—	27.1	—	—	0.1	15.0	—	0.0	1.3	1.0	0.0	300.0	0.0	—	—	—	11.2	—	USDASR14
284			100.0	—	—	0.4	55.4	—	0.0	4.8	3.7	0.0	1108.2	0.0	—	—	—	41.4	—	

(continues)

TABLE 12-3 (*continued*)

Entry Number	Description	International Feed Number[b]	Dry Matter (%)	Biotin (mg/kg)	Choline (mg/kg)	Folacin (mg/kg)	Niacin[c] (mg/kg)	Pantothenic Acid (mg/kg)	Thiamin (mg/kg)	Riboflavin (mg/kg)	Vitamin B6 (mg/kg)	Vitamin B12 (mg/kg)	Vitamin C (mg/kg)	Vitamin A (IU/kg)	Beta-Carotene (mg/kg)	Vitamin D2 (IU/kg)	Vitamin D3 (IU/kg)	Vitamin E (mg/kg)	Vitamin K (mg/kg)	Data Source
	Grape, European type *Vitis* spp																			
285	fruit, raw, ep	—	19.4	—	—	0.0	3.0	0.2	0.9	0.6	1.1	0.0	108.0	0.0	—	—	—	7.0	—	USDASR14
286			100.0	—	—	0.0	15.4	1.0	4.6	3.1	5.7	0.0	555.6	0.0	—	—	—	36.0	—	
	Grapefruit *Citrus paradisi*																			
287	fruit, raw, ep	—	9.1	—	—	0.1	3.0	3.0	0.4	0.2	0.4	0.0	344.0	0.0	—	—	—	2.5	—	USDASR14
288			100.0	—	—	1.1	32.9	32.9	4.4	2.2	4.4	0.0	3776.1	0.0	—	—	—	27.4	—	
289	peel	—	29.1																	Schmidt et al., 1999
290			100.0																	
	Grasshopper *Melanoplus femurrubrum*																			
291	adult	—	30.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Bird et al., 1982
292			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Guava, common or lemon *Psidium guajava*																			
293	fruit, raw, ep	—	13.9	—	—	0.1	12.0	2.0	0.5	0.5	1.4	0.0	1835.0	0.0	4.2	—	—	11.2	—	USDASR14
294			100.0	—	—	0.7	86.3	14.4	3.6	3.6	10.1	0.0	13201.4	0.0	29.9	—	—	80.6	—	
	Guava, strawberry *Psidium cattleianum*																			
295	fruit, raw, ep	—	19.3	—	—	—	6.0	—	0.3	0.3	0.0	0.0	370.0	0.0	—	—	—	—	—	USDASR14
296			100.0	—	—	—	31.0	—	1.6	1.6	0.0	0.0	1913.1	0.0	—	—	—	—	—	
	Hemicellulose extract																			
297		4-08-030	76.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1982
298			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—		
	Hibiscus, tropical *Hibiscus rosa-sinensis*																			
299	leaves, mature, fresh	—	21.9	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Janeke, 1995
300			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Honeysuckle *Lonicera albiflora*																			
301	leaves, fresh	2-29-875	33.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1981
302			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Jack fruit *Artocarpus heterophyllus*																			
303	fruit, raw, ep	—	26.8	—	—	0.1	4.0	—	0.3	1.1	1.1	0.0	67.0	0.0	—	—	—	1.5	—	USDASR14
304			100.0	—	—	0.4	14.9	—	1.1	4.1	4.1	0.0	250.3	0.0	—	—	—	5.6	—	
	Jujube *Zizyphus jujuba*																			
305	browse, fresh	2-30-091	32.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1981
306			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
307	fruit, raw, ep	—	22.1	—	—	—	9.0	—	0.2	0.4	0.8	0.0	690.0	0.0	—	—	—	—	—	USDASR14
308			100.0	—	—	—	40.7	—	0.9	1.8	3.6	0.0	3116.5	0.0	—	—	—	—	—	
	Kale *Brassica oleracea* var. *acephala*																			
309	leaves and stems, fresh	—	15.5	—	—	0.3	10.0	0.9	1.1	1.3	2.7	0.0	1200.0	0.0	—	—	—	8.0	—	USDASR14; Schmidt et al., 1999
310			100.0	—	—	1.9	64.4	5.8	7.1	8.4	17.4	0.0	7722.0	0.0	—	—	—	51.5	—	
	Kiwifruit *Actinidia chinensis*																			
311	raw	—	17.0	—	—	0.4	5.0	—	0.2	0.5	0.9	0.0	980.0	0.0	—	—	—	11.2	—	USDASR14; Schmidt et al., 1999
312			100.0	—	—	2.4	29.5	—	1.2	2.9	5.3	0.0	5781.7	0.0	—	—	—	66.1	—	
	Kohlrabi *Brassica oleracea* var. *gongylodes*																			
313	tubers, fresh	—	9.0	—	—	0.2	4.0	1.7	0.5	0.2	1.5	0.0	620.0	0.0	—	—	—	4.8	—	USDASR14
314			100.0	—	—	2.2	44.4	18.9	5.6	2.2	16.7	0.0	6888.9	0.0	—	—	—	53.3	—	
	Kudzu *Pueraria lobata*																			
315	aerial part, fresh	2-02-482	26.4	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1971
316			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Kumquat *Fortunella* spp																			
317	fruit, raw, ep	—	18.3	—	—	0.2	5.0	—	0.8	1.0	0.6	0.0	374.0	0.0	—	—	—	2.4	—	USDASR14
318			100.0	—	—	1.1	27.3	—	4.4	5.5	3.3	0.0	2043.7	0.0	—	—	—	13.1	—	
	Lactose																			
319		4-07-881	96.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1998
320			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Lentil *Len culinaris*																			
321	seeds	5-02-506	89.0	0.13		0.7	22.0	14.9	3.9	2.4	5.5	0.0	—	0.0	1.0	—	—	0.0	—	NRC, 1998
322			100.0	0.15	0	0.8	24.7	16.7	4.4	2.7	6.2	0.0	—	0.0	1.1	—	—	0.0	—	
	Lettuce, endive *Cichorium endiva*																			
323	leaves, fresh	—	6.2	—	—	1.4	4.0	9.0	0.8	0.8	0.2	0.0	65.0	0.0	—	—	—	4.4	—	USDASR14
324			100.0	—	—	22.5	64.4	144.9	12.9	12.9	3.2	0.0	1046.7	0.0	—	—	—	70.9	—	

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	Lettuce, iceberg *Lactuca sativa*																			
325	leaves, fresh	—	4.1	—	—	0.6	2.0	0.5	0.5	0.3	0.0	0.0	39.0	0.0	—	—	—	2.8	—	USDASR11; Schmidt et al., 1999
326			100.0	—	—	14.6	48.7	12.2	12.2	7.3	0.0	0.0	948.9	0.0	—	—	—	68.1	—	
	Lettuce, romaine																			
327	leaves, fresh	—	5.1	—	—	1.4	5.0	2.0	1.0	1.0	0.4	0.0	240.0	0.0	19.0	—	—	4.4	—	USDASR14; Schmidt et al., 1999
328			100.0	—	—	26.7	98.0	33.0	19.6	19.6	5.8	0.0	4715.1	0.0	373.3	—	—	86.4	—	
	Longan *Nephelium longana*																			
329	fruit, raw, ep	—	17.3	—	—	—	3.0	—	0.3	1.4	0.5	0.0	840.0	0.0	—	—	—	—	—	USDASR14
330			100.0	—	—	—	17.4	—	1.7	8.1	2.9	0.0	4869.6	0.0	—	—	—	—	—	
	Loquat *Eriobotrya japonica*																			
331	fruit, raw, ep	—	13.3	—	—	0.1	2.0	—	0.2	0.2	0.0	0.0	10.0	0.0	—	—	—	8.9	—	USDASR14
332			100.0	—	—	0.8	15.1	—	1.5	1.5	0.0	0.0	75.4	0.0	—	—	—	67.1	—	
	Lupin (sweet white) *Lupinus albus*																			
333	seeds	5-27-717	89.0	0.05	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	—	0.0	0.0	—	—	7.5	—	NRC, 1998
334			100.0	0.06	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	—	0.0	0.0	—	—	8.4	—	
	Lychee *Litchi chinensis*																			
335	fruit, raw, ep	—	18.2	—	—	0.1	6.0	—	0.1	0.7	1.0	0.0	715.0	0.0	—	—	—	7.0	—	USDASR14
336			100.0	—	—	0.5	32.9	—	0.5	3.8	5.5	0.0	3920.0	0.0	—	—	—	38.4	—	
	Mango *Mangifera indica*																			
337	fruit, raw, ep	—	18.3	—	—	0.1	6.0	2.0	0.6	0.6	1.3	0.0	277.0	0.0	15.1	—	—	11.2	—	USDASR14; Schmidt et al., 1999
338			100.0	—	—	0.5	32.8	10.9	3.3	3.3	7.1	0.0	1514.5	0.0	82.3	—	—	61.2	—	
	Maple, sugar *Acer saccharum*																			
339	leaves	—	—	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Robbins and Moen, 1975
340			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Mealworm *Tenebrio molitor*																			
341	larvae	—	38.1	0.30	1844	1.6	40.7	26.2	2.4	8.1	8.1	<0.01	12.0	<1000	<0.2	—	<256	<5.0	—	Finke, 2002
342			100.0	0.79	4840	4.1	106.8	68.8	6.3	21.3	21.3	0.01	31.5	—	—	—	—	—	—	
343	larvae, gut loaded with high (8%) Ca diet	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
344			—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
345	oversized	—	39.0	0.37	1712	1.2	41.3	14.5	1.2	16.1	5.8	<0.01	24.0	<1000	<0.2	—	<256	<5.0	—	Finke, 2002
346			100.0	0.95	4390	3.0	105.9	37.2	3.1	41.3	14.9	<0.01	61.5	—	—	—	—	—	—	
	Mealworm *Zophobas morio*																			
347	larvae	—	42.1	0.35	1736	0.7	32.3	19.4	0.6	7.5	3.2	<0.01	12.0	<1000	<0.2	—	<256	7.7	—	Finke, 2002
348			100.0	0.83	4124	1.6	76.7	46.1	1.4	17.8	7.6	0.01	28.5	—	—	—	—	18.3	—	
	Meat																			
349	meal rendered	5-00-385	94.0	0.08	2077	0.5	57.0	5.0	0.6	4.7	2.4	80.0	—	—	—	—	—	1.2	—	NRC, 1998
350			100.0	0.09	2210	0.5	60.6	5.3	0.6	5.0	2.6	85.1	—	—	—	—	—	1.3	—	
351	meal rendered with bone	5-00-388	93.0	0.08	1996	0.4	49.0	4.1	0.4	4.7	4.6	90.0	—	—	—	—	—	1.6	—	NRC, 1998
352			100.0	0.09	2146	0.4	52.7	4.4	0.4	5.1	4.9	96.8	—	—	—	—	—	1.7	—	
	Melon, cantaloupe *Cucumis melo*																			
353	fruit, raw, ep	—	10.2	—	—	0.2	6.0	1.0	0.4	0.2	1.2	0.0	422.0		—	—	—	1.5	—	USDASR14; Schmidt et al., 1999
354			100.0	—	—	2.0	58.7	9.8	3.9	2.0	11.7	0.0	4129.2	0.0	—	—	—	14.7	—	
355	fruit, raw, with peel	—	7.5	—	—	—	—	—	—	—	—	0.0	—	—	—	—	—	—	—	Schmidt et al., 1999
356			100.0	—	—	—	—	—	—	—	—	0.0	—	—	—	—	—	—	—	
	Melon, casaba *Cucumis melo*																			
357	fruit, raw, ep	—	8.0	—	—	0.2	4.0	—	0.6	0.2	1.2	0.0	160.0	0.0	—	—	—	1.5	—	USDASR14
358			100.0	—	—	2.5	50.0	—	7.5	2.5	15.0	0.0	2000.0	0.0	—	—	—	18.8	—	
	Melon, honeydew *Cucumis melo*																			
359	fruit, raw, ep	—	10.3	—	—	0.1	6.0	2.0	0.8	0.2	0.6	0.0	248.0	0.0	—	—	—	1.5	—	USDASR14; Schmidt et al., 1999
360			100.0	—	—	1.0	58.0	19.3	7.7	1.9	5.8	0.0	2398.5	0.0	—	—	—	14.5	—	
361	fruit, raw, with peel	—	8.1	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Schmidt et al., 1999
362			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Milk, cattle *Bos taurus*																			
363	dehy	5-01-167	96.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1982
364			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
365	fresh	5-01-168	12.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1982
366			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
367	skimmed, dehy	5-01-175	94.0	0.25	1393	0.5	12.0	36.4	3.7	19.1	4.1	36.0	—	—	—	—	—	4.1	—	NRC, 1998
368			100.0	0.27	1482	0.5	12.8	38.7	3.9	20.3	4.4	38.3	—	—	—	—	—	4.4	—	
369	skimmed, fresh	5-01-170	10.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1982
370			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	

(continues)

TABLE 12-3 (*continued*)

Entry Number	Description	International Feed Number[b]	Dry Matter (%)	Biotin (mg/kg)	Choline (mg/kg)	Folacin (mg/kg)	Niacin[c] (mg/kg)	Pantothenic Acid (mg/kg)	Thiamin (mg/kg)	Riboflavin (mg/kg)	Vitamin B6 (mg/kg)	Vitamin B12 (mg/kg)	Vitamin C (mg/kg)	Vitamin A (IU/kg)	Beta-Carotene (mg/kg)	Vitamin D2 (IU/kg)	Vitamin D3 (IU/kg)	Vitamin E (mg/kg)	Vitamin K (mg/kg)	Data Source
	Milk, human *Homo sapiens*																			
371	fresh	—	12.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Jensen, 1995
372			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Milk, baboon *Papio*																			
373	fresh, days 0-5	—	14.6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Hummer, 1970
374			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
375	fresh, days 6-11	—	15.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Hummer, 1970
376			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
377	fresh, days 12-35	—	14.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Hummer, 1970
378			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
379	fresh, days 36-279	—	14.4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Hummer, 1970
380			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Millet *Panicum miliaceum*																			
381	grain	4-03-120	90.0	0.16	440	0.2	23.0	11.0	7.3	3.8	5.8	0.0	—	0.0	0.0	—	—	0.0	—	NRC, 1998
382			100.0	0.18	489	0.3	25.6	12.2	8.1	4.2	6.4	0.0	—	0.0	0.0	—	—	0.0	—	
	Mirror plant *Coprosma repens*																			
383	leaves, mature, fresh	—	17.5	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Janeke, 1995
384			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Molasses and syrup																			
385	beet, sugar, molasses	4-00-668	78.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1982
386			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
387	citrus, syrup	4-01-241	68.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1982
388			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
389	sugarcane, molasses, dehy	4-04-695	94.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1982
390			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
391	sugarcane, molasses, more than 46%	4-04-696	75.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1982
392			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Mulberry *Morus* spp.																			
393	browse, fresh	2-03-150	40.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1981
394			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
395	fruit, raw, ep	—	12.3	—	—	0.1	6.0	—	0.3	1.0	0.5	0.0	364.0	0.0	—	—	—	4.5	—	USDASR14
396			100.0	—	—	0.8	48.7	—	2.4	8.1	4.1	0.0	2954.5	0.0	—	—	—	36.5	—	
	Mulberry, white *Morus alba*																			
397	leaves, mature, fresh	—	31.1	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Janeke, 1995
398			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Mustard *Brassica oleracea* var.																			
399	leaves and stems, fresh	—	9.2	—	—	1.9	8.0	2.0	0.8	1.1	1.8	0.0	700.0	0.0	—	—	—	20.1	—	USDASR14; Schmidt et al., 1999
400			100.0	—	—	20.7	87.0	21.7	8.7	12.0	19.6	0.0	7608.7	0.0	—	—	—	218.5	—	
	Nectarine *Prunus persica*																			
401	fruit, raw, ep	—	13.7	—	—	0.0	10.0	2.0	0.2	0.4	0.3	0.0	54.0	0.0	—	—	—	8.9	—	USDASR14; Schmidt et al., 1999
402			100.0	—	—	0.0	72.9	14.6	1.5	2.9	2.2	0.0	393.6	0.0	—	—	—	64.9	—	
	Oat *Avena sativa*																			
403	grain	4-03-309	89.0	0.24	946	0.3	19.0	13.0	6.0	1.7	2.0	0.0	—	0.0	3.7	—	—	7.8	—	NRC, 1998
404			100.0	0.27	1063	0.3	21.3	14.6	6.7	1.9	2.2	0.0	—	0.0	4.2	—	—	8.8	—	
405	grain, naked	4-25-101	86.0	0.12	1240	0.5	20.0	7.1	5.2	1.3	9.6	0.0	—	0.0	—	—	—	2.0	—	NRC, 1998
406			100.0	0.14	1442	0.6	23.3	8.3	6.0	1.5	11.2	0.0	—	0.0	—	—	—	2.3	—	
407	groat	4-03-331	90.0	0.20	1139	0.5	14.0	13.4	6.5	1.5	1.1	0.0	—	0.0	—	—	—	—	—	NRC, 1998
408			100.0	0.22	1266	0.6	15.6	14.9	7.2	1.7	1.2	0.0	—	0.0	—	—	—	—	—	
409	hulls	1-03-281	92.0																	NRC, 1982
410			100.0																	
	Olive *Olea europaea*																			
411	oil	—	100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1998
412			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Okra *Hibiscus esculentus*																			
413		—	12.6	—	—	0.9	10.0	3.0	2.0	0.6	2.2	0.0	211.0	0.0	—	—	—	6.9	0.0	USDASR14; Schmidt et al., 1999
414			100.0	—	—	7.2	79.6	23.9	15.9	4.8	17.5	0.0	1679.9	0.0	—	—	—	54.9	0.0	
	Onion *Allium cepa*																			
415	green	—	9.1	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Schmidt et al., 1999
416			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	

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417	red	—	9.1	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Schmidt et al., 1999
418			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
419	yellow	—	10.3	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Schmidt et al., 1999
420			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Orange *Citrus* spp																			
421	fruit, raw, ep	—	13.3	—	—	0.3	3.0	3.0	0.9	0.4	0.6	0.0	532.0	0.0	—	—	—	2.4	—	USDASR14
422			100.0	—	—	2.3	22.6	22.6	6.8	3.0	4.5	0.0	4015.1	0.0	—	—	—	18.1	—	
423	fruit, raw, with peel	—	17.7	—	—	0.3	5.0	3.0	1.0	0.5	0.9	0.0	710.0	0.0	—	—	—	2.4	—	USDASR14; Bath et al., 1999
424			100.0	—	—	1.7	28.2	16.9	5.6	2.8	5.1	0.0	4011.3	0.0	—	—	—	13.6	—	
425	peel	—	27.5	—	—	0.3	9.0	5.0	1.2	0.9	1.8	0.0	1360.0	0.0	—	—	—	2.4	—	USDASR14; Schmidt et al., 1999
426			100.0	—	—	1.1	32.7	18.2	4.4	3.3	6.5	0.0	4945.5	0.0	—	—	—	8.7	—	
	Papaya *Carica papaya*																			
427	fruit, raw, ep	—	11.2	—	—	0.4	3.0	2.0	0.3	0.3	0.2	0.0	618.0	0.0	1.3	—	—	11.2	—	USDASR14; Schmidt et al., 1999
428			100.0	—	—	3.6	26.9	17.9	2.7	2.7	1.8	0.0	5532.7	0.0	11.3	—	—	100.3	—	
	Parsley																			
429	leaves and stems, fresh	—	12.0	—	—	1.5	13.0	4.0	0.9	1.0	0.9	0.0	1330.0	0.0	—	—	—	17.9	—	USDASR14; Schmidt et al., 1999
430			100.0	—	—	12.5	108.1	33.3	7.5	8.3	7.5	0.0	11055.7	0.0	—	—	—	148.8	—	
	Parsnip *Pastinaca sativa*																			
431	roots, fresh	—	20.5	—	—	37.0	7.0	6.0	39.0	0.5	0.9	0.0	170.0	0.0	—	—	—	—	—	USDASR14
432			100.0	—	—	180.8	34.2	29.3	190.5	2.4	4.4	0.0	830.5	0.0	—	—	—	—	—	
	Pea *Pisum* spp																			
433	seeds	5-03-600	89.0	0.15	547	0.2	31.0	18.7	4.6	1.8	1.0	0.0	—	0.0	1.0	—	—	0.2	—	NRC, 1998
434			100.0	0.17	615	0.2	34.8	21.0	5.2	2.0	1.1	0.0	—	0.0	1.1	—	—	0.2	—	
	Peach *Prunus persica*																			
435	fruit, raw, ep	—	12.3	—	—	0.0	10.0	2.0	0.2	0.4	0.2	0.0	66.0	0.0	—	—	—	7.0	0.0	USDASR14
436			100.0	—	—	0.0	81.0	16.2	1.6	3.2	1.6	0.0	534.8	0.0	—	—	—	56.7	0.0	
	Pear *Pyrus communis*																			
437	fruit, raw, ep	—	16.2	—	—	0.1	1.0	1.0	0.2	0.4	0.2	0.0	40.0	0.0	—	—	—	5.0	—	USDASR14; Schmidt et al., 1999
438			100.0	—	—	0.6	6.2	6.2	1.2	2.5	1.2	0.0	247.1	0.0	—	—	—	30.9	—	
	Peanut (Groundnut) *Arachis hypogaea*																			
439	butter	—	98.8	—	—	0.7	134.0	8.0	0.8	1.1	4.5	0.0	0.0	0.0	—	—	—	100.0	—	USDASR14
440			100.0	—	—	0.7	135.7	8.1	0.8	1.1	4.6	0.0	0.0	0.0	—	—	—	101.2	—	
441	hulls	1-08-028	91.0																	NRC, 1982
442			100.0																	
443	kernels, meal mech extr	5-03-649	92.0	0.35	1848	0.7	166.0	47.0	7.1	5.2	7.4	0.0	—	0.0	0.0	—	—	2.7	—	NRC, 1998
444			100.0	0.38	2009	0.8	180.4	51.1	7.7	5.7	8.0	0.0	—	0.0	0.0	—	—	2.9	—	
445	kernels, meal solv extr	5-03-650	92.0	0.39	1854	0.5	170.0	53.0	5.7	7.0	6.0	0.0	—	0.0	0.0	—	—	2.7	—	NRC, 1998
446			100.0	0.42	2015	0.5	184.8	57.6	6.2	7.6	6.5	0.0	—	0.0	0.0	—	—	2.9	—	
	Peepultree *Ficus religiosa*																			
447	leaves, fresh	2-27-207	17.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1981
448			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Pepper, sweet, green *Capsicum annuum*																			
449	fruit, raw, ep	—	5.3	—	—	0.2	5.0	1.0	0.7	0.3	2.5	0.0	893.0	0.0	—	—	—	6.9	—	USDASR14; Schmidt et al., 1999
450			100.0	—	—	3.8	95.2	19.0	13.3	5.7	47.6	0.0	17009.5	0.0	—	—	—	131.4	—	
	Persimmon, American *Diospyros virginiana*																			
451	fruit, raw, ep	—	35.6	—	—	—	—	—	—	—	0.0	0.0	660.0	0.0	—	—	—	—	—	USDASR14
452			100.0	—	—	—	—	—	—	—	0.0	0.0	1853.9	0.0	—	—	—	—	—	
	Persimmon, Oriental (Kaki) *Diospyros kaki*																			
453	fruit, raw, ep	—	19.7	—	—	0.1	1.0	—	0.3	0.2	1.0	0.0	75.0	0.0	—	—	—	5.9	—	USDASR14
454			100.0	—	—	0.5	5.1	—	1.5	1.0	5.1	0.0	381.1	0.0	—	—	—	30.0	—	
	Pineapple *Ananas comosus*																			
455	fruit, raw, ep	—	13.5	—	—	0.1	4.0	2.0	0.9	0.4	0.9	0.0	154.0	0.0	—	—	—	1.0	—	USDASR14; Schmidt et al., 1999
456			100.0	—	—	0.7	29.6	14.8	6.7	3.0	6.7	0.0	1140.7	0.0	—	—	—	7.4	—	
	Plantain *Musa sapientum*																			
457	fruit, raw, ep	—	34.7	—	—	0.2	7.0	2.6	0.5	0.5	3.0	0.0	184.0	0.0	—	—	—	2.7	—	USDASR14; Schmidt et al., 1999
458			100.0	—	—	0.6	20.2	7.5	1.4	1.4	8.6	0.0	530.0	0.0	—	—	—	7.8	—	
	Plum *Prunus domestica*																			
459	fruit, raw, ep	—	14.8	—	—	0.0	5.0	2.0	0.4	1.0	0.8	0.0	95.0	0.0	—	—	—	6.0	—	USDASR14; Schmidt et al., 1999
460			100.0	—	—	0.0	33.8	13.5	2.7	6.8	5.4	0.0	641.9	0.0	—	—	—	40.5	—	
	Pomegranate *Punica granatum*																			
461	fruit, raw, ep	—	19.0	—	—	0.1	3.0	6.0	0.3	0.3	1.1	0.0	61.0	0.0	—	—	—	5.5	—	USDASR14
462			100.0	—	—	0.5	15.8	31.5	1.6	1.6	5.8	0.0	320.5	0.0	—	—	—	28.9	—	
	Poplar, black *Populus nigra*																			
463	leaves, sun-cured	1-03-750	85.4	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1971
464			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	

(continues)

TABLE 12-3 (*continued*)

Entry Number	Description	International Feed Number[b]	Dry Matter (%)	Biotin (mg/kg)	Choline (mg/kg)	Folacin (mg/kg)	Niacin[c] (mg/kg)	Pantothenic Acid (mg/kg)	Thiamin (mg/kg)	Riboflavin (mg/kg)	Vitamin B6 (mg/kg)	Vitamin B12 (mg/kg)	Vitamin C (mg/kg)	Vitamin A (IU/kg)	Beta-Carotene (mg/kg)	Vitamin D2 (IU/kg)	Vitamin D3 (IU/kg)	Vitamin E (mg/kg)	Vitamin K (mg/kg)	Data Source
	Potato *Solanum tuberosum*																			
465	protein concentrate	5-25-392	91.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1998
466			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
467	tubers, fresh	—	28.0																	USDASR11; Schmidt et al., 1999
468			100.0																	
	Poultry																			
469	by-product, meal rendered	5-03-798	93.0	0.09	6029	0.5	47.0	11.1	0.2	10.5	4.4	—	—	—	—	—	—	—	—	NRC, 1998
470			100.0	0.10	6483	0.5	50.5	11.9	0.2	11.3	4.7	—	—	—	—	—	—	—	—	
	Prune																			
471	with pits	—	82.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Bath et al., 1999
472			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
473	without pits	—	80.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Bath et al., 1999
474			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Pummelo *Citrus grandis*																			
475	fruit, raw, ep	—	10.9	—	—	—	2.0	—	0.3	0.3	0.4	0.0	610.0	0.0	—	—	—	—	—	USDASR14
476			100.0	—	—	—	18.3	—	2.8	2.8	3.7	0.0	5596.3	0.0	—	—	—	—	—	
	Pumpkin *Cucurbita pepo*																			
477		—	20.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Schmidt et al., 1999
478			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Quince *Cydonia oblonga*																			
479	fruit, raw, ep	—	16.2	—	—	0.0	2.0	0.8	0.2	0.3	0.4	0.0	150.0	0.0	—	—	—	5.5	—	USDASR14
480			100.0	—	—	0.0	12.3	4.9	1.2	1.9	2.5	0.0	925.9	0.0	—	—	—	34.0	—	
	Radicchio *Cichorium intybus* var. *foliosum*																			
481	raw	—	6.9	—	—	0.6	3.0	3.0	0.2	0.3	0.6	0.0	80.0	0.0	—	—	—	22.6	—	USDASR14
482			100.0	—	—	8.7	43.7	43.7	2.9	4.4	8.7	0.0	1166.2	0.0	—	—	—	329.4	—	
	Radish *Raphanus sativus*																			
483	raw	—	5.2	—	—	0.3	3.0	1.0	0.1	0.5	0.7	0.0	228.0	0.0	—	—	—	0.0	—	USDASR14; Schmidt et al., 1999
484			100.0	—	—	5.8	58.1	19.4	1.9	9.7	13.6	0.0	4418.6	0.0	—	—	—	0.2	—	
	Raisin, golden seedless *Vitis vinifera*																			
485	fruit, raw, ep	—	85.0	—	—	0.0	11.0	1.0	0.1	1.9	3.2	0.0	32.0	0.0	—	—	—	7.0	—	USDASR14
486			100.0	—	—	0.0	12.9	1.2	0.1	2.2	3.8	0.0	37.6	0.0	—	—	—	8.2	—	
	Raisin, seeded *Vitis vinifera*																			
487	fruit, raw, ep	—	83.4	—	—	0.0	11.0	1.0	1.1	1.8	1.9	0.0	54.0	0.0	—	—	—	7.0	—	USDASR14
488			100.0	—	—	0.0	13.2	1.2	1.3	2.2	2.3	0.0	64.7	0.0	—	—	—	8.4	—	
	Raisin, seedless *Vitis vinifera*																			
489	fruit, raw, ep	—	84.6	—	—	0.0	8.0	1.0	1.6	0.9	2.5	0.0	33.0	0.0	—	—	—	7.0	—	USDASR14
490			100.0	—	—	0.0	9.5	1.2	1.9	1.1	3.0	0.0	39.0	0.0	—	—	—	8.3	—	
	Raspberry *Rubus idaeus*																			
491	fruit, raw, ep	—	13.4	—	—	0.3	9.0	2.0	0.3	0.9	0.6	0.0	250.0	0.0	—	—	—	4.5	—	USDASR14; Schmidt et al., 1999
492			100.0	—	—	2.2	67.0	14.9	2.2	6.7	4.5	0.0	1861.5	0.0	—	—	—	33.5	—	
	Rice *Oryza sativa*																			
493	bran	4-03-928	90.0	0.35	1135	2.2	293.0	23.0	22.5	2.5	26.0	0.0	—	0.0	—	—	—	9.7	—	NRC, 1998
494			100.0	0.39	1261	2.4	325.6	25.6	25.0	2.8	28.9	0.0	—	0.0	—	—	—	10.8	—	
495	flour	—	88.1	—	—	0.0	26.0	8.0	1.4	0.2	4.4	0.0	0.0	0.0	—	—	—	1.3	—	USDASR14
496			100.0	—	—	0.0	29.5	9.1	1.6	0.2	5.0	0.0	0.0	0.0	—	—	—	1.5	—	
497	grain, polished and broken	4-03-932	89.0	0.08	1003	0.2	25.0	3.3	1.4	0.4	28.0	0.0	—	0.0	—	—	—	2.0	—	NRC, 1998
498	(Brewer's Rice)		100.0	0.09	1127	0.2	28.1	3.7	1.6	0.4	31.5	0.0	—	0.0	—	—	—	2.2	—	
499	hulls	1-08-075	92.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1982
500			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
501	polishings	4-03-943	90.0	0.37	1237	0.2	520.0	47.0	1.8	19.8	27.6	0.0	—	0.0	0.1	—	—	61.0	—	NRC, 1998
502			100.0	0.41	1374	0.2	577.8	52.2	2.0	22.0	30.7	0.0	—	0.0	0.1	—	—	67.8	—	
	Rocket *Eruca sativa*																			
503	aerial part, fresh	2-03-949	15.8	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1971
504			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Rutabaga *Brassica campestris* var. *rutabaga*																			
505	raw	—	10.3	—	—	0.2	7.0	2.0	0.9	0.4	1.0	0.0	250.0	0.0	—	—	—	3.0	—	USDASR14; Schmidt et al., 1999
506			100.0	—	—	1.9	67.7	19.3	8.7	3.9	9.7	0.0	2417.8	0.0	—	—	—	29.0	—	
507	tops, fresh	—	10.9	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Bath et al., 1999
508			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	

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	Rye *Secale cereale*																			
509	grain	4-04-047	88.0	0.08	419	0.6	19.0	8.0	3.6	1.6	2.6	0.0	—	0.0	—	—	—	9.0	—	NRC, 1998
510			100.0	0.09	476	0.7	21.6	9.1	4.1	1.8	3.0	0.0	—	0.0	—	—	—	10.2	—	
	Safflower *Carthamus tinctorius*																			
511	hulls	—	91.3	1.03	820	0.5	11.0	33.9	4.6	2.3	12.0	0.0	—	0.0	0.0	—	—	16.0	—	Bath et al., 1999
512			100.0	1.13	898	0.5	12.0	37.1	5.0	2.5	13.1	0.0	—	0.0	0.0	—	—	17.5	—	
513	meal, sol. extr.	5-04-110	92.0	1.03	3248	1.6	22.0	39.1	4.5	2.4	11.3	0.0	—	0.0	0.0	—	—	16.0	—	NRC, 1998
514			100.0	1.12	3530	1.7	23.9	42.5	4.9	2.6	12.3	0.0	—	0.0	0.0	—	—	17.4	—	
515	meal without hulls, sol. extr.	5-07-959	92.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1998
516			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
517	oil	4-20-526	100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1998
518			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
519	seeds	—	94.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Bath et al., 1999
520			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Sapote *Achras sapotas*																			
521	fruit, raw, ep	—	22.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Schmidt et al., 1999
522			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Sesame *Sesamum indicum*																			
523	meal, mech. extr.	5-04-220	93.0	0.24	1536	0.0	30.0	6.0	2.8	3.6	12.5	0.0	—	0.0	0.2	—	—	1.0	—	NRC, 1998
524			100.0	0.26	1652	0.0	32.3	6.5	3.0	3.9	13.4	0.0	—	0.0	0.2	—	—	1.1	—	
525	seeds	—	92.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Bath et al., 1999
526			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Sorghum *Sorghum bicolor*																			
527	grain	4-20-893	89.0	0.26	668	0.2	41.0	12.4	3.0	1.3	5.2	0.0	—	0.0	0.0	—	—	5.0	—	NRC, 1998
528			100.0	0.29	751	0.2	46.1	13.9	3.4	1.5	5.8	0.0	—	0.0	0.0	—	—	5.6	—	
	Soybean *Glycine max*																			
529	flour, full-fat, raw	—	94.8	—	—	3.5	43.0	16.0	5.8	11.6	4.6	0.0	0.0	0.0	—	—	—	19.5	—	USDASR14
530			100.0	—	—	3.7	45.3	16.9	6.1	12.2	4.9	0.0	0.0	0.0	—	—	—	20.6	—	
531	hulls	1-4-560	91.0																	NRC, 1982
532			100.0																	
533	meal, sol. extr.	5-04-604	89.0	0.27	2794	1.4	34.0	16.0	4.5	2.9	6.0	0.0	—	0.0	0.2	—	—	2.3	—	NRC, 1998
534			100.0	0.30	3139	1.5	38.2	18.0	5.1	3.3	6.7	0.0	—	0.0	0.2	—	—	2.6	—	
535	meal without hulls, sol. extr.	5-04-612	90.0	0.26	2731	1.4	22.0	15.0	3.2	3.1	6.4	0.0	—	0.0	0.2	—	—	2.3	—	NRC, 1998
536			100.0	0.29	3034	1.5	24.4	16.7	3.6	3.4	7.1	0.0	—	0.0	0.2	—	—	2.6	—	
537	protein concentrate	—	90.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1998
538			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
539	protein isolate	5-08-038	92.0	0.30	2	2.5	6.0	4.2	0.3	1.7	5.4	0.0	—	0.0		—	—		—	NRC, 1998
540			100.0	0.33	2	2.7	6.5	4.6	0.3	1.8	5.9	0.0	—	0.0	0.0	—	—	0.0	—	
541	seeds, heat processed	5-04-597	90.0	0.24	2307	3.6	22.0	15.0	11.0	2.6	10.8	0.0	—	0.0	1.9	—	—	18.1	—	NRC, 1998
542			100.0	0.27	2563	4.0	24.4	16.7	12.2	2.9	12.0	0.0	—	0.0	2.1	—	—	20.1	—	
	Spinach *Spinacia oleracea*																			
543	raw	—	8.4	—	—	1.9	7.0	0.7	0.8	1.9	2.0	0.0	281.0	0.0	—	—	—	18.9	—	USDASR14; Schmidt et al., 1999
544			100.0	—	—	22.6	83.1	8.3	9.5	22.6	23.8	0.0	3337.3	0.0	—	—	—	224.5	—	
	Squash, acorn *Cucurbita maxima*																			
545	raw	—	12.2	—	—	0.2	7.0	4.0	1.4	0.1	1.5	0.0	110.0	0.0	—	—	—	—	—	USDASR14; Schmidt et al., 1999
546			100.0	—	—	1.6	57.3	32.7	11.5	0.8	12.3	0.0	900.2	0.0	—	—	—	—	—	
	Squash, butternut *Cucurbita maxima*																			
547	raw	—	13.6	—	—	0.3	12.0	4.0	1.0	0.2	1.5	0.0	210.0	0.0	—	—	—	—	—	USDASR14; Schmidt et al., 1999
548			100.0	—	—	2.2	88.3	29.4	7.4	1.5	11.0	0.0	1545.3	0.0	—	—	—	—	—	
	Squash, spaghetti *Cucurbita maxima*																			
549	raw	—	8.4	—	—	0.1	10.0	4.0	0.4	0.2	1.0	0.0	21.0	0.0	—	—	—	—	—	USDASR14; Schmidt et al., 1999
550			100.0	—	—	1.2	119.0	47.6	4.8	2.4	11.9	0.0	250.0	0.0	—	—	—	—	—	
	Squash, zucchini *Cucurbita pepo*																			
551	raw, with peel	—	4.7	—	—	0.2	4.0	1.0	0.7	0.3	0.9	0.0	90.0	0.0	—	—	—	1.2	—	USDASR14; Schmidt et al., 1999
552			100.0	—	—	4.2	84.7	21.2	14.8	6.4	19.1	0.0	1906.8	0.0	—	—	—	25.4	—	
	Strawberry *Fragaria* spp																			
553	fruit, raw, ep	—	8.4	—	—	0.2	2.0	3.0	0.2	0.7	0.6	0.0	567.0	0.0	—	—	—	1.4	—	USDASR14; Schmidt et al., 1999
554			100.0	—	—	2.4	23.7	35.6	2.4	8.3	7.1	0.0	6726.0	0.0	—	—	—	16.6	—	
	Sucrose																			
555		4-04-701	99.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1998
556			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Sugarcane *Saccharum officinarum*																			
557	stems, fresh	2-13-248	15.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1982
558			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
559	sugar	4-04-701	100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1982
560			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	

(continues)

TABLE 12-3 (*continued*)

Entry Number	Description	International Feed Number[b]	Dry Matter (%)	Biotin (mg/kg)	Choline (mg/kg)	Folacin (mg/kg)	Niacin[c] (mg/kg)	Pantothenic Acid (mg/kg)	Thiamin (mg/kg)	Riboflavin (mg/kg)	Vitamin B6 (mg/kg)	Vitamin B12 (mg/kg)	Vitamin C (mg/kg)	Vitamin A (IU/kg)	Beta-Carotene (mg/kg)	Vitamin D2 (IU/kg)	Vitamin D3 (IU/kg)	Vitamin E (mg/kg)	Vitamin K (mg/kg)	Data Source
	Sunflower, common *Helianthus annuus*																			
561	kernels	—	95.0	1.40	3791	1.1	264.0	29.9	3.0	3.0	11.1	0.0	—	0.0	0.0	—	—	9.1	—	Bath et al., 1999
562			100.0	1.47	3991	1.2	277.9	31.5	3.2	3.2	11.7	0.0	—	0.0	0.0	—	—	9.6	—	
563	meal, sol. extr.	5-09-340	90.0	1.45	3150	1.1	220.0	24.0	3.5	3.6	13.7	0.0	—	0.0	0.0	—	—	9.1	—	NRC, 1998
564			100.0	1.61	3500	1.3	244.4	26.7	3.9	4.0	15.2	0.0	—	0.0	0.0	—	—	10.1	—	
565	meal without hulls, sol. extr.	5-04-739	93.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1998
566			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
567	seeds	—	94.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Bath et al., 1999
568			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Sweet potato *Ipomoea batatas*																			
569	tubers, fresh	—	27.2	—	—	0.1	7.0	6.0	0.7	1.5	2.6	0.0	227.0	0.0	—	—	—	2.8	—	USDASR14; Schmidt et al., 1999
570			100.0	—	—	0.4	25.8	22.1	2.6	5.5	9.6	0.0	835.8	0.0	—	—	—	10.3	—	
	Tamarind *Tamarindus indica*																			
571	pulp	—	68.6	—	—	0.1	19.0	1.0	4.3	1.5	0.7	0.0	35.0	0.0	—	—	—	7.0	—	USDASR14
572			100.0	—	—	0.1	27.7	1.5	6.3	2.2	1.0	0.0	51.0	0.0	—	—	—	10.2	—	
573	seed	—	—	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Glew et al., 1997
574			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Tomatillo																			
575	fruit, raw, ep	—	8.0	—	—	0.1	19.0	2.0	0.4	0.4	0.6	0.0	117.0	0.0	—	—	—	3.8	—	USDASR14; Schmidt et al., 1999
576			100.0	—	—	1.3	239.0	25.2	5.0	5.0	7.5	0.0	1471.7	0.0	—	—	—	47.8	—	
	Tomato *Lycopersicon esculentum*																			
577	pomace, dehy	—	92.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1982; Bath et al., 1999
578			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
579	red, ripe, raw, year-round average	—	6.2	—	—	0.2	6.0	3.0	0.6	0.5	0.8	0.0	100.0	0.0	—	—	—	3.8	—	USDASR14; Schmidt et al., 1999
580			100.0	—	—	3.2	96.2	48.1	9.6	8.0	12.8	0.0	1602.6	0.0	—	—	—	60.9	—	
	Triticale *Triticale hexaploide*																			
581	grain	4-20-362	90.0	0.00	462	0.0	0.0	0.0	0.0	0.4	0.0	0.0	—	0.0	0.0	—	—	1.7	—	NRC, 1998
582			100.0	0.00	513	0.0	0.0	0.0	0.0	0.4	0.0	0.0	—	0.0	0.0	—	—	1.9	—	
	Turnip *Brassica rapa rapa*																			
583	greens, raw	—	8.9	—	—	1.9	6.0	4.0	0.7	1.0	2.6	0.0	600.0	0.0	—	—	—	29.0	—	USDASR14; Schmidt et al., 1999
584			100.0	—	—	21.3	67.2	44.8	7.8	11.2	29.1	0.0	6718.9	0.0	—	—	—	324.7	—	
585	tubers, fresh	—	8.1	—	—	0.2	4.0	2.0	0.4	0.3	0.9	0.0	210.0	0.0	—	—	—	0.3	—	USDASR14; Schmidt et al., 1999
586			100.0	—	—	2.5	49.2	24.6	4.9	3.7	11.1	0.0	2583.0	0.0	—	—	—	3.7	—	
	Walnut																			
587	meats, ground	—	91.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Bath et al., 1999
588			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Watermelon *Citrullus vulgaris*																			
589	fruit, raw, ep	—	8.5	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Schmidt et al., 1999
590			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
591	fruit, raw, with peel	—	6.7	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	Schmidt et al., 1999
592			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Waxmoth *Galleria mellonella*																			
593	larvae	—	41.5	0.29	1641	0.44	37.5	20.2	2.3	7.3	1.3	<1.2	<10.0	<1000	—	—	<256	13.3	—	Finke, 2002
594			100.0	0.70	3954	1.06	90.4	48.7	5.5	17.6	3.1	—	—	—	—	—	—	32.0	—	
	Wheat *Triticum aestivum*																			
595	bran	4-05-190	89.0	0.36	1232	0.6	186.0	31.0	8.0	4.6	12.0	0.0	—	0.0	1.0	—	—	16.5	—	NRC, 1998
596			100.0	0.40	1384	0.7	209.0	34.8	9.0	5.2	13.5	0.0	—	0.0	1.1	—	—	18.5	—	
597	flour, less than 2% fiber (feed flour)	4-28-221	88.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1982
598			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
599	germs, ground	5-05-218	88.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1982
600			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
601	grain	4-05-211	89.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1982
602			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
603	grain, hard red spring	4-05-258	88.0	0.11	1026	0.4	56.0	12.5	5.1	1.3	3.6	0.0	—	0.0		—	—		—	NRC, 1998
604			100.0	0.13	1166	0.5	63.6	14.2	5.8	1.5	4.1	0.0	—	0.0	0.0	—	—	0.0	—	
605	grain, hard red winter	4-05-268	88.0	0.11	778	0.2	48.0	9.9	4.5	1.4	3.4	0.0	—	0.0	0.4	—	—	11.6	—	NRC, 1998
606			100.0	0.13	884	0.3	54.5	11.3	5.1	1.6	3.9	0.0	—	0.0	0.5	—	—	13.2	—	
607	grain, soft red winter	4-05-294	88.0	0.11	1092	0.4	48.0	9.9	4.5	1.4	2.2	0.0	—	0.0	0.0	—	—	0.0	—	NRC, 1998
608			100.0	0.13	1241	0.4	54.5	11.3	5.1	1.6	2.5	0.0	—	0.0	0.0	—	—	0.0	—	

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609	grain, soft white winter	4-05-337	89.0	0.11	1002	0.2	57.0	11.0	4.3	1.3	4.0	0.0	—	0.0	0.4	—	—	11.6	—	NRC, 1998
610			100.0	0.12	1126	0.2	64.0	12.4	4.8	1.5	4.5	0.0	—	0.0	0.4	—	—	13.0	—	
611	middlings, < 9.5% fiber	4-05-205	89.0	0.33	1187	0.8	72.0	15.6	16.5	1.8	9.0	0.0	—	0.0	3.0	—	—	20.1	—	NRC, 1998
612			100.0	0.37	1334	0.9	80.9	17.5	18.5	2.0	10.1	0.0	—	0.0	3.4	—	—	22.6	—	
613	mill run, less than 9.5% fiber	4-05-206	90.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1982
614			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
615	red dog, < 4% fiber	4-05-203	88.0	0.11	1534	0.8	42.0	13.3	2.2	22.8	4.6	0.0	—	0.0	0.0	—	—	0.0	—	NRC, 1998
616			100.0	.13	1743	0.9	47.7	15.1	2.5	25.9	5.2	0.0	—	0.0	0.0	—	—	0.0	—	
617	shorts, < 7% fiber	4-05-201	88.0	0.24	1170	1.4	107.0	22.3	18.1	3.3	7.2	0.0	—	0.0	0.0	—	—	0.0	—	NRC, 1998
618			100.0	0.27	1330	1.6	121.6	25.3	20.6	3.8	8.2	0.0	—	0.0	0.0	—	—	0.0	—	
	Whey (cattle)																			
619	dried	4-01-182	96.0	0.27	1820	0.9	10.0	47.0	4.1	27.1	4.0	23.0	—	—	0.0	—	—	0.3	—	NRC, 1998
620			100.0	0.28	1896	0.9	10.4	49.0	4.3	28.2	4.2	24.0	—	—	0.0	—	—	0.3	—	
621	low lactose, dried	4-01-186	96.0	0.27	3571	0.7	19.0	69.0	5.7	37.2	4.4	25.0	—	—	0.0	—	—	0.3	—	NRC, 1998
622			100.0	0.28	3720	0.7	19.8	71.9	5.9	38.8	4.6	26.0	—	—	0.0	—	—	0.3	—	
623	permeate, dried	—	96.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1998
624			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Willow *Salix* spp.																			
625	browse, fresh	2-05-472	41.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1971
626			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Willow, yellow *Salix lutea*																			
627	browse	2-05-475	—	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1971
628			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Wood																			
629	sawdust	1-07-714	90.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	NRC, 1971
630			100.0	—	—	—	—	—	—	—	—	0.0	—	0.0	—	—	—	—	—	
	Yam *Dioscorea alata*																			
631	tubers, fresh	—	30.4	—	—	0.2	6.0	3.0	1.1	0.3	2.9	0.0	171.0	0.0	—	—	—	1.6	—	USDASR14
632			100.0	—	—	0.7	19.7	9.9	3.6	1.0	9.5	0.0	562.5	0.0	—	—	—	5.3	—	
	Yeast, brewer's *Saccharomyces cerevisiae*																			
633	dried	7-05-527	93.0	0.63	3984	9.9	448.0	109.0	91.8	37.0	42.8	1.0	—	—	0.0	—	—	10.0	—	NRC, 1998
634			100.0	0.68	4284	10.6	481.7	117.2	98.7	39.8	46.0	1.1	—	—	0.0	—	—	10.8	—	
	Yeast, torula *Torulopsis utilis*																			
635	dried	7-05-534	93.0	0.58	2881	22.4	492.0	84.2	6.2	49.9	36.3	0.0	—	—	0.0	—	—	0.0	—	NRC, 1998
636			100.0	0.62	3098	24.1	529.0	90.5	6.7	53.7	39.0	0.0	—	—	0.0	—	—	0.0	—	

[a] Dash indicates that no data were available.

[b] First digit is class of feed: 1, dry forages and roughages; 2, pasture, range plants, and forages fed green; 3, silages; 4, energy feeds; 5, protein supplements; 6, minerals; 7, vitamins; 8, additives; the other five digits are the International Feed Number.

[c] The niacin in corn, oats, sorghum, and wheat grain is poorly available. The bioavailability of niacin in most by-products produced from these grains is probably also low.

TABLE 12-4 Composition of Important Feeds: Amino Acids, Data Expressed As-Fed and Dry (100% Dry Matter)[a]

Entry Number	Description	International Feed Number[b]	Dry Matter (%)	Crude Protein (%)	Arginine (%)	Histidine (%)	Isoleucine (%)	Leucine (%)	Lysine (%)	Methionine (%)	Cystine (%)	Phenylalanine (%)	Taurine (%)	Tyrosine (%)	Threonine (%)	Tryptophan (%)	Valine (%)	Data Source
	Alder *Alnus* sp																	
1	leaves, sun-cured	—	85.0	18.7	—	—	—	—	—	—	—	—	—	—	—	—	—	Bath et al., 1999
2			100.0	22.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Alfalfa *Medicago sativa*																	
3	meal dehy, 15% CP	1-00-022	90.0	15.6	0.59	0.27	0.64	1.02	0.59	0.22	0.21	0.62	—	0.41	0.56	0.38	0.75	NRC, 1982
4			100.0	17.3	0.65	0.30	0.71	1.13	0.66	0.24	0.23	0.69	—	0.45	0.62	0.42	0.83	
5	meal dehy, 17% CP	1-00-023	92.0	17.0	0.71	0.37	0.68	1.21	0.74	0.25	0.18	0.84	—	0.55	0.70	0.24	0.86	NRC, 1998; NRC, 1982
6			100.0	18.5	0.84	0.36	0.88	1.39	0.93	0.29	0.31	0.87	—	0.59	0.77	0.37	0.96	
7	meal dehy, 20% CP	1-00-024	92.0	19.6	0.91	0.38	0.89	1.40	0.90	0.34	0.26	0.93	—	0.60	0.82	0.35	1.05	NRC, 1998; NRC, 1982
8			100.0	21.3	1.05	0.41	0.97	1.54	0.98	0.34	0.35	1.03	—	0.67	0.88	0.45	1.13	
9	meal dehy, 22% CP	1-07-851	93.0	22.2	0.96	0.44	1.06	1.63	0.97	0.34	0.30	1.13	—	0.64	0.97	0.49	1.29	NRC, 1982
10			100.0	23.9	1.04	0.47	1.15	1.75	1.05	0.37	0.32	1.22	—	0.69	1.04	0.52	1.39	
	Almond *Prunus amygdalus*																	
11	hulls	4-00-359	90.0	1.9	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1982
12			100.0	2.1	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Apple *Malus sylvestris*																	
13	fruit, raw, with peel	—	16.1	0.2	0.01	0.00	0.01	0.01	0.01	0.00	0.00	0.01	—	0.00	0.01	0.00	0.01	USDASR14; Schmidt et al., 1999
14			100.0	1.2	0.04	0.02	0.05	0.07	0.08	0.01	0.02	0.03	—	0.02	0.04	0.01	0.06	
15	pomace, dehy	—	89.0	4.4	—	—	—	—	—	—	—	—	—	—	—	—	—	Bath et al., 1999
16			100.0	4.9	—	—	—	—	—	—	—	—	—	—	—	—	—	
17	pomace, oat hulls added, dehy	4-28-096	89.0	4.6	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1982
18			100.0	5.2	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Apricot *Prunus armeniaca*																	
19	fruit, dried, sulfured	—	68.9	3.7	0.14	0.06	0.11	0.21	0.25	0.02	0.01	0.15	—	0.09	0.13	0.07	0.13	USDASR14
20			100.0	5.3	0.21	0.09	0.16	0.31	0.37	0.03	0.02	0.22	—	0.12	0.19	0.09	0.19	
21	fruit, raw, ep	—	13.7	1.4	0.05	0.03	0.04	0.08	0.10	0.01	0.00	0.05	—	0.03	0.05	0.02	0.05	USDASR14; Schmidt et al., 1999
22			100.0	10.3	0.33	0.20	0.30	0.56	0.71	0.04	0.02	0.38	—	0.21	0.34	0.11	0.34	
	Ash *Fraxinus* spp.																	
23	leaves, sun-cured	—	85.0	12.4	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1971
24			100.0	14.6	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Asparagus *Asparagus officinalis*																	
25	spear, raw	—	7.6	2.3	0.11	0.04	0.08	0.10	0.11	0.02	0.03	0.05	—	0.04	0.06	0.02	0.09	USDASR14; Schmidt et al., 1999
26			100.0	30.0	1.41	0.46	1.11	1.30	1.42	0.29	0.36	0.71	—	0.47	0.84	0.29	1.16	
	Aspen *Populus* spp																	
27	leaves, sun-cured	—	85.0	14.6	—	—	—	—	—	—	—	—	—	—	—	—	—	Bath et al., 1999
28			100.0	17.2	—	—	—	—	—	—	—	—	—	—	—	—	—	
29	flower buds, spring	—	38.2	5.2	—	—	—	—	—	—	—	—	—	—	—	—	—	Guglielmo and Karasov, 1995
30			100.0	13.5	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Avocado *Persea americana*																	
31	fruit, raw, ep, all commerical varieties	—	25.7	2.0	0.06	0.03	0.07	0.12	0.09	0.04	0.02	0.07	—	0.05	0.07	0.02	0.10	USDASR14
32			100.0	7.7	0.23	0.11	0.28	0.48	0.37	0.14	0.08	0.26	—	0.19	0.26	0.08	0.38	
	Bamboo, arrow *Psuedosasa japonica*																	
33	leaves	—	24.1	3.1	—	—	—	—	—	—	—	—	—	—	—	—	—	Warnell, 1988
34			100.0	12.7	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Banyan, weeping Chinese *Ficus benjamina*																	
35	leaves, mature, fresh	—	39.9	3.4	—	—	—	—	—	—	—	—	—	—	—	—	—	Janeke, 1995
36			100.0	8.5	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Banyantree *Ficus benghalensis*																	
37	leaves, fresh	2-27-208	32.0	3.1	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1981
38			100.0	9.6	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Bakery waste																	
39	dried bakery product	4-00-466	92.0	10.8	0.45	0.24	0.38	0.80	0.27	0.18	0.23	0.50	—	0.36	0.33	0.10	0.46	NRC, 1998
40			100.0	11.7	0.49	0.26	0.41	0.87	0.29	0.20	0.25	0.54	—	0.39	0.36	0.11	0.50	
	Banana *Musa sapientum*																	
41	aerial part, fresh	2-00-483	16.0	1.0	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1971
42			100.0	6.4	—	—	—	—	—	—	—	—	—	—	—	—	—	
43	flower	—	8.7	1.4	—	—	—	—	—	—	—	—	—	—	—	—	—	Schmidt et al., 1999
44			100.0	15.8	—	—	—	—	—	—	—	—	—	—	—	—	—	
45	fruit, raw, ep	—	25.7	1.0	0.05	0.08	0.03	0.07	0.05	0.01	0.02	0.04	—	0.02	0.03	0.01	0.05	USDASR14
46			100.0	4.0	0.18	0.31	0.13	0.28	0.19	0.04	0.07	0.15	—	0.09	0.13	0.05	0.18	

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47	fruit, raw, with peel	—	19.9	1.1	—	—	—	—	—	—	—	—	—	—	—	—	—	Schmidt et al., 1999
48			100.0	5.7	—	—	—	—	—	—	—	—	—	—	—	—	—	
49	leaves, fresh	2-09-902	19.0	2.9	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1981
50			100.0	15.7	—	—	—	—	—	—	—	—	—	—	—	—	—	
51	peel	—	16.2	1.0	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1971
52			100.0	6.1	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Barley *Hordeum distichon*																	
53	grain, two row	4-00-572	89.0	11.3	0.54	0.25	0.39	0.77	0.41	0.20	0.28	0.55	—	0.29	0.35	0.11	0.52	NRC, 1998
54			100.0	12.7	0.61	0.28	0.44	0.87	0.46	0.22	0.31	0.62	—	0.33	0.39	0.12	0.58	
	Barley *Hordeum vulgare*																	
55	grain, six row	4-00-574	89.0	10.5	0.48	0.22	0.37	0.68	0.36	0.17	0.20	0.49	—	0.32	0.34	0.13	0.49	NRC, 1998
56			100.0	11.8	0.54	0.25	0.42	0.76	0.40	0.19	0.22	0.55	—	0.36	0.38	0.15	0.55	
57	grain, hulless	4-00-552	88.0	14.9	0.56	0.23	0.41	0.77	0.44	0.16	0.24	0.61	—	0.40	0.40	0.13	0.55	NRC, 1998
58			100.0	16.9	0.64	0.26	0.47	0.88	0.50	0.18	0.27	0.69	—	0.45	0.45	0.15	0.63	
	Bean, snap Phaseolus spp																	
59	green, raw	—	9.7	1.8	0.07	0.03	0.07	0.11	0.09	0.02	0.02	0.07	—	0.04	0.08	0.02	0.09	USDASR14; Schmidt et al., 1999
60			100.0	18.7	0.75	0.35	0.68	1.15	0.90	0.23	0.19	0.69	—	0.43	0.81	0.20	0.92	
61	yellow, raw	—	9.7	1.8	0.07	0.03	0.07	0.11	0.09	0.02	0.02	0.07	—	0.04	0.08	0.02	0.09	USDASR14
62			100.0	18.7	0.75	0.35	0.68	1.15	0.90	0.23	0.19	0.69	—	0.43	0.81	0.20	0.92	
	Beech, American *Fagus grandifolia*																	
63	leaves, sun-cured	1-00-628	86.0	10.5	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1971; Robbins and Moen, 1975
64			100.0	12.2	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Beet, sugar *Beta vulgaris altissima*																	
65	greens, raw	—	7.9	1.8	0.05	0.03	0.04	0.08	0.05	0.02	0.02	0.05	—	0.04	0.05	0.03	0.05	USDASR14
66			100.0	23.2	0.66	0.36	0.48	1.03	0.68	0.19	0.22	0.61	—	0.55	0.69	0.37	0.69	
67	pulp, dehy	4-00-669	91.0	8.6	0.32	0.23	0.31	0.53	0.52	0.07	0.06	0.30	—	0.40	0.38	0.10	0.45	NRC, 1998
68			100.0	9.5	0.35	0.25	0.34	0.58	0.57	0.08	0.07	0.33	—	0.44	0.42	0.11	0.49	
69	tops, fresh	—	17.0	2.6	—	—	—	—	—	—	—	—	—	—	—	—	—	Bath et al., 1999
70			100.0	15.1	—	—	—	—	—	—	—	—	—	—	—	—	—	
71	tubers, raw	—	12.4	1.6	0.04	0.02	0.05	0.07	0.06	0.02	0.02	0.05	—	0.04	0.05	0.02	0.06	USDASR14
72			100.0	13.0	0.34	1.69	0.39	0.55	0.47	0.15	0.15	0.37	—	0.31	0.38	0.15	0.45	
	Birch, paper *Betula papyrifera*																	
73	leaves	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Robbins and Moen, 1975
74			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Birch, sweet *Betula lenta*																	
75	browse, immature, fresh	2-00-724	92.4	26.0	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1971
76			100.0	28.1	—	—	—	—	—	—	—	—	—	—	—	—	—	
77	browse, mid-bloom, fresh	2-00-725	93.7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1971
78			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Blackberry *Rubus ulmifolius*																	
79	fruit, raw	—	14.4	0.7	—	—	—	—	—	—	—	—	—	—	—	—	—	USDASR14; Schmidt et al., 1999
80			100.0	5.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Blood																	
81	meal, conventional	5-00-380	92.0	77.1	3.34	5.06	0.91	10.99	7.04	0.99	1.09	5.34	—	2.29	4.05	1.08	7.05	NRC, 1998
82			100.0	83.8	3.63	5.50	0.99	11.95	7.65	1.08	1.18	5.80	—	2.49	4.40	1.17	7.66	
83	meal, flash dried	5-26-006	92.0	87.6	3.37	4.57	0.88	11.48	7.56	0.95	1.20	6.41	—	2.32	4.07	1.06	8.03	NRC, 1998
84			100.0	95.2	3.66	4.97	0.96	12.48	8.22	1.03	1.30	6.97	—	2.52	4.42	1.15	8.73	
85	meal, spray or ring dried	5-00-381	93.0	88.8	3.69	5.30	1.03	10.81	7.45	0.99	1.04	5.81	—	2.71	3.78	1.48	7.03	NRC, 1998
86			100.0	95.5	3.97	5.70	1.11	11.62	8.01	1.06	1.12	6.25	—	2.91	4.06	1.59	7.56	
87	plasma, spray dried	—	91.0	78.0	4.55	2.55	2.71	7.61	6.84	0.75	2.63	4.41	—	3.53	4.72	1.36	4.94	NRC, 1998
88			100.0	85.7	5.00	2.80	2.98	8.36	7.52	0.82	2.89	4.85	—	3.88	5.19	1.49	5.43	
89	cells, spray dried	—	92.0	92.0	3.77	6.99	0.49	12.70	8.51	0.81	0.61	6.69	—	2.14	3.38	1.37	8.50	NRC, 1998
90			100.0	100.0	4.10	7.60	0.53	13.80	9.25	0.88	0.66	7.27	—	2.33	3.67	1.49	9.24	
	Blueberries *Vaccinium* spp.																	
91	fruit, raw	—	15.4	0.7	0.03	0.01	0.02	0.04	0.01	0.01	0.01	0.02		0.01	0.02	0.00	0.03	USDASR14; Schmidt et al., 1999
92			100.0	4.4	0.22	0.06	0.14	0.26	0.08	0.07	0.05	0.16		0.05	0.12	0.02	0.18	
	Breadfruit *Artocarpus altilis*																	
93	fruit, raw	—	29.4	1.1	—	—	0.06	0.07	0.04	0.10	0.01	0.03	—	0.02	0.05	—	0.05	USDASR14
94			100.0	3.7	—	—	0.22	0.22	0.13	0.34	0.03	0.09	—	0.06	0.18	—	0.16	
	Brewer's grain																	
95	dried	5-02-141	92.0	26.5	1.53	0.53	1.02	2.08	1.08	0.45	0.49	1.22	—	0.88	0.95	0.26	1.26	NRC, 1998
96			100.0	28.8	1.66	0.58	1.11	2.26	1.17	0.49	0.53	1.33	—	0.96	1.03	0.28	1.37	
	Broccoli *Brassica oleracea* var. *italicca*																	
97	raw	—	9.3	3.0	0.15	0.05	0.11	0.13	0.14	0.03	0.02	0.08	—	0.06	0.09	0.03	0.13	USDASR14; Schmidt et al., 1999
98			100.0	32.0	1.56	0.54	1.17	1.41	1.51	0.37	0.21	0.90	—	0.68	0.98	0.31	1.37	
	Brush cherry *Syzygium paniculata*																	
99	leaves, mature, fresh	—	31.6	3.3	—	—	—	—	—	—	—	—	—	—	—	—	—	Janeke, 1995
100			100.0	10.3	—	—	—	—	—	—	—	—	—	—	—	—	—	

(continues)

TABLE 12-4 *(continued)*

Entry Number	Description	International Feed Number[b]	Dry Matter (%)	Crude Protein (%)	Arginine (%)	Histidine (%)	Isoleucine (%)	Leucine (%)	Lysine (%)	Methionine (%)	Cystine (%)	Phenylalanine (%)	Taurine (%)	Tyrosine (%)	Threonine (%)	Tryptophan (%)	Valine (%)	Data Source
	Brussel sprouts *Brassica oleracea* var. *bullata gemmifera*																	
101	raw	—	14.0	3.8	0.20	0.08	0.13	0.15	0.15	0.03	0.02	0.10	—	—	0.12	0.04	0.16	USDASR14; Schmidt et al., 1999
102			100.0	27.2	1.45	0.54	0.94	1.09	1.10	0.23	0.16	0.70	—	—	0.86	0.26	1.11	
	Buckwheat, common *Fagopyrum sagittatum*																	
103	grain	4-00-994	88.0	11.1	0.92	0.25	0.40	0.64	0.57	0.19	0.23	0.45	—	0.31	0.41	0.17	0.56	NRC, 1998
104			100.0	12.6	1.05	0.28	0.45	0.73	0.65	0.22	0.26	0.51	—	0.35	0.47	0.19	0.64	
105	middlings	5-00-991	89.0	29.8	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1982
106			100.0	33.5	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Cabbage *Brassica oleracea* var. *capitata*																	
107	raw	—	7.9	1.4	0.08	0.03	0.07	0.07	0.07	0.01	0.01	0.05	—	0.02	0.05	0.02	0.06	USDASR14; Schmidt et al., 1999
108			100.0	18.3	1.03	0.37	0.92	0.93	0.85	0.18	0.15	0.57	—	0.31	0.62	0.19	0.78	
	Cabbage, bok choy																	
109	raw	—	4.8	1.1	—	—	—	—	—	—	—	—	—	—	—	—	—	Schmidt et al., 1999
110			100.0	23.7	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Cabbage, napa *Brassica pekinensis*																	
111	raw	—	3.5	1.0	—	—	—	—	—	—	—	—	—	—	—	—	—	Schmidt et al., 1999
112			100.0	27.6	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Carambola *Averrhoa carambola*																	
113	fruit, raw	—	9.1	0.5	0.01	0.00	0.02	0.04	0.04	0.01	—	0.02	—	0.02	0.02	0.00	0.03	USDASR14
114			100.0	6.0	0.12	0.04	0.25	0.44	0.44	0.12	—	0.21	—	0.25	0.25	0.04	0.29	
	Carrot *Daucus carota*																	
115	roots, fresh	—	12.2	1.0	0.04	0.02	0.04	0.04	0.04	0.01	0.01	0.03	—	0.02	0.04	0.01	0.04	USDASR14; Schmidt et al., 1999
116			100.0	8.4	0.35	0.13	0.34	0.35	0.33	0.06	0.07	0.26	—	0.16	0.31	0.09	0.36	
117	tops, fresh	—	16.0	2.1	—	—	—	—	—	—	—	—	—	—	—	—	—	Bath et al., 1999
118			100.0	13.1	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Canola *Brassica napa*																	
119	meal, sol. extr.	5-06-145	90.0	35.6	2.21	0.96	1.43	2.58	2.08	0.74	0.91	1.43	—	1.13	1.59	0.45	1.82	NRC, 1998
120			100.0	39.6	2.46	1.07	1.59	2.87	2.31	0.82	1.01	1.59	—	1.26	1.77	0.50	2.02	
121	oil	4-06-144	100.0	0.0	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1998
122			100.0	0.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Casein (cattle)																	
123	dehy	5-01-162	91.0	88.7	3.26	2.82	4.66	8.79	7.35	2.70	0.41	4.79	—	4.77	3.98	1.14	6.10	NRC, 1998
124			100.0	97.5	3.58	3.10	5.12	9.66	8.08	2.97	0.45	5.26	—	5.24	4.37	1.25	6.70	
	Cassava *Manihot esculenta*																	
125	meal, dehydrated	4-01-152	88.0	3.3	0.18	0.08	0.11	0.19	0.12	0.04	0.05	0.15	—	0.04	0.11	0.04	0.14	NRC, 1998
126			100.0	3.8	0.20	0.09	0.13	0.22	0.14	0.05	0.06	0.17	—	0.05	0.13	0.05	0.16	
127	tubers, fresh	4-09-599	31.5	1.3	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1982; Schmidt et al., 1999
128			100.0	3.6	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Cauliflower *Brassica oleracea* var. *botrytis*																	
129	raw	—	8.1	2.0	0.10	0.04	0.08	0.12	0.11	0.03	0.02	0.07	—	0.04	0.07	0.03	0.10	USDASR14; Schmidt et al., 1999
130			100.0	24.5	1.17	0.49	0.93	1.43	1.31	0.35	0.28	0.88	—	0.53	0.89	0.32	1.22	
131	green, raw	—	10.2	3.0	0.14	0.06	0.11	0.17	0.16	0.04	0.03	0.11	—	0.06	0.11	0.04	0.15	USDASR14
132			100.0	28.9	1.39	0.58	1.10	1.68	1.55	0.41	0.33	1.03	—	0.63	1.05	0.38	1.45	
	Celery *Apium graveolens* var. *dulce*																	
133	raw	—	5.4	0.8	0.02	0.01	0.02	0.04	0.03	0.01	0.00	0.02	—	0.01	0.02	0.01	0.03	USDASR14; Schmidt et al., 1999
134			100.0	14.0	0.41	0.24	0.43	0.65	0.54	0.11	0.07	0.41	—	0.19	0.41	0.19	0.56	
	Cereal																	
135	screenings	4-02-156	90.0	12.1									—					NRC, 1982
136			100.0	13.4									—					
	Chalum *Inga* spp																	
137	dehy, fruit	—	96.8	12.5	—	—	—	—	—	—	—	—	—	—	—	—	—	
138			100.0	12.9	—	—	—	—	—	—	—	—	—	—	—	—	—	
139	dehy, pod	—	97.8	9.8	—	—	—	—	—	—	—	—	—	—	—	—	—	
140			100.0	10.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
141	dehy, seeds	—	93.5	20.2	—	—	—	—	—	—	—	—	—	—	—	—	—	
142			100.0	21.6	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Chayote *Cucurbita pepo*																	
143	fruit, raw, with peel	—	7.0	0.9	0.04	0.02	0.04	0.07	0.04	0.00	—	0.05	—	0.03	0.04	0.01	0.06	USDASR14; Schmidt et al., 1999
144			100.0	12.9	0.57	0.24	0.57	1.0	0.57	0.00	—	0.71	—	0.43	0.57	0.14	0.86	

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	Cherimoya *Annona cherimolia*																		
145	fruit, raw	—	26.5	1.3	—	—	—	—	—	—	—	—	—	—	—	—	—	USDASR14
146			100.0	4.9	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Cherry *Prunus* spp																		
147	fruit, raw	—	13.9	1.0	—	—	—	—	—	—	—	—	—	—	—	—	—	USDASR14
148			100.0	7.2	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Chicory *Cichorium intybus*																		
149	greens, raw	—	8.0	1.7	0.12	0.03	0.10	0.01	0.07	301.00	—	0.04	—	—	0.05	0.03	0.08	USDASR14
150			100.0	21.3	1.50	0.38	1.25	0.09	0.88	3762.50	—	0.50	—	—	0.63	0.38	1.00	
	Cockroach, American *Periplaneta americana*																		
151	adult	—	33.3	21.1	—	—	—	—	—	—	—	—	—	—	—	—	—	Allen, 1989
152			100.0	63.5	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Cockroach, Haitian *Blaberus discoidalus*																		
153	adult	—	30.3	19.0	—	—	—	—	—	—	—	—	—	—	—	—	—	Allen, 1989
154			100.0	62.8	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Coconut *Cocos nucifera*																		
155	meal, sol. extr.	5-01-573	92.0	21.9	2.38	0.39	0.75	1.36	0.58	0.35	0.29	0.84	—	0.57	0.67	0.19	1.07	NRC, 1998
156			100.0	23.8	2.59	0.42	0.82	1.48	0.63	0.38	0.32	0.91	—	0.62	0.73	0.21	1.16	
157	oil	4-09-320	100.0	0.0									—					NRC, 1998
158			100.0	0.0									—					
	Collard *Brassica oleracea* var.																		
159	greens, raw	—	9.5	1.6	0.13	0.05	0.10	0.15	0.12	0.03	0.03	0.09	—	0.07	0.09	0.03	0.12	USDASR14; Schmidt et al., 1999
160			100.0	16.6	1.38	0.53	1.06	1.59	1.27	0.32	0.32	0.95	—	0.74	0.95	0.32	1.27	
	Corn, yellow *Zea mays indentata*																		
161	bran	—	95.3	8.4	—	—	—	—	—	—	—	—	—	—	—	—	—	USDASR14
162			100.0	8.8	—	—	—	—	—	—	—	—	—	—	—	—	—	
163	cobs, ground	1-28-234	90.0	2.8	—	—	—	—	—	—	—	—	—	—	—	—	—	
164			100.0	3.2	—	—	—	—	—	—	—	—	—	—	—	—	—	
165	distillers' grain	5-02-842	94.0	24.8	0.90	0.63	0.95	2.63	0.74	0.43	0.28	0.99	—	0.82	0.62	0.20	1.24	NRC, 1998
166			100.0	26.4	0.96	0.67	1.01	2.80	0.79	0.46	0.30	1.05	—	0.87	0.66	0.21	1.32	
167	distillers' grain with solubles	5-02-843	93.0	27.7	1.13	0.69	1.03	2.50	0.62	0.50	0.52	1.34	—	0.83	0.94	0.25	1.30	NRC, 1998
168			100.0	29.8	1.22	0.74	1.11	2.69	0.67	0.54	0.56	1.44	—	0.89	1.01	0.27	1.40	
169	distillers' solubles	5-02-844	92.0	26.7	0.90	0.66	1.21	2.25	0.82	0.51	0.46	1.38	—	0.80	1.03	0.23	1.50	NRC, 1998
170			100.0	29.0	0.98	0.72	1.32	2.45	0.89	0.55	0.50	1.50	—	0.87	1.12	0.25	1.63	
171	flour, whole grain	—	89.1	6.9	0.35	0.21	0.25	0.85	0.20	0.15	0.12	0.34	—	0.28	0.26	0.05	0.35	USDASR14
172			100.0	7.8	0.39	0.24	0.28	0.95	0.22	0.16	0.14	0.38	—	0.32	0.29	0.06	0.39	
173	gluten feed	5-02-903	90.0	21.5	1.04	0.67	0.66	1.96	0.63	0.35	0.46	0.76	—	0.58	0.74	0.07	1.01	NRC, 1998
174			100.0	23.9	1.16	0.74	0.73	2.18	0.70	0.39	0.51	0.84	—	0.64	0.82	0.08	1.12	
175	gluten meal, 60% CP	5-28-242	90.0	60.2	1.93	1.28	2.48	10.19	1.02	1.43	1.09	3.84	—	3.25	2.08	0.31	2.79	NRC, 1998
176			100.0	66.9	2.14	1.42	2.76	11.32	1.13	1.59	1.21	4.27	—	3.61	2.31	0.34	3.10	
177	grain	4-02-935	89.0	8.3	0.37	0.23	0.28	0.99	0.26	0.17	0.19	0.39	—	0.25	0.29	0.06	0.39	NRC, 1998
178			100.0	9.3	0.42	0.26	0.31	1.11	0.29	0.19	0.21	0.44	—	0.28	0.33	0.07	0.44	
179	grits by-product (Hominy Feed)	4-03-011	90.0	10.3	0.56	0.28	0.36	0.98	0.38	0.18	0.18	0.43	—	0.40	0.40	0.10	0.52	NRC, 1998
180			100.0	11.4	0.62	0.31	0.40	1.09	0.42	0.20	0.20	0.48	—	0.44	0.44	0.11	0.58	
181	oil	4-07-882	100.0	0.0	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1998
182			100.0	0.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
183	starch	4-02-889	99.0	0.3	0.01	0.01	0.01	0.04	0.01	0.01	0.01	0.01	—	0.01	0.01	0.00	0.01	USDASR14
184			100.0	0.3	0.01	0.01	0.01	0.04	0.01	0.01	0.01	0.01	—	0.01	0.01	0.00	0.01	
185	syrup, light	—	77.2	0.0	—	—	—	—	—	—	—	—	—	—	—	—	—	USDASR14
186			100.0	0.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Corn, sweet *Zea mays saccharata*																		
187	cobs, fresh	—	31.7	1.4	—	—	—	—	—	—	—	—	—	—	—	—	—	Schmidt et al., 1999
188			100.0	4.5	—	—	—	—	—	—	—	—	—	—	—	—	—	
189	ear, whole, with husk, fresh	—	20.8	2.3	—	—	—	—	—	—	—	—	—	—	—	—	—	Schmidt et al., 1999
190			100.0	10.9	—	—	—	—	—	—	—	—	—	—	—	—	—	
191	husk, fresh	—	26.1	2.9	—	—	—	—	—	—	—	—	—	—	—	—	—	Schmidt et al., 1999
192			100.0	11.1	—	—	—	—	—	—	—	—	—	—	—	—	—	
193	white, raw, ep	—	24.0	3.2	0.47	0.29	0.34	1.16	0.27	0.20	0.17	0.46	—	0.38	0.35	0.07	0.48	USDASR14
194			100.0	13.4	1.96	1.21	1.42	4.83	1.13	0.83	0.71	1.92	—	1.58	1.46	0.29	2.00	
195	yellow, raw, ep	—	24.0	3.2	0.47	0.29	0.34	1.16	0.27	0.20	0.17	0.46	—	0.38	0.35	0.07	0.48	USDASR14
196			100.0	13.4	1.96	1.21	1.41	4.83	1.12	0.83	0.71	1.91	—	1.58	1.46	0.29	2.00	
	Corn borer, European *Ostrinia nubilalis*																		
197	larvae	—	27.3	16.5	—	—	—	—	—	—	—	—	—	—	—	—	—	Allen, 1989
198			100.0	60.4	—	—	—	—	—	—	—	—	—	—	—	—	—	
199	pupae	—	28.0	18.0	—	—	—	—	—	—	—	—	—	—	—	—	—	Allen, 1989
200			100.0	64.2	—	—	—	—	—	—	—	—	—	—	—	—	—	

(continues)

TABLE 12-4 *(continued)*

Entry Number	Description	International Feed Number[b]	Dry Matter (%)	Crude Protein (%)	Arginine (%)	Histidine (%)	Isoleucine (%)	Leucine (%)	Lysine (%)	Methionine (%)	Cystine (%)	Phenylalanine (%)	Taurine (%)	Tyrosine (%)	Threonine (%)	Tryptophan (%)	Valine (%)	Data Source
	Cottonseed *Gossypium* spp																	
201	meal, mech. extr., 41% CP	5-01-617	92.0	42.4	4.26	1.11	1.29	2.45	1.65	0.67	0.69	1.97	—	1.23	1.34	0.54	1.76	NRC, 1998
202			100.0	46.1	4.63	1.21	1.40	2.66	1.79	0.73	0.75	2.14	—	1.34	1.46	0.59	1.91	
203	meal, sol. extr. 41% CP	5-07-872	90.0	41.4	4.55	1.17	1.30	2.47	1.72	0.67	0.70	2.20	—	1.22	1.36	0.48	1.78	NRC, 1998
204			100.0	46.0	5.06	1.30	1.44	2.74	1.91	0.74	0.78	2.44	—	1.36	1.51	0.53	1.98	
	Crayfish, Mexico *Cambrus* sp., *Aegiale hesperiaris*																	
205	adult	—	33.5	17.2	—	—	—	—	—	—	—	—	—	—	—	—	—	Massieu et al., 1951
206			100.0	51.3	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Cricket, house *Acheta domesticus*																	
207	adult	—	30.8	20.5	1.25	0.48	0.94	2.05	1.10	0.30	0.17	0.65	0.14	1.00	0.74	0.13	1.07	Finke, 2002
208			100.0	66.6	4.06	1.56	3.05	6.66	3.57	0.97	0.55	2.11	0.45	3.25	2.40	0.42	3.47	
209	juvenile	—	22.9	15.4	0.94	0.34	0.66	1.47	0.83	0.20	0.13	0.43	0.08	0.85	0.55	0.08	0.76	Finke, 2002
210			100.0	67.2	4.10	1.48	2.88	6.42	3.62	0.87	0.57	1.88	0.35	3.71	2.40	0.35	3.32	
	Cricket, mormon *Anabrus simplex*																	
211	adult, both sexes	—	29.7	17.2	—	—	—	—	—	—	—	—	—	—	—	—	—	DeFoliart et al., 1982
212			100.0	58.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Cucumber *Cucumis sativus*																	
213	raw, with peel	—	4.0	0.7	0.04	0.01	0.02	0.03	0.03	0.01	0.01	0.02	—	0.01	0.02	0.01	0.02	USDASR14; Schmidt et al., 1999
214			100.0	17.3	1.00	0.25	0.50	0.75	0.75	0.25	0.25	0.50	—	0.25	0.50	0.25	0.50	
	Custard apple *Annona* spp																	
215	fruit, raw	—	28.5	1.7	—	—	—	—	0.04	0.00	—	—	—	—	—	0.01	—	USDASR14
216			100.0	6.0	—	—	—	—	0.14	0.00	—	—	—	—	—	0.04	—	
	Dandelion *Taraxacum officinale*																	
217	greens, raw	2-01-748	14.4	2.7	—	—	—	—	—	—	—	—	—	—	—	—	—	USDASR14
218			100.0	18.8	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Dock *Rumex* spp.																	
219	greens, raw	—	7.0	2.0	0.11	0.05	0.10	0.17	0.12	0.04	—	0.11	—	0.08	0.09	—	0.13	USDASR14
220			100.0	28.6	1.57	0.71	1.43	2.42	1.71	0.57		1.57	—	1.14	1.29		1.86	
	Egg (Chicken)																	
221	dehy, whole	—	96.9	47.4	2.84	1.12	2.58	4.05	3.40	1.48	1.10	2.52	—	1.93	2.27	0.58	2.89	USDASR14
222			100.0	48.9	2.93	1.16	2.66	4.18	3.51	1.53	1.14	2.60	—	1.99	2.34	0.60	2.98	
	Eggplant *Solanum melongena*																	
223	fruit, raw	—	8.0	1.0	0.06	0.02	0.05	0.06	0.05	0.01	0.01	0.04	—	0.03	0.04	0.01	0.05	USDASR14; Schmidt et al., 1999
224			100.0	12.8	0.75	0.25	0.63	0.75	0.63	0.13	0.13	0.50	—	0.38	0.50	0.13	0.63	
	Fababean (Broadbean) *Phaseolus* spp																	
225	seeds	5-09-262	87.0	25.4	2.28	0.67	1.03	1.89	1.62	0.20	0.32	1.03	—	0.87	0.89	0.22	1.14	NRC, 1998
226			100.0	29.2	2.62	0.77	1.18	2.17	1.86	0.23	0.37	1.18	—	1.00	1.02	0.25	1.31	
	Fat																	
227	animal, hydrolyzed	4-00-376	100.0	0.0	—	—	—	—	—	—	—	—	—	—	—	—	—	USDASR11
228			100.0	0.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
229	animal, poultry	4-00-409	99.8	0.0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	—	0.00	0.00	0.00	0.00	USDASR14
230			100.0	0.0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	—	0.00	0.00	0.00	0.00	
231	animal, swine (lard)	4-04-790	100.0	0.0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	—	0.00	0.00	0.00	0.00	USDASR14
232			100.0	0.0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	—	0.00	0.00	0.00	0.00	
	Feather																	
233	meal, hydrolyzed	5-03-795	93.0	84.5	5.62	0.93	3.86	6.79	2.08	0.61	4.13	4.01	—	2.41	3.82	0.54	5.88	NRC, 1981
234			100.0	90.9	6.04	1.00	4.15	7.30	2.24	0.66	4.44	4.31	—	2.59	4.11	0.58	6.32	
	Feijoa *Feijoa sellowiana*																	
235	fruit, raw	—	13.4	1.2	—	—	—	—	—	—	—	—	—	—	—	—	—	USDASR14
236			100.0	9.3	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Ficus nitida																	
237	leaves, mature, fresh	—	35.3	3.1	—	—	—	—	—	—	—	—	—	—	—	—	—	Janeke, 1995
238			100.0	8.8	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Ficus rumphii																	
239	leaves, mature, fresh	—	29.6	4.3	—	—	—	—	—	—	—	—	—	—	—	—	—	Janeke, 1995
240			100.0	14.4	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Ficus thonningii																	
241	leaves, mature, fresh	—	27.7	4.2	—	—	—	—	—	—	—	—	—	—	—	—	—	Janeke, 1995
242			100.0	15.1	—	—	—	—	—	—	—	—	—	—	—	—	—	

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	Fig *Ficus carica*																		
243	fruit, raw	—	20.9	0.8	0.02	0.01	0.02	0.03	0.03	0.01	0.01	0.01	—	0.03	0.02	0.01	0.03	USDASR14
244			100.0	3.6	0.1	0.05	0.01	0.14	0.14	0.05	0.05	0.05		0.14	0.01	0.01	0.14	
245	fruit, dried	—	64.9	2.7	—	—	—	—	—	—	—	—	—	—	—	—	—	Schmidt et al., 1999
246			100.0	4.2	—	—	—	—	—	—	—	—	—	—	—	—	—	
247	leaves, mature, fresh	—	23.5	3.7	—	—	—	—	—	—	—	—	—	—	—	—	—	Janeke, 1995
248			100.0	15.8	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Fig, cluster *Ficus glomerata*																	
249	leaves, fresh	2-27-209	30.0	3.4	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1981
250			100.0	11.2	—	—	—	—	—	—	—	—	—	—	—	—	—	
251	leaves, mature, fresh	—	32.8	3.7	—	—	—	—	—	—	—	—	—	—	—	—	—	Janeke, 1995
252			100.0	11.4	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Fig, Indian laurel *Ficus retusa*																	
253	leaves, mature, fresh	—	38.0	3.2	—	—	—	—	—	—	—	—	—	—	—	—	—	Janeke, 1995
254			100.0	8.5	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Fig, Moreton Bay *Ficus macrophylla*																	
255	leaves, mature, fresh	—	37.0	3.2	—	—	—	—	—	—	—	—	—	—	—	—	—	Janeke, 1995
256			100.0	8.6	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Fig, Roxburgh *Ficus roxburghii*																	
257	leaves, fresh	2-30-177	33.0	4.5	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1981
258			100.0	13.4	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Fig, rustyleaf *Ficus rubiginosa*																	
259	leaves, mature, fresh	—	30.6	3.1	—	—	—	—	—	—	—	—	—	—	—	—	—	Janeke, 1995
260			100.0	10.1	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Fig, spotted *Ficus virens*																	
261	leaves, fresh	2-28-704	15.0	1.7	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1981
262			100.0	11.2	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Fish																	
263	solubles, condensed	5-01-969	51.0	32.7	1.61	1.56	1.06	1.86	1.73	0.50	0.30	0.93	—	0.40	0.86	0.31	1.16	NRC, 1998
264			100.0	64.1	3.16	3.06	2.08	3.65	3.39	0.98	0.59	1.82	—	0.78	1.69	0.61	2.27	
265	solubles, dried	5-01-971	92.0	64.2	2.67	1.23	1.56	2.68	2.84	0.98	0.49	1.22	—	0.62	1.40	0.34	1.94	NRC, 1998
266			100.0	69.8	2.90	1.34	1.70	2.91	3.09	1.07	0.53	1.33	—	0.67	1.52	0.37	2.11	
	Fish, anchovy *Engraulis ringen*																	
267	meal, mech. extr.	5-01-985	92.0	64.6	3.68	1.56	3.06	5.00	5.11	1.95	0.61	2.66	—	2.15	2.82	0.76	3.51	NRC, 1998
268			100.0	70.2	4.00	1.70	3.33	5.43	5.55	2.12	0.66	2.89	—	2.34	3.07	0.83	3.82	
	Fish, herring *Clupea harengus*																	
269	meal, mech. extr.	5-02-000	93.0	68.1	4.01	1.52	2.91	5.20	5.46	2.04	0.66	2.75	—	2.18	3.02	0.74	3.46	NRC, 1998
270			100.0	73.2	4.31	1.63	3.13	5.59	5.87	2.19	0.71	2.96	—	2.34	3.25	0.80	3.72	
	Fish, menhaden *Brevoortia tyrannus*																	
271	meal, mech. extr.	5-02-009	92.0	62.3	3.66	1.78	2.57	4.54	4.81	1.77	0.57	2.51	—	2.04	2.64	0.66	3.03	NRC, 1998
272			100.0	67.7	3.98	1.93	2.79	4.93	5.23	1.92	0.62	2.73	—	2.22	2.87	0.72	3.29	
	Fish, white Gadidae (family); Lophiidae (family)																	
273	meal, mech. extr.	5-02-025	91.0	63.3	4.04	1.34	2.61	4.39	4.51	1.76	0.68	2.32	—	2.03	2.60	0.66	3.06	NRC, 1998
274			100.0	69.6	4.44	1.47	2.87	4.82	4.96	1.93	0.75	2.55	—	2.23	2.86	0.73	3.36	
	Flax *Linum usitatissinum*																	
275	meal, sol. extr.	5-02-048	90.0	33.6	2.97	0.68	1.56	2.06	1.24	0.59	0.59	1.57		1.03	1.26	0.52	1.74	NRC, 1998
276			100.0	37.3	3.30	0.76	1.73	2.29	1.38	0.66	0.66	1.74		1.14	1.40	0.58	1.93	
	Fructose																	
277		—	99.5	0.0	—	—	—	—	—	—	—	—	—	—	—	—	—	IOM, 1996
278			100.0	0.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Gelatin																	
279		5-14-503	90.0	88.6	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1998
280			100.0	98.4	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Glucose																	
281	monohydrate	4-02-125	90.0	0.3	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1998
282			100.0	0.3	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Granadilla, purple *Passiflora edulis*																	
283	fruit, raw, ep	—	27.1	2.2	—	—	—	—	—	—	—	—	—	—	—	—	—	USDASR14
284			100.0	8.1	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Grape, European type *Vitis* spp																	
285	fruit, raw, ep	—	19.4	0.7	0.05	0.02	0.01	0.01	0.02	0.02	0.01	0.01	—	0.01	0.02	0.00	0.02	USDASR14
286			100.0	3.4	0.26	0.10	0.05	0.05	0.10	0.10	0.05	0.05	—	0.05	0.10	0.00	0.10	
	Grapefruit *Citrus paradisi*																	
287	fruit, raw, ep	—	9.1	0.6	—	—	—	—	0.02	0.00	—	—	—	—	—	0.00	—	USDASR14
288			100.0	6.9	—	—	—	—	0.22	0.00	—	—	—	—	—	0.00	—	
289	peel	—	29.1	1.5	—	—	—	—	—	—	—	—	—	—	—	—	—	Schmidt et al., 1999
290			100.0	5.0	—	—	—	—	—	—	—	—	—	—	—	—	—	

(continues)

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TABLE 12-4 *(continued)*

Entry Number	Description	International Feed Number[b]	Dry Matter (%)	Crude Protein (%)	Arginine (%)	Histidine (%)	Isoleucine (%)	Leucine (%)	Lysine (%)	Methionine (%)	Cystine (%)	Phenylalanine (%)	Taurine (%)	Tyrosine (%)	Threonine (%)	Tryptophan (%)	Valine (%)	Data Source
	Grasshopper *Melanoplus femurrubrum*																	
291	adult	—	30.5	24.2	—	—	—	—	—	—	—	—	—	—	—	—	—	Bird et al., 1982
292			100.0	79.2	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Guava, common or lemon *Psidium guajava*																	
293	fruit, raw, ep	—	13.9	0.8	0.02	0.01	0.03	0.06	0.02	0.01	—	0.00	—	0.01	0.03	0.01	0.03	USDASR14
294			100.0	5.9	0.14	0.07	0.22	0.43	0.14	0.07	—	0.00	—	0.07	0.22	0.07	0.22	
	Guava, strawberry *Psidium cattleianum*																	
295	fruit, raw, ep	—	19.3	0.6	0.02	0.01	0.02	0.04	0.02	0.00	—	0.00	—	0.01	0.02	0.01	0.02	USDASR14
296			100.0	3.0	0.10	0.05	0.10	0.21	0.10	0.00	—	0.00	—	0.05	0.10	0.05	0.10	
	Hemicellulose extract																	
297		4-08-030	76.0	0.6	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1982
298			100.0	0.7	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Hibiscus, tropical *Hibiscus rosa-sinensis*																	
299	leaves, mature, fresh	—	21.9	3.3	—	—	—	—	—	—	—	—	—	—	—	—	—	Janeke, 1995
300			100.0	15.1	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Honeysuckle *Lonicera albiflora*																	
301	leaves, fresh	2-29-875	33.0	3.3	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1981
302			100.0	10.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Jack fruit *Artocarpus heterophyllus*																	
303	fruit, raw, ep	—	26.8	1.5	—	—	—	—	—	—	—	—	—	—	—	—	—	USDASR14
304			100.0	5.5	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Jujube *Zizyphus jujuba*																	
305	browse, fresh	2-30-091	32.0	2.7	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1981
306			100.0	8.6	—	—	—	—	—	—	—	—	—	—	—	—	—	
307	fruit, raw, ep	—	22.1	1.2	—	—	—	—	—	—	—	—	—	—	—	—	—	USDASR14
308			100.0	5.4	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Kale *Brassica oleracea* var. *acephala*																	
309	leaves and stems, fresh	—	15.5	3.3	0.18	0.07	0.20	0.23	0.20	0.03	0.04	0.17	—	0.12	0.15	0.04	0.18	USDASR14; Schmidt et al., 1999
310			100.0	21.2	1.16	0.45	1.29	1.48	1.29	0.19	0.26	1.09	—	0.77	0.97	0.26	1.16	
	Kiwifruit *Actinidia chinensis*																	
311	raw	—	17.0	1.0	—	—	—	—	—	—	—	—	—	—	—	—	—	USDASR14; Schmidt et al., 1999
312			100.0	5.8	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Kohlrabi *Brassica oleracea* var. *gongylodes*																	
313	tubers, fresh	—	9.0	1.7	0.11	0.02	0.08	0.07	0.06	0.01	0.01	0.04	—	—	0.05	0.01	0.05	USDASR14
314			100.0	18.9	1.22	0.22	0.89	0.78	0.67	0.11	0.11	0.44	—	—	0.56	0.11	0.56	
	Kudzu *Pueraria lobata*																	
315	aerial part, fresh	2-02-482	26.4	4.6	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1971
316			100.0	17.6	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Kumquat *Fortunella* spp																	
317	fruit, raw, ep	—	18.3	0.9	—	—	—	—	—	—	—	—	—	—	—	—	—	USDASR14
318			100.0	4.9	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Lactose																	
319		4-07-881	96.0	0.3	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1998
320			100.0	0.3	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Lentil *Len culinaris*																	
321	seeds	5-02-506	89.0	24.4	2.05	0.78	1.00	1.84	1.71	0.18	0.27	1.29	—	0.70	0.84	0.21	1.27	NRC, 1998
322			100.0	27.4	2.30	0.88	1.12	2.07	1.92	0.20	0.30	1.45	—	0.79	0.94	0.24	1.43	
	Lettuce, endive *Cichorium endiva*																	
323	leaves, fresh	—	6.2	1.3	0.06	0.02	0.07	0.10	0.06	0.01	0.01	0.05	—	0.04	0.05	0.01	0.06	USDASR14
324			100.0	20.1	0.97	0.32	1.13	1.61	0.97	0.16	0.16	0.81	—	0.64	0.81	0.16	0.97	
	Lettuce, iceberg *Lactuca sativa*																	
325	leaves, fresh	—	4.1	1.0	0.06	0.02	0.08	0.07	0.08	0.01	0.01	0.05	—	0.03	0.05	0.01	0.06	USDASR14; Schmidt et al., 1999
326			100.0	24.6	1.46	0.49	1.95	1.70	1.95	0.24	0.24	1.22	—	0.73	1.22	0.24	1.46	
	Lettuce, romaine																	
327	leaves, fresh	—	7.0	2.2	0.09	0.03	0.11	0.10	0.11	0.02	0.02	0.07	—	0.04	0.07	0.01	0.09	USDASR14; Schmidt et al., 1999
328			100.0	31.8	1.73	0.55	2.08	1.94	2.08	0.40	0.38	1.35	—	0.79	1.47	0.24	1.72	
	Longan *Nephelium longana*																	
329	fruit, raw, ep	—	17.3	1.3	0.04	0.01	0.03	0.05	0.05	0.01	—	0.03	—	0.03	0.03	—	0.06	USDASR14
330			100.0	7.6	0.23	0.06	0.17	0.29	0.29	0.06	—	0.17	—	0.17	0.17	—	0.35	

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	Loquat *Eriobotrya japonica*																	
331	fruit, raw, ep	—	13.3	0.4	0.01	0.01	0.02	0.03	0.02	0.00	0.01	0.01	—	0.01	0.02	0.01	0.02	USDASR14
332			100.0	3.2	0.08	0.08	0.15	0.23	0.15	0.00	0.08	0.08	—	0.08	0.15	0.08	0.15	
	Lupin (sweet white) *Lupinus albus*																	
333	seeds	5-27-717	89.0	34.9	3.38	0.77	1.40	2.43	1.54	0.27	0.51	1.22		1.35	1.20	0.26	1.29	NRC, 1998
334			100.0	39.2	3.80	0.87	1.57	2.73	1.73	0.30	0.57	1.37		1.52	1.35	0.29	1.45	
	Lychee *Litchi chinnsis*																	
335	fruit, raw, ep	—	18.2	0.8	—	—	—	—	0.04	0.01	—	—	—	—	—	0.01	—	USDASR14
336			100.0	4.6	—	—	—	—	0.22	0.05	—	—	—	—	—	0.05	—	
	Mango *Mangifera indica*																	
337	fruit, raw, ep	—	18.3	0.5	0.02	0.01	0.02	0.03	0.04	0.01	—	0.02	—	0.01	0.02	0.01	0.03	USDASR14; Schmidt et al., 1999
338			100.0	2.8	0.11	0.05	0.11	0.16	0.22	0.05	—	0.11	—	0.05	0.11	0.05	0.16	
	Maple, sugar *Acer saccharum*																	
339	leaves	—	—	—														Robbins and Moen, 1975
340			100.0	—														
	Mealworm *Tenebrio molitor*																	
341	larvae	—	38.1	18.7	0.97	0.59	0.94	1.99	1.02	0.24	0.16	0.66	0.01	1.37	0.77	0.15	1.10	Finke, 2002
342			100.0	49.1	2.55	1.55	2.47	5.22	2.68	0.63	0.42	1.73	0.02	3.60	2.02	0.39	2.89	
343	larvae, gut loaded with high (8%) Ca diet	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
344			—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
345	oversized	—	39.0	18.4	1.03	0.65	0.86	1.43	1.12	0.26	0.15	0.75	0.01	1.43	0.64	0.17	1.22	Finke, 2002
346			100.0	47.2	2.64	1.67	2.21	3.67	2.87	0.67	0.38	1.92	0.01	3.67	1.64	0.44	3.13	
	Mealworm *Zophobas morio*																	
347	larvae	—	42.1	19.7	0.96	0.60	0.93	1.91	1.03	0.21	0.15	0.68	<0.01	1.37	0.78	0.18	1.03	Finke, 2002
348			100.0	46.8	2.28	1.43	2.21	4.54	2.45	0.50	0.36	1.62	—	3.25	1.85	0.43	2.45	
	Meat																	
349	meal rendered	5-00-385	94.0	54.0	3.60	1.14	1.60	3.84	3.07	0.80	0.60	2.17	—	1.40	1.97	0.35	2.66	NRC, 1998
350			100.0	57.4	3.83	1.21	1.70	4.09	3.27	0.85	0.64	2.31	—	1.49	2.10	0.37	2.83	
351	meal rendered with bone	5-00-388	93.0	51.5	3.45	0.91	1.34	2.98	2.51	0.68	0.50	1.62	—	1.07	1.59	0.28	2.04	NRC, 1998
352			100.0	55.4	3.71	0.98	1.44	3.20	2.70	0.73	0.54	1.74	—	1.15	1.71	0.30	2.19	
	Melon, cantaloupe *Cucumis melo*																	
353	fruit, raw, ep	—	10.2	0.9	—	—	—	—	—	—	—	—	—	—	—	—	—	USDASR14; Schmidt et al., 1999
354			100.0	8.6	—	—	—	—	—	—	—	—	—	—	—	—	—	
355	fruit, raw, with peel	—	7.5	1.0														Schmidt et al., 1999
356			100.0	13.1														
	Melon, casaba *Cucumis melo*																	
357	fruit, raw, ep	—	8.0	0.9	—	—	—	—	—	—	—	—	—	—	—	—	—	USDASR14
358			100.0	11.3	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Melon, honeydew *Cucumis melo*																	
359	fruit, raw, ep	—	10.3	0.5	—	—	—	—	—	—	—	—	—	—	—	—	—	USDASR14; Schmidt et al., 1999
360			100.0	4.5	—	—	—	—	—	—	—	—	—	—	—	—	—	
361	fruit, raw, with peel	—	8.1	0.7														Schmidt et al., 1999
362			100.0	8.9														
	Milk, cattle *Bos taurus*																	
363	dehy	5-01-167	96.0	25.4	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1982
364			100.0	26.5	—	—	—	—	—	—	—	—	—	—	—	—	—	
365	fresh	5-01-168	12.0	3.3	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1982
366			100.0	26.7	—	—	—	—	—	—	—	—	—	—	—	—	—	
367	skimmed, dehy	5-01-175	94.0	33.7	1.24	1.05	1.87	3.67	2.86	0.92	0.30	1.78		1.87	1.62	0.51	2.33	NRC, 1998
368			100.0	35.9	1.32	1.12	1.99	3.90	3.04	0.98	0.32	1.89		1.99	1.72	0.54	2.48	
369	skimmed, fresh	5-01-170	10.0	3.0	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1982
370			100.0	31.2	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Milk, human *Homo sapiens*																	
371	fresh	—	12.5	1.0	—	—	—	—	—	—	—	—	—	—	—	—	—	Jensen, 1995
372			100.0	8.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Milk, baboon *Papio*																	
373	fresh, days 0-5	—	14.6	2.3	—	—	—	—	—	—	—	—	—	—	—	—	—	Hummer, 1970
374			100.0	15.8	—	—	—	—	—	—	—	—	—	—	—	—	—	
375	fresh, days 6-11	—	15.3	1.7	—	—	—	—	—	—	—	—	—	—	—	—	—	Hummer, 1970
376			100.0	11.1	—	—	—	—	—	—	—	—	—	—	—	—	—	
377	fresh, days 12-35	—	14.0	1.5	—	—	—	—	—	—	—	—	—	—	—	—	—	Hummer, 1970
378			100.0	10.7	—	—	—	—	—	—	—	—	—	—	—	—	—	
379	fresh, days 36-279	—	14.4	1.6	—	—	—	—	—	—	—	—	—	—	—	—	—	Hummer, 1970
380			100.0	11.1	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Millet *Panicum miliaceum*																	
381	grain	4-03-120	90.0	11.1	0.41	0.20	0.46	1.24	0.23	0.31	0.18	0.56	—	0.31	0.40	0.16	0.57	NRC, 1998
382			100.0	12.3	0.46	0.22	0.51	1.38	0.26	0.34	0.20	0.62	—	0.34	0.44	0.18	0.63	

(continues)

TABLE 12-4 *(continued)*

Entry Number	Description	International Feed Number[b]	Dry Matter (%)	Crude Protein (%)	Arginine (%)	Histidine (%)	Isoleucine (%)	Leucine (%)	Lysine (%)	Methionine (%)	Cystine (%)	Phenylalanine (%)	Taurine (%)	Tyrosine (%)	Threonine (%)	Tryptophan (%)	Valine (%)	Data Source
	Mirror plant *Coprosma repens*																	
383	leaves, mature, fresh	—	17.5	2.2	—	—	—	—	—	—	—	—	—	—	—	—	—	Janeke, 1995
384			100.0	12.6	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Molasses and syrup																	
385	beet, sugar, molasses	4-00-668	78.0	6.6	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1982
386			100.0	8.5	—	—	—	—	—	—	—	—	—	—	—	—	—	
387	citrus, syrup	4-01-241	68.0	5.5	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1982
388			100.0	8.2	—	—	—	—	—	—	—	—	—	—	—	—	—	
389	sugarcane, molasses, dehy	4-04-695	94.0	9.7	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1982
390			100.0	10.3	—	—	—	—	—	—	—	—	—	—	—	—	—	
391	sugarcane, molasses, more than 46%	4-04-696	75.0	4.4	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1982
392			100.0	5.8	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Mulberry *Morus* spp.																	
393	browse, fresh	2-03-150	40.0	7.3	—	—	—	—	—	—	—	—		—	—	—	—	NRC, 1981
394			100.0	18.1	—	—	—	—	—	—	—	—		—	—	—	—	
395	fruit, raw, ep	—	12.3	1.4	—	—	—	—	—	—	—	—	—	—	—	—	—	USDASR14
396			100.0	11.7	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Mulberry, white *Morus alba*																	
397	leaves, mature, fresh	—	31.1	6.4	—	—	—	—	—	—	—	—	—	—	—	—	—	Janeke, 1995
398			100.0	20.6	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Mustard *Brassica oleracea* var.																	
399	leaves and stems, fresh	—	9.2	2.7	0.20	0.05	0.10	0.08	0.12	0.03	0.04	0.07	—	0.14	0.07	0.03	0.11	USDASR14; Schmidt et al., 1999
400			100.0	29.3	2.17	0.54	1.09	0.87	1.30	0.33	0.43	0.76	—	1.52	0.76	0.33	1.20	
	Nectarine *Prunus persica*																	
401	fruit, raw, ep	—	13.7	0.9	—	—	—	—	—	—	—	—	—	—	—	—	—	USDASR14; Schmidt et al., 1999
402			100.0	6.9	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Oat *Avena sativa*																	
403	grain	4-03-309	89.0	11.5	0.87	0.31	0.48	0.92	0.40	0.22	0.36	0.65	—	0.41	0.44	0.14	0.66	NRC, 1998
404			100.0	12.9	0.98	0.35	0.54	1.03	0.45	0.25	0.40	0.73	—	0.46	0.49	0.16	0.74	
405	grain, naked	4-25-101	86.0	17.1	0.77	0.26	0.48	0.86	0.47	0.19	0.32	0.60	—	0.42	0.40	0.16	0.63	NRC, 1998
406			100.0	19.9	0.90	0.30	0.56	1.00	0.55	0.22	0.37	0.70	—	0.49	0.47	0.19	0.73	
407	groat	4-03-331	90.0	13.9	0.85	0.24	0.55	0.98	0.48	0.20	0.22	0.66	—	0.51	0.44	0.18	0.72	NRC, 1998
408			100.0	15.4	0.94	0.27	0.61	1.09	0.53	0.22	0.24	0.73	—	0.57	0.49	0.20	0.80	
409	hulls	1-03-281	92.0	3.6	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1982
410			100.0	3.9	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Olive *Olea europaea*																	
411	oil	—	100.0	0.0	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1998
412			100.0	0.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Okra *Hibiscus esculentus*																	
413		—	12.6	2.2	0.08	0.03	0.07	0.11	0.08	0.02	0.02	0.07	—	0.09	0.07	0.02	0.09	USDASR14; Schmidt et al., 1999
414			100.0	17.4	0.63	0.24	0.56	0.87	0.63	0.16	0.16	0.56	—	0.71	0.56	0.16	0.71	
	Onion *Allium cepa*																	
415	green	—	9.1	1.9	—	—	—	—	—	—	—	—	—	—	—	—	—	Schmidt et al., 1999
416			100.0	20.7	—	—	—	—	—	—	—	—	—	—	—	—	—	
417	red	—	9.1	1.4	—	—	—	—	—	—	—	—	—	—	—	—	—	Schmidt et al., 1999
418			100.0	15.5	—	—	—	—	—	—	—	—	—	—	—	—	—	
419	yellow	—	10.3	0.9	—	—	—	—	—	—	—	—	—	—	—	—	—	Schmidt et al., 1999
420			100.0	9.1	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Orange *Citrus* spp																	
421	fruit, raw, ep	—	13.3	0.9	0.07	0.02	0.03	0.02	0.05	0.02	0.01	0.03	—	0.02	0.02	0.01	0.04	USDASR14
422			100.0	7.1	0.53	0.15	0.00	0.15	0.38	0.15	0.08	0.38	—	0.15	0.15	0.08	0.30	
423	fruit, raw, with peel	—	17.7	1.3	0.09	0.02	0.04	0.03	07.03	0.01	0.04	0.04	—	0.02	0.02	0.01	0.06	USDASR14; Bath et al., 1999
424			100.0	7.3									—					
425	peel	—	27.5	1.5	—	—	—	—	—	—	—	—	—	—	—	—	—	USDASR14; Schmidt et al., 1999
426			100.0	5.5	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Papaya *Carica papaya*																	
427	fruit, raw, ep	—	11.2	0.6	0.01	0.01	0.01	0.02	0.03	0.00	—	0.01	—	0.01	0.01	0.01	0.00	USDASR14; Schmidt et al., 1999
428			100.0	5.5	0.09	0.09	0.09	0.18	0.27	0.00	—	0.09	—	0.09	0.09	0.09	0.00	
	Parsley																	
429	leaves and stems, fresh	—	12.0	2.9	0.12	0.06	0.12	0.20	0.18	0.04	0.01	0.15	—	0.08	0.12	0.05	0.17	USDASR14; Schmidt et al., 1999
430			100.0	24.0	1.00	0.50	1.00	1.66	1.50	0.33	0.08	1.25	—	0.67	1.00	0.42	1.41	

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	Parsnip *Pastinaca sativa*																		
431	roots, fresh	—	20.5	1.2	—	—	—	—	—	—	—	—	—	—	—	—	—	USDASR14
432			100.0	5.9	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Pea *Pisum* spp																		
433	seeds	5-03-600	89.0	22.8	1.87	0.54	0.86	1.51	0.15	0.21	0.31	0.98	—	0.71	0.78	0.19	0.98	NRC, 1998
434			100.0	25.6	2.10	0.61	0.97	1.70	0.17	0.24	0.35	1.10	—	0.80	0.88	0.21	1.10	
	Peach *Prunus persica*																		
435	fruit, raw, ep	—	12.3	0.7	0.02	0.01	0.02	0.04	0.02	0.02	0.01	0.02	—	0.02	0.03	0.00	0.04	USDASR14
436			100.0	5.7	0.16	0.08	0.16	0.32	0.16	0.16	0.08	0.16	—	0.16	0.24	0.00	0.32	
	Pear *Pyrus communis*																		
437	fruit, raw, ep	—	16.2	0.4	0.01	0.00	0.01	0.02	0.01	0.01	0.00	0.01	—	0.00	0.01	—	0.01	USDASR14; Schmidt et al., 1999
438			100.0	2.4	0.06	0.00	0.06	0.12	0.06	0.06	0.00	0.06	—	0.00	0.06	—	0.06	
	Peanut (Groundnut) *Arachis hypogaea*																		
439	butter	—	98.8	25.2	3.02	0.64	0.88	1.64	0.91	0.31	0.32	1.31	—	1.09	0.86	0.25	1.06	USDASR14
440			100.0	25.5	3.06	0.65	0.89	1.66	0.92	0.31	0.32	1.33	—	1.10	0.87	0.25	1.07	
441	hulls	1-08-028	91.0	7.1														NRC, 1982
442			100.0	7.8														
443	kernels, meal mech extr	5-03-649	92.0	43.2	4.79	1.01	1.41	2.77	1.48	0.50	0.60	2.02	—	1.74	1.16	0.41	1.70	NRC, 1998
444			100.0	47.0	5.21	1.10	1.53	3.01	1.61	0.54	0.65	2.20	—	1.89	1.26	0.45	1.85	
445	kernels, meal solv extr	5-03-650	92.0	49.1	5.09	1.06	1.78	2.83	1.66	0.52	0.69	2.35	—	1.80	1.27	0.48	1.98	NRC, 1998
446			100.0	53.4	5.53	1.15	1.93	3.08	1.80	0.57	0.75	2.55	—	1.96	1.38	0.52	2.15	
	Peepultree *Ficus religiosa*																		
447	leaves, fresh	2-27-207	17.0	3.4	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1981
448			100.0	11.2	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Pepper, sweet, green *Capsicum annuum*																		
449	fruit, raw, ep	—	5.3	0.9	0.04	0.02	0.03	0.05	0.04	0.01	0.02	0.03	—	0.02	0.03	0.01	0.04	USDASR14; Schmidt et al., 1999
450			100.0	17.7	0.76	0.38	0.57	0.95	0.76	0.19	0.38	0.57	—	0.38	0.57	0.19	0.76	
	Persimmon, American *Diospyros virginiana*																		
451	fruit, raw, ep	—	35.6	0.8	0.03	0.02	0.04	0.06	0.05	0.01	0.02	0.04	—	0.02	0.04	0.01	0.04	USDASR14
452			100.0	2.2	0.08	0.06	0.11	0.17	0.14	0.03	0.06	0.11	—	0.06	0.11	0.03	0.11	
	Persimmon, Oriental (Kaki) *Diospyros kaki*																		
453	fruit, raw, ep	—	19.7	0.6	0.03	0.01	0.03	0.04	0.03	0.01	0.01	0.05	—	0.02	0.03	0.01	0.03	USDASR14
454			100.0	2.9	0.15	0.05	0.15	0.20	0.15	0.05	0.05	0.25	—	0.10	0.15	0.05	0.15	
	Pineapple *Ananas comosus*																		
455	fruit, raw, ep	—	13.5	0.4	0.02	0.01	0.01	0.02	0.03	0.01	0.00	0.01	—	0.01	0.01	0.01	0.02	USDASR14; Schmidt et al., 1999
456			100.0	2.9	0.15	0.07	0.07	0.15	0.22	0.07	0.00	0.07	—	0.07	0.07	0.07	0.15	
	Plantain *Musa sapientum*																		
457	fruit, raw, ep	—	34.7	1.3	0.11	0.06	0.04	0.60	0.06	0.02	0.02	0.04	—	0.03	0.03	0.02	0.05	USDASR14; Schmidt et al., 1999
458			100.0	3.7	0.32	0.17	0.12	1.73	0.17	0.06	0.06	0.12	—	0.09	0.09	0.06	0.14	
	Plum *Prunus domestica*																		
459	fruit, raw, ep	—	14.8	0.8	0.01	0.01	0.02	0.02	0.02	0.01	0.00	0.02	—	0.01	0.02	—	0.02	USDASR14; Schmidt et al., 1999
460			100.0	5.3	0.07	0.07	0.14	0.14	0.14	0.07	0.00	0.14	—	0.07	0.14	—		
	Pomegranate *Punica granatum*																		
461	fruit, raw, ep	—	19.0	1.0	—	—	—	—	—	—	—	—	—	—	—	—	—	USDASR14
462			100.0	5.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Poplar, black *Populus nigra*																		
463	leaves, sun-cured	1-03-750	85.4	16.1	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1971
464			100.0	18.8	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Potato *Solanum tuberosum*																		
465	protein concentrate	5-25-392	91.0	73.8	3.80	1.71	4.09	7.61	5.83	1.68	1.20	4.89		4.27	4.30	1.02	4.89	NRC, 1998
466			100.0	81.1	4.18	1.88	4.49	8.36	6.41	1.85	1.32	5.37		4.69	4.73	1.12	5.37	
467	tubers, fresh	—	28.0	2.7	—	—	—	—	—	—	—	—	—	—	—	—	—	USDASR11; Schmidt et al., 1999
468			100.0	9.7	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Poultry																		
469	by-product, meal rendered	5-03-798	93.0	64.1	3.94	1.25	2.01	3.89	3.32	1.11	0.65	2.26		1.56	2.18	0.48	2.51	NRC, 1998
470			100.0	68.9	4.24	1.34	2.16	4.18	3.57	1.19	0.70	2.43		1.68	2.34	0.52	2.70	
	Prune																		
471	with pits	—	82.0	4.3	—	—	—	—	—	—	—	—	—	—	—	—	—	Bath et al., 1999
472			100.0	5.3	—	—	—	—	—	—	—	—	—	—	—	—	—	
473	without pits	—	80.0	3.3	—	—	—	—	—	—	—	—	—	—	—	—	—	Bath et al., 1999
474			100.0	4.1	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Pummelo *Citrus grandis*																		
475	fruit, raw, ep	—	10.9	0.8	—	—	—	—	—	—	—	—	—	—	—	—	—	USDASR14
476			100.0	7.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Pumpkin *Cucurbita pepo*																		
477		—	20.0	1.5	—	—	—	—	—	—	—	—	—	—	—	—	—	Schmidt et al., 1999
478			100.0	7.3	—	—	—	—	—	—	—	—	—	—	—	—	—	

(continues)

TABLE 12-4 *(continued)*

Entry Number	Description	International Feed Number[b]	Dry Matter (%)	Crude Protein (%)	Arginine (%)	Histidine (%)	Isoleucine (%)	Leucine (%)	Lysine (%)	Methionine (%)	Cystine (%)	Phenylalanine (%)	Taurine (%)	Tyrosine (%)	Threonine (%)	Tryptophan (%)	Valine (%)	Data Source
	Quince *Cydonia oblonga*																	
479	fruit, raw, ep	—	16.2	0.4	—	—	—	—	—	—	—	—	—	—	—	—	—	USDASR14
480			100.0	2.5	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Radicchio *Cichorium intybus* var. *foliosum*																	
481	raw	—	6.9	1.4	0.11	0.02	0.09	0.06	0.06	0.01	—	0.03	—	—	0.04	0.03	0.07	USDASR14
482			100.0	20.8	1.60	0.29	1.31	0.87	0.87	0.15	—	0.44	—	—	0.58	0.44	1.02	
	Radish *Raphanus sativus*																	
483	raw	—	5.2	0.6	0.04	0.10	0.03	0.04	0.04	0.01	0.01	0.02	—	0.01	0.03	0.00	0.03	USDASR14; Schmidt et al., 1999
484			100.0	11.6	0.78	1.94	0.58	0.78	0.78	0.19	0.19	0.39	—	0.19	0.58	0.00	0.58	
	Raisin, golden seedless *Vitis vinifera*																	
485	fruit, raw, ep	—	85.0	3.4	—	—	—	—	—	—	—	—	—	—	—	—	—	USDASR14
486			100.0	4.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Raisin, seeded *Vitis vinifera*																	
487	fruit, raw, ep	—	83.4	2.5	—	—	—	—	—	—	—	—	—	—	—	—	—	USDASR14
488			100.0	3.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Raisin, seedless *Vitis vinifera*																	
489	fruit, raw, ep	—	84.6	3.2	—	—	—	—	—	—	—	—	—	—	—	—	—	USDASR14
490			100.0	3.8	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Raspberry *Rubus idaeus*																	
491	fruit, raw, ep	—	13.4	0.9	—	—	—	—	—	—	—	—	—	—	—	—	—	USDASR14; Schmidt et al., 1999
492			100.0	6.8	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Rice *Oryza sativa*																	
493	bran	4-03-928	90.0	13.3	1.00	0.34	0.44	0.92	0.57	0.26	0.27	0.56		0.40	0.48	0.14	0.68	NRC, 1998
494			100.0	14.8	1.11	0.38	0.49	1.02	0.63	0.29	0.30	0.62		0.44	0.53	0.16	0.76	
495	flour	—	88.1	6.0	0.52	0.15	0.24	0.49	0.21	0.14	0.11	0.32	—	0.31	0.21	0.07	0.35	USDASR14
496			100.0	6.8	0.59	0.17	0.27	0.56	0.24	0.16	0.12	0.36	—	0.35	0.24	0.08	0.40	
497	grain, polished and broken	4-03-932	89.0	7.9	0.52	0.18	0.34	0.67	0.30	0.18	0.11	0.39	—	0.38	0.26	0.10	0.49	NRC, 1998
498	(Brewer's Rice)		100.0	8.9	0.58	0.20	0.38	0.75	0.34	0.20	0.12	0.44	—	0.43	0.29	0.11	0.55	
499	hulls	1-08-075	92.0	3.0	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1982
500			100.0	3.3	—	—	—	—	—	—	—	—	—	—	—	—	—	
501	polishings	4-03-943	90.0	13.0	0.82	0.28	0.43	0.82	0.58	0.23	0.22	0.49	—	0.44	0.44	0.13	0.75	NRC, 1998
502			100.0	14.4	0.91	0.31	0.48	0.91	0.64	0.26	0.24	0.54	—	0.49	0.49	0.14	0.83	
	Rocket *Eruca sativa*																	
503	aerial part, fresh	2-03-949	15.8	1.8	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1971
504			100.0	11.4	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Rutabaga *Brassica campestris* var. *rutabaga*																	
505	raw	—	10.3	1.2	0.15	0.03	0.05	0.04	0.04	0.01	0.01	0.03	—	0.02	0.05	0.01	0.05	USDASR14; Schmidt et al., 1999
506			100.0	11.6	1.46	0.29	0.49	0.39	0.34	0.10	0.10	0.29	—	0.20	0.49	0.10	0.49	
507	tops, fresh	—	10.9	2.0	—	—	—	—	—	—	—	—	—	—	—	—	—	Bath et al., 1999
508			100.0	18.6	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Rye *Secale cereale*																	
509	grain	4-04-047	88.0	11.8	0.50	0.24	0.37	0.64	0.38	0.17	0.19	0.50	—	0.26	0.32	0.12	0.51	NRC, 1998
510			100.0	13.4	0.57	0.27	0.42	0.73	0.43	0.19	0.22	0.57	—	0.30	0.36	0.14	0.58	
	Safflower *Carthamus tinctorius*																	
511	hulls	—	91.3	3.3	2.04	0.59	0.67	1.52	0.74	0.34	0.38	1.07	—	0.77	0.65	0.33	1.18	Bath et al., 1999
512			100.0	3.6	2.23	0.65	0.73	1.66	0.81	0.37	0.42	1.17	—	0.84	0.71	0.36	1.29	
513	meal, sol. extr.	5-04-110	92.0	23.4	3.59	1.07	1.69	2.57	1.17	0.66	0.69	2.00	—	1.08	1.28	0.54	2.33	NRC, 1998
514			100.0	25.4	3.90	1.16	1.84	2.79	1.27	0.72	0.75	2.17	—	1.17	1.39	0.59	2.53	
515	meal without hulls, sol. extr.	5-07-959	92.0	42.5	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1998
516			100.0	46.2	—	—	—	—	—	—	—	—	—	—	—	—	—	
517	oil	4-20-526	100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1998
518			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
519	seeds	—	94.0	16.4	—	—	—	—	—	—	—	—	—	—	—	—	—	Bath et al., 1999
520			100.0	17.4	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Sapote *Achras sapotas*																	
521	fruit, raw, ep	—	22.0	0.4	—	—	—	—	—	—	—	—	—	—	—	—	—	Schmidt et al., 1999
522			100.0	2.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Sesame *Sesamum indicum*																	
523	meal, mech. extr.	5-04-220	93.0	42.6	4.86	0.98	1.47	2.74	1.01	1.15	0.82	1.77	—	1.52	1.44	0.54	1.85	NRC, 1998
524			100.0	45.8	5.23	1.05	1.58	2.95	1.09	1.24	0.88	1.90	—	1.63	1.55	0.58	1.99	
525	seeds	—	92.0	22.3	—	—	—	—	—	—	—	—	—	—	—	—	—	Bath et al., 1999
526			100.0	24.2	—	—	—	—	—	—	—	—	—	—	—	—	—	

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	Sorghum *Sorghum bicolor*																		
527	grain	4-20-893	89.0	9.2	0.38	0.23	0.37	1.21	0.22	0.17	0.17	0.49	—	0.35	0.31	0.10	0.46	NRC, 1998
528			100.0	10.3	0.43	0.26	0.42	1.36	0.25	0.19	0.19	0.55	—	0.39	0.35	0.11	0.52	
	Soybean *Glycine max*																	
529	flour, full-fat, raw	—	94.8	34.5	2.68	0.93	1.68	2.81	2.30	0.47	0.56	1.80	—	1.31	1.50	0.50	1.72	USDASR14
530			100.0	36.4	2.83	0.98	1.77	2.96	2.43	0.50	0.54	1.90	—	1.38	1.58	0.53	1.81	
531	hulls	1-4-560	91.0	11.0	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1982
532			100.0	12.1	—	—	—	—	—	—	—	—	—	—	—	—	—	
533	meal, sol. extr.	5-04-604	89.0	43.8	3.23	1.17	1.99	3.42	2.83	0.61	0.70	2.18	—	1.69	1.73	0.61	2.06	NRC, 1998
534			100.0	49.2	3.63	1.31	2.24	3.84	3.18	0.69	0.79	2.45	—	1.90	1.94	0.69	2.31	
535	meal without hulls, sol. extr.	5-04-612	90.0	47.5	3.48	1.28	2.16	3.66	3.02	0.67	0.74	2.39	—	1.82	1.85	0.65	2.27	NRC, 1998
536			100.0	52.8	3.87	1.42	2.40	4.07	3.36	0.74	0.82	2.66	—	2.02	2.06	0.72	2.52	
537	protein concentrate	—	90.0	64.0	5.79	1.80	3.30	5.30	4.20	0.90	1.00	3.40	—	2.50	2.80	0.90	3.40	NRC, 1998
538			100.0	71.1	6.43	2.00	3.67	5.89	4.67	1.00	1.11	3.78	—	2.78	3.11	1.00	3.78	
539	protein isolate	5-08-038	92.0	85.8	6.87	2.25	4.25	6.64	5.26	1.01	1.19	4.34	—	3.10	3.17	1.08	4.21	NRC, 1998
540			100.0	93.3	7.47	2.45	4.62	7.22	5.72	1.10	1.29	4.72	—	3.37	3.45	1.17	4.58	
541	seeds, heat processed	5-04-597	90.0	35.2	2.60	0.96	1.61	2.75	2.22	0.53	0.55	1.83	—	1.32	1.41	0.48	1.68	NRC, 1998
542			100.0	39.1	2.89	1.07	1.79	3.06	2.47	0.59	0.61	2.03	—	1.47	1.57	0.53	1.87	
	Spinach *Spinacia oleracea*																	
543	raw	—	8.4	2.9	0.16	0.06	0.15	0.22	0.17	0.05	0.04	0.13	—	0.11	0.12	0.04	0.16	USDASR14; Schmidt et al., 1999
544			100.0	34.0	1.90	0.71	1.78	2.61	2.02	0.59	0.48	1.54	—	1.31	1.43	0.48	1.90	
	Squash, acorn *Cucurbita maxima*																	
545	raw	—	12.2	0.8	0.04	0.02	0.03	0.04	0.03	0.01	0.01	0.03	—	0.03	0.02	0.01	0.03	USDASR14; Schmidt et al., 1999
546			100.0	6.5	0.33	0.16	0.25	0.33	0.25	0.08	0.08	0.25	—	0.25	0.16	0.08	0.25	
	Squash, butternut *Cucurbita maxima*																	
547	raw	—	13.6	1.0	0.06	0.02	0.04	0.06	0.04	0.01	0.01	0.04	—	0.03	0.03	0.01	0.04	USDASR14; Schmidt et al., 1999
548			100.0	7.4	0.44	0.15	0.29	0.44	0.29	0.07	0.07	0.29	—	0.22	0.22	0.07	0.29	
	Squash, spaghetti *Cucurbita maxima*																	
549	raw	—	8.4	0.6	0.03	0.01	0.02	0.03	0.02	0.01	0.01	0.02	—	0.02	0.02	0.01	0.03	USDASR14; Schmidt et al., 1999
550			100.0	7.6	0.36	0.12	0.24	0.36	0.24	0.12	0.12	0.24	—	0.24	0.24	0.12	0.36	
	Squash, zucchini *Cucurbita pepo*																	
551	raw, with peel	—	4.7	1.2	0.05	0.03	0.04	0.07	0.06	0.02	0.01	0.04	—	0.03	0.03	0.01	0.05	USDASR14; Schmidt et al., 1999
552			100.0	25.4	1.06	0.64	0.85	1.48	1.27	0.42	0.21	0.85	—	0.64	0.64	0.21	1.06	
	Strawberry *Fragaria* spp																	
553	fruit, raw, ep	—	8.4	0.6	0.03	0.01	0.01	0.03	0.03	0.00	0.01	0.02	—	0.02	0.02	0.01	0.02	USDASR14; Schmidt et al., 1999
554			100.0	7.2	0.36	0.12	0.12	0.36	0.36	0.00	0.12	0.24	—	0.24	0.24	0.12	0.24	
	Sucrose																	
555		4-04-701	99.0	0.0	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1998
556			100.0	0.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Sugarcane *Saccharum officinarum*																	
557	stems, fresh	2-13-248	15.0	1.2	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1982
558			100.0	7.6	—	—	—	—	—	—	—	—	—	—	—	—	—	
559	sugar	4-04-701	100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1982
560			100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Sunflower, common *Helianthus annuus*																	
561	kernels	—	95.0	25.7	2.38	0.66	1.29	1.86	1.01	0.59	0.48	1.23	—	0.76	1.04	0.38	1.49	Bath et al., 1999
562			100.0	27.1	2.51	0.69	1.36	1.96	1.06	0.62	0.51	1.29	—	0.80	1.09	0.40	1.57	
563	meal, sol. extr.	5-09-340	90.0	26.8	2.93	0.92	1.44	2.31	1.20	0.82	0.66	1.66	—	1.03	1.33	0.44	1.74	NRC, 1998
564			100.0	29.8	3.26	1.02	1.60	2.57	1.33	0.91	0.73	1.84	—	1.14	1.48	0.49	1.93	
565	meal without hulls, sol. extr.	5-04-739	93.0	42.2														NRC, 1998
566			100.0	45.4														
567	seeds	—	94.0	16.8														Bath et al., 1999
568			100.0	17.9														
	Sweet potato *Ipomoea batatas*																	
569	tubers, fresh	—	27.2	1.7	0.08	0.03	0.08	0.12	0.08	0.04	0.01	0.10	—	0.07	0.08	0.08	0.11	USDASR14; Schmidt et al., 1999
570			100.0	6.1	0.29	0.11	0.29	0.44	0.29	0.15	0.04	0.37	—	0.26	0.29	0.29	0.41	
	Tamarind *Tamarindus indica*																	
571	pulp	—	68.6	2.8	—	—	—	—	0.14	0.01	—	—	—	—	—	0.02	—	USDASR14
572			100.0	4.1	—	—	—	—	0.20	0.01	—	—	—	—	—	0.03	—	
573	seed	—	—	—														Glew et al., 1997
574			100.0	17.3														
	Tomatillo																	
575	fruit, raw, ep	—	8.0	1.1	—	—	—	—	—	—	—	—	—	—	—	—	—	USDASR14; Schmidt et al., 1999
576			100.0	14.3	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Tomato *Lycopersicon esculentum*																	
577	pomace, dehy	—	92.0	21.6														NRC, 1982; Bath et al., 1999
578			100.0	23.5														
579	red, ripe, raw, year-round average	—	6.2	0.9	0.02	0.01	0.02	0.03	0.03	0.01	0.01	0.02	—	0.02	0.02	0.01	0.02	USDASR14; Schmidt et al., 1999
580			100.0	13.6	0.32	0.16	0.32	0.48	0.48	0.16	0.16	0.32	—	0.32	0.32	0.16	0.32	

(continues)

TABLE 12-4 *(continued)*

Entry Number	Description	International Feed Number[b]	Dry Matter (%)	Crude Protein (%)	Arginine (%)	Histidine (%)	Isoleucine (%)	Leucine (%)	Lysine (%)	Methionine (%)	Cystine (%)	Phenylalanine (%)	Taurine (%)	Tyrosine (%)	Threonine (%)	Tryptophan (%)	Valine (%)	Data Source
	Triticale *Triticale hexaploide*																	
581	grain	4-20-362	90.0	12.5	0.57	0.26	0.39	0.76	0.39	0.20	0.26	0.49	—	0.32	0.36	0.14	0.51	NRC, 1998
582			100.0	13.9	0.63	0.29	0.43	0.84	0.43	0.22	0.29	0.54	—	0.36	0.40	0.16	0.57	
	Turnip *Brassica rapa rapa*																	
583	greens, raw	—	8.9	1.5	0.09	0.04	0.08	0.14	0.10	0.03	0.02	0.09	—	0.06	0.08	0.03	0.10	USDASR14; Schmidt et al., 1999
584			100.0	16.8	1.01	0.45	0.90	1.57	1.12	0.34	0.22	1.01	—	0.67	0.90	0.34	1.12	
585	tubers, fresh	—	8.1	0.9	0.02	0.01	0.04	0.03	0.04	0.01	0.01	0.02	—	0.01	0.03	0.01	0.03	USDASR14; Schmidt et al., 1999
586			100.0	11.1	0.25	0.12	0.49	0.37	0.49	0.12	0.12	0.25	—	0.12	0.37	0.12	0.37	
	Walnut																	
587	meats, ground	—	91.0	41.7	—	—	—	—	—	—	—	—	—	—	—	—	—	Bath et al., 1999
588			100.0	45.8	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Watermelon *Citrullus vulgaris*																	
589	fruit, raw, ep	—	8.5	0.6	—	—	—	—	—	—	—	—	—	—	—	—	—	Schmidt et al., 1999
590			100.0	7.3	—	—	—	—	—	—	—	—	—	—	—	—	—	
591	fruit, raw, with peel	—	6.7	0.5	—	—	—	—	—	—	—	—	—	—	—	—	—	Schmidt et al., 1999
592			100.0	7.8	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Waxmoth *Galleria mellonella*																	
593	larvae	—	41.5	14.1	0.71	0.33	0.63	1.24	0.79	0.22	0.11	0.53	<0.01	0.88	0.59	0.12	0.68	Finke, 2002
594			100.0	34.0	1.71	0.80	1.52	2.99	1.90	0.53	0.27	1.28	—	2.12	1.42	0.29	1.64	
	Wheat *Triticum aestivum*																	
595	bran	4-05-190	89.0	15.7	1.07	0.44	0.49	0.98	0.64	0.25	0.33	0.62	—	0.43	0.52	0.22	0.72	NRC, 1998
596			100.0	17.6	1.20	0.49	0.55	1.10	0.72	0.28	0.37	0.70	—	0.48	0.58	0.25	0.81	
597	flour, less than 2% fiber (feed flour)	4-28-221	88.0	11.0	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1982
598			100.0	12.5	—	—	—	—	—	—	—	—	—	—	—	—	—	
599	germs, ground	5-05-218	88.0	24.8	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1982
600			100.0	28.1	—	—	—	—	—	—	—	—	—	—	—	—	—	
601	grain	4-05-211	89.0	14.2	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1982
602			100.0	16.0	—	—	—	—	—	—	—	—	—	—	—	—	—	
603	grain, hard red spring	4-05-258	88.0	14.1	0.67	0.34	0.47	0.93	0.38	0.23	0.30	0.67	—	0.40	0.41	0.16	0.61	NRC, 1998
604			100.0	16.0	0.76	0.39	0.53	1.06	0.43	0.26	0.34	0.76	—	0.45	0.47	0.18	0.69	
605	grain, hard red winter	4-05-268	88.0	13.5	0.60	0.32	0.41	0.86	0.34	0.20	0.29	0.60	—	0.38	0.37	0.15	0.54	NRC, 1998
606			100.0	15.3	0.68	0.36	0.47	0.98	0.39	0.23	0.33	0.68	—	0.43	0.42	0.17	0.61	
607	grain, soft red winter	4-05-294	88.0	11.5	0.50	0.20	0.45	0.90	0.38	0.22	0.27	0.63	—	0.37	0.39	0.26	0.57	NRC, 1998
608			100.0	13.1	0.57	0.23	0.51	1.02	0.43	0.25	0.31	0.72	—	0.42	0.44	0.30	0.65	
609	grain, soft white winter	4-05-337	89.0	11.8	0.55	0.27	0.44	0.79	0.33	0.20	0.28	0.55	—	0.36	0.35	0.15	0.53	NRC, 1998
610			100.0	13.3	0.62	0.30	0.49	0.89	0.37	0.22	0.31	0.62	—	0.40	0.39	0.17	0.60	
611	middlings, < 9.5% fiber	4-05-205	89.0	15.9	0.97	0.44	0.53	1.06	0.57	0.26	0.32	0.70	—	0.29	0.51	0.20	0.75	NRC, 1998
612			100.0	17.9	1.09	0.49	0.60	1.19	0.64	0.29	0.36	0.79	—	0.33	0.57	0.22	0.84	
613	mill run, less than 9.5% fiber	4-05-206	90.0	15.4	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1982
614			100.0	17.2	—	—	—	—	—	—	—	—	—	—	—	—	—	
615	red dog, < 4% fiber	4-05-203	88.0	15.3	0.96	0.41	0.55	1.06	0.59	0.23	0.37	0.66	—	0.46	0.50	0.10	0.72	NRC, 1998
616			100.0	17.4	1.09	0.47	0.63	1.20	0.67	0.26	0.42	0.75	—	0.52	0.57	0.11	0.82	
617	shorts, < 7% fiber	4-05-201	88.0	16.0	1.07	0.43	0.58	1.02	0.70	0.25	0.28	0.70	—	0.51	0.57	0.22	0.87	NRC, 1998
618			100.0	18.2	1.22	0.49	0.66	1.16	0.80	0.28	0.32	0.80	—	0.58	0.65	0.25	0.99	
	Whey (cattle)																	
619	dried	4-01-182	96.0	12.1	0.26	0.23	0.62	1.08	0.90	0.17	0.25	0.36	—	0.25	0.72	0.18	0.60	NRC, 1998
620			100.0	12.6	0.27	0.24	0.65	1.13	0.94	0.18	0.26	0.38	—	0.26	0.75	0.19	0.63	
621	low lactose, dried	4-01-186	96.0	17.6	0.53	0.33	1.16	1.61	1.51	0.39	0.46	0.63	—	0.52	1.17	0.31	1.15	NRC, 1998
622			100.0	18.3	0.55	0.34	1.21	1.68	1.57	0.41	0.48	0.66	—	0.54	1.22	0.32	1.20	
623	permeate, dried	—	96.0	3.8	0.06	0.05	0.17	0.22	0.18	0.03	0.04	0.06	—	0.00	0.14	0.03	0.13	NRC, 1998
624			100.0	4.0	0.06	0.05	0.18	0.23	0.19	0.03	0.04	0.06	—	0.00	0.15	0.03	0.14	
	Willow *Salix* spp.																	
625	browse, fresh	2-05-472	41.0	4.0	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1971
626			100.0	9.8	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Willow, yellow *Salix lutea*																	
627	browse	2-05-475	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1971
628			100.0	14.4	—	—	—	—	—	—	—	—	—	—	—	—	—	
	Wood																	
629	sawdust	1-07-714	90.0	2.8	—	—	—	—	—	—	—	—	—	—	—	—	—	NRC, 1971
630			100.0	3.2	—	—	—	—	—	—	—	—	—	—	—	—	—	

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631	Yam Dioscorea alata tubers, fresh	—	30.4	1.5	0.13	0.03	0.05	0.10	0.06	0.02	0.02	0.07	—	0.04	0.05	0.01	0.06	USDASR14
632			100.0	5.0	0.43	0.10	0.16	0.33	0.20	0.07	0.07	0.23	—	0.13	0.16	0.03	0.20	
633	Yeast, brewer's *Saccharomyces cerevisiae* dried	7-05-527	93.0	45.9	2.20	1.09	2.15	3.13	3.22	0.74	0.50	1.83	—	1.55	2.20	0.56	2.39	NRC, 1998
634			100.0	49.4	2.37	1.17	2.31	3.37	3.46	0.80	0.54	1.97	—	1.67	2.37	0.60	2.57	
635	Yeast, torula *Torulopsis utilis* dried	7-05-534	93.0	46.4	2.48	1.09	2.50	3.32	3.47	0.69	0.50	2.33	—	1.65	2.30	0.51	2.60	NRC, 1998
636			100.0	49.9	2.67	1.17	2.69	3.57	3.73	0.74	0.54	2.51	—	1.77	2.47	0.55	2.80	

[a] Dash indicates that no data were available.

[b] First digit is class of feed: 1, dry forages and roughages; 2, pasture, range plants, and forages fed green; 3, silages; 4, energy feeds; 5, protein supplements; 6, minerals; 7, vitamins; 8, additives; the other five digits are the International Feed Number

TABLE 12-5 Mineral Concentrations in Macro- and Micromineral Sources

Entry Number	Description	International Feed No.	Dry Matter (%)	Calcium[a] (Ca) (%)	Phosphorus (P) (%)	Sodium (Na) (%)	Chlorine (Cl) (%)	Potassium (K) (%)	Magnesium (Mg) (%)	Sulfur (S) (%)	Copper (Cu) (%)	Iron (Fe) (%)	Manganese (Mn) (%)	Selenium (Se) (%)	Zinc (Zn) (%)	Data Source
	Bone															
1	meal, steamed	6-00-400	97	29.80	12.50	0.04	—	0.20	0.30	2.40	—	—	0.03	—	0.01	NRC, 1981;
2			100	30.72	12.89	0.04	—	0.21	0.31	2.47	—	—	0.03	—	0.01	NRC, 1998
	Calcium															
3	carbonate, $CaCO_3$	6-01-069	100	38.50	0.02	0.08	0.02	0.08	1.61	0.08	—	0.06	0.02	—	—	
4			100	38.50	0.02	0.08	0.02	0.08	1.61	0.08	—	0.06	0.02	—	—	
5	iodate, $Ca(IO_3)_2$			—	—	—	—	—	—	—	—	—	—	—	—	
6				—	—	—	—	—	—	—	—	—	—	—	—	
7	phosphate (dicalcium)	6-01-080	97	20 to 24	18.50	0.18	0.47	0.15	0.80	0.80	—	0.79	0.14	—	—	
8			100	—	—	—	—	—	—	—	—	—	—	—	—	
9	phosphate (monocalcium)	6-26-334	96	17.00	21.10	0.20	—	0.16	0.90	0.80	—	0.75	0.01	—	—	
10			100				—				—			—	—	
11	sulfate, dihydrate	6-01-090		21.85	—	—	—	—	0.48	16.19	—	—	—	—	—	
12			100		—	—	—	—			—	—	—	—	—	
	Copper (Cupric)															
13	oxide, CuO		—	—	—	—	—	—	—	—	75.00	—	—	—	—	
14			—	—	—	—	—	—	—	—	—	—	—	—	—	
15	sulfate, pentahydrate, $CuSO_4 \cdot 5H_2O$	6-01-719	100	—	—	—	—	—	—	12.80	25.40	—	—	—	—	
16			100	—	—	—	—	—	—	12.80	25.40	—	—	—	—	
	Iron (Ferric)															
17	oxide, Fe_2O_3	6-02-431	92	0.30	—	—	—	—	0.40	—	—	57.00	0.30	—	—	
18			100	0.32	—	—	—	—	0.43	—	—	61.95	0.32	—	—	
	Iron (Ferrous)															
19	carbonate, $FeCO_3$	6-01-863	99	—	—	—	—	—	—	—	—	39.60	—	—	—	
20			100	—	—	—	—	—	—	—	—	40.00	—	—	—	
21	oxide, FeO	6-20-728	97	—	—	—	—	—	—	—	—	75.37	—	—	—	
22			100	—	—	—	—	—	—	—	—	77.70	—	—	—	
23	sulfate, heptahydrate, $FeSO_4 \cdot 7H_2O$	6-20-734	98	—	—	—	—	—	—	12.10	—	21.40	—	—	—	
24			100	—	—	—	—	—	—	12.35	—	21.84	—	—	—	
	Limestone															
25	ground[b]	6-02-632	100	35.84	0.01	0.06	0.02	0.11	2.06	0.04	—	0.35	0.02	—	—	
26			100	35.84	0.01	0.06	0.02	0.11	2.06	0.04	—	0.35	0.02	—	—	
27	magnesium (Dolomitic)	6-02-633	99	22.08	0.04	—	0.12	0.36	9.89	—	—	0.08	—	—	—	
28			100	22.30	0.04	—	0.12	0.36	9.99	—	—	0.08	—	—	—	
	Magnesium															
29	carbonate	6-02-754	98	0.02	—	—	—	—	30.20	—	—	—	0.01	—	—	
30			100	0.02	—	—	—	—	30.82	—	—	—	0.01	—	—	
31	oxide	6-02-756	98	1.69	—	—	—	0.02	55.00	0.10	—	1.06	—	—	—	
32			100	1.72	—	—	—	0.02	56.12	0.10	—	1.08	—	—	—	
33	sulfate, heptahydrate	6-02-758	98	0.02	—	—	0.01	—	9.60	13.04	—	—	—	—	—	
34			100	0.02	—	—	0.01	—	9.80	13.31	—	—	—	—	—	
	Phosphate															
35	defluorinated	6-01-780	100	32.00	18.00	3.27	—	0.10	0.29	0.13	—	0.84[c]	0.05	—	—	
36			100	32.00	18.00	3.27	—	0.10	0.29	0.13	—	0.84[c]	0.05	—	—	
37	monoammonium	6-09-338		0.35	24.20	0.20	—	0.16	0.75	1.50	—	0.41	0.01	—	—	
38			100	—	—	—	—	—	—	—	—	—	—	—	—	
39	rock curaçao, ground	6-05-586	99	35.09	14.23	0.20	—	—	0.80	—	—	0.35	—	—	—	
40			100	—	—	—	—	—		—	—		—	—	—	
41	rock, soft	6-03-947	100	16.09	9.05	0.10	—	—	0.38	—	—	1.92	0.10	—	—	
42			100	16.09	9.05	0.10	—	—	0.38	—	—	1.92	0.10	—	—	

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	Potassium														
43	chloride, KCl	6-03-755	100	0.05	—	1.00	46.93	51.37	0.23	0.32	—	0.06	0.00	—	—
44			100	0.05	—	1.00	46.93	51.37	0.23	0.32	—	0.06	0.00	—	—
45	and magnesium sulfate	6-06-177	98	0.06	—	0.76	1.25	18.45	11.58	21.97	—	0.01	0.00	—	—
46			100	—	—	—	—	—	—	—	—	—	—	—	—
47	sulfate, K_2SO_4	6-08-098	98	0.15	—	0.09	1.50	43.04	0.60	17.64	—	0.07	0.00	—	—
48			100	—	—	—	—	—	—	—	—	—	—	—	—
	Sodium														
49	bicarbonate, $NaHCO_3$	6-04-272	100	0.01	—	27.00	—	0.01	—	—	—	—	—	—	—
50			100	0.01	—	27.00	—	0.01	—	—	—	—	—	—	—
51	carbonate	6-12-316	—	—	—	43.30	—	—	—	—	—	—	—	—	—
52			—	—	—	—	—	—	—	—	—	—	—	—	
53	chloride, NaCl	6-04-152	100	0.30	—	39.50	59.00	—	0.01	0.20	—	0.01	—	—	—
54			100	0.30	—	39.50	59.00	—	0.01	0.20	—	0.01	—	—	—
55	phosphate, dibasic, Na_2HPO_4	6-04-286	—	—	21.15	31.04	—	—	—	—	—	—	—	—	—
56			—	—	—	—	—	—	—	—	—	—	—	—	—
57	phosphate, monobasic	6-04-288	97	0.09	24.94	18.65	0.02	0.01	0.01	—	—	—	—	—	—
58			100	—	—	—	—	—	—	—	—	—	—	—	—
59	selenite, Na_2SeO_3	6-26-013	98	—	—	26.1	—	—	—	—	—	—	—	44.7	—
60			100	—	—	26.6	—	—	—	—	—	—	—	45.6	—
61	selenate, Na_2SeO_4		98	—	—	23.8	—	—	—	—	—	—	—	41.0	—
62			100	—	—	24.3	—	—	—	—	—	—	—	41.8	—
63	sulfate, decahydrate, $Na_2SO_4 \cdot 10H_2O$	6-04-291	—	—	—	13.80	—	—	—	9.70	—	—	—	—	—
64			—	—	—		—	—	—	—	—	—	—	—	—
	Zinc														
65	carbonate, $ZnCO_3$		99	—	—	—	—	—	—	—	—	—	—	—	51.63
66			100	—	—	—	—	—	—	—	—	—	—	—	52.15
67	oxide, ZnO		100	—	—	—	—	—	—	—	—	—	—	—	78.00
68			100	—	—	—	—	—	—	—	—	—	—	—	78.00
69	sulfate, monohydrate, $ZnSO_4 \cdot H_2O$		99	0.02	—	—	0.02	—	—	17.50	—	0.00	0.00	—	36.00
70			100	0.02	—	—	0.02	—	—	17.68	—	0.00	0.00	—	36.36
71	sulfate, heptahydrate, $ZnSO_4 \cdot 7H_2O$		98	—	—	—	—	—	—	10.93	—	—	—	—	22.25
72			100	—	—	—	—	—	—	11.15	—	—	—	—	22.70

NOTE: The mineral sources used as feed supplements are not chemically pure compounds, and the composition may vary substantially among sources. The supplier's analysis should be used if it is available. For example, feed-grade dicalcium phosphate contains some monocalcium phosphate and feed-grade monocalcium phosphate contains some dicalcium phosphate. Dashes indicate no available data.

[a] Estimates suggest 90 to 100% bioavailability of calcium in most sources of monocalcium phosphate, dicalcium phosphate, tricalcium phosphate, defluorinated phosphate, calcium carbonate, calcium sulfate, and calcitic limestone. The calcium in high-magnesium limestone or dolomitic limestone is less bioavailable (50-80%).

[b] Most calcitic limestones will contain 38% or more calcium and less magnesium than shown.

[c] Iron in defluorinated phosphate is about 65% as available as the iron in ferrous sulfate.

TABLE 12-6 Characteristics of Various Sources of Fats and Oils (data on as-fed basis)[a,b]

Entry Number	Description	International Feed Number[c]	Selected Fatty Acids (% of Total Fatty Acids)										Total sat.	Total unsat.	U:S[d] ratio	Iodine value	Total n-6	Total n-3
			<C10	C12:0	C14:0	C16:0	C16:1	C18:0	C18:1	C18:2	C18:3	>C20						
	Animal Fats																	
1	Beef Tallow	4-08-127	0.0	0.9	3.7	24.9	4.2	18.9	36.0	3.1	0.6	0.3	52.1	47.9	0.92	44	3.1	0.6
2	Choice White Grease	—	0.2	0.2	1.9	21.5	5.7	14.9	41.1	11.6	0.4	1.8	40.8	59.2	1.45	60	11.6	0.4
3	Lard	4-04-790	0.1	0.2	1.3	23.8	2.7	13.5	41.2	10.2	1.0	1.0	41.1	58.9	1.44	64	10.2	1.0
4	Poultry Fat	4-09-319	0.0	0.1	0.9	21.6	5.7	6.0	37.3	19.5	1.0	1.2	31.2	68.8	2.20	78	19.5	1.0
5	Restaurant Grease	—	—	—	1.9	16.2	2.5	10.5	47.5	17.5	1.9	1.0	29.9	70.1	2.34	75	17.5	1.9
	Fish Oils																	
6	Anchovy	—	—	—	7.4	17.4	10.5	4.0	11.6	1.2	0.8	30.3	34.6	65.4	1.89	—	1.3	31.2
7	Herring	7-08-048	—	0.2	7.1	11.7	9.6	0.8	11.9	1.1	0.8	45.6	22.8	77.2	3.39	—	1.4	17.8
8	Menhaden	7-08-049	—	—	8.0	15.1	10.5	3.8	14.5	2.1	1.5	29.5	33.3	66.7	2.00	—	1.5	25.1
	Vegetable Oils																	
9	Canola (Rapeseed)	4-06-144	0.0	0.0	0.0	4.0	0.2	1.8	56.1	20.3	9.3	3.6	7.4	92.6	12.46	118	20.3	9.3
10	Coconut	4-09-320	14.1	44.6	16.8	8.2	0.0	2.8	5.8	1.8	0.0	0.0	91.9	8.1	0.09	10	1.8	0.0
11	Corn	4-07-882	0.0	0.0	0.0	10.9	0.0	1.8	24.2	59.0	0.7	0.0	13.3	86.7	6.53	125	58.0	0.7
12	Cottonseed	4-20-836	0.0	0.0	0.8	22.7	0.8	2.3	17.0	51.5	0.2	0.1	27.1	72.9	2.69	105	51.5	0.2
13	Olive	—	0.0	0.0	0.0	11.0	0.8	2.2	72.5	7.9	0.6	0.3	14.1	85.9	6.08	86	7.9	0.6
14	Palm	—	0.0	0.1	1.0	43.5	0.3	4.3	36.6	9.1	0.2	0.1	51.6	48.4	0.94	50	9.1	0.2
15	Peanut	4-03-658	0.0	0.0	0.1	9.5	0.1	2.2	44.8	32.0	0.0	6.4	17.8	82.2	4.63	92	32.0	0.0
16	Safflower	4-20-526	0.0	0.0	0.1	6.2	0.4	2.3	11.7	74.1	0.4	0.0	9.5	90.5	9.52	140	74.1	0.4
17	Sesame	—	0.0	0.0	0.0	8.9	0.2	4.8	39.3	41.3	0.3	0.2	14.8	85.2	5.73	110	41.3	0.3
18	Soybean	4-07-983	0.0	0.0	0.1	10.3	0.2	3.8	22.8	51.0	6.8	0.2	15.1	84.9	5.64	130	51.0	6.8
19	Sunflower	4-20-833	0.0	0.0	0.0	5.4	0.2	3.5	45.3	39.8	0.2	0.0	10.6	89.4	8.47	133	39.8	0.2

[a] Dash indicates that no data were available.

[b] The fatty acid data were obtained from Pearl (1995) of the Fats and Protein Research Foundation and USDA Food Composition Standard Release 14 (2001). Values for fatty acid content do not always total 100% but represent means as obtained from various fat analysis conducted by gas-liquid chromatography.

[c] First digit is class of feed: 1, dry forages and roughages; 2, pasture, range plants, and forages fed green; 3, silages; 4, energy feeds; 5, protein supplements; 6, minerals; 7, vitamins; 8, additives; the other five digits are the International Feed Number.

[d] Unsaturated: saturated fatty acid ratio.

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13 Food as a Component of Environmental Enhancement

Those who conduct research with nonhuman primates or exhibit and view them are increasingly concerned about the psychological well-being of the animals. Psychological well-being is not easily defined and has been interpreted in various ways by those who view, use, display, or regulate nonhuman primates. US Public Law 89-544 (as amended in 1970, 1976, and 1985) specifies that all research facilities in the United States that maintain nonhuman primates must develop a plan for environmental enhancement adequate to promote the psychological well-being of captive animals. The plan must address social needs and provide for group housing of compatible animals when possible. In 1991, the Animal and Plant Health Inspection Service (APHIS) of the US Department of Agriculture (USDA) adopted Title 9 of the *Code of Federal Regulations (CFR)*, Part 3, Subpart D, "Specifications for the Humane Handling, Care, Treatment, and Transportation of Nonhuman Primates." The subject of Section 3.81 is, "Environment enhancement to promote psychological well-being of nonhuman primates." Because of concern about the lack of clarity and specificity in the regulations and a perceived lack of enforceability, an APHIS Animal Care Primate Environment Enhancement Team developed a final report on this subject that served as the basis of the USDA APHIS draft policy published in the *Federal Register* on July 15, 1999 (APHIS, 1999). The 79-page final report includes background on the intent and language of the Animal Welfare Act, the response of the public and the research and exhibit communities, a review of primate-care practices in other countries, and a discussion of the difficulties inherent in measuring psychological well-being. The report also contains a literature review dealing with behaviors of primate species in their natural environments and responses of captive primates to various environmental enhancements. The Institute for Laboratory Animal Research of the National Research Council has published a comprehensive document, *The Psychological Well-Being of Nonhuman Primates* (National Research Council, 1998).

GOAL OF ENVIRONMENTAL ENHANCEMENT

The consensus of the literature is that "species-typical" or "species-appropriate" behavior should be the goal of environmental-enhancement programs, as should a full range of normal behavior. It is clear that normal behavior depends on the species. APHIS policy states that to adequately promote psychological well-being, consideration should be given to species-specific requirements for social grouping, social needs of infants, environmental structures and substrate, foraging opportunities, and manipulanda. These issues are too complex for full discussion here, and the reader is referred to the APHIS final report (APHIS, 1999).

ROLE OF FOOD AND FORAGING

Food and foraging for food are clearly involved in the psychological well-being of captive nonhuman primates. It has been shown that food and nonfood items can be used in ways that stimulate natural feeding behaviors, extend feeding activity, and inhibit stereotypy (Fajzi et al., 1989; Knapka et al., 1995). Foraging enrichment can be used to disperse animals, occupy their time, and reduce tension and aggressive interactions (Boccia, 1989). Social aggression in chimpanzees has been reduced by behavior modification with food (Bloomsmith et al., 1994), but it is clear that methods of food distribution that are appropriate for one species might be inappropriate for another. As opposed to floor- or ground-based feeding by terrestrial species, vertical clinging is a normal feeding posture for many arboreal primates, such as nocturnal prosimians, tarsiers, and callitrichids (Fleagle, 1998). Tail length and tail-suspension postures during feeding also influence enclosure design and food placement (Poole, 1991; Reinhardt et al., 1996).

Enclosure size can interact with nutrient and energy needs and influence diet composition. Enclosures that are

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too small can restrict growth and movement enough to produce noticeable muscle atrophy (Faucheaux et al., 1978). That effect can be a reflection both of limited exercise and an associated lower energy need, which lead to lower food consumption and inadequate protein intake by young primates from low-protein, high-energy diets.

Substrates used on enclosure floors are manipulable items, can provide comfort, and can be part of foraging enrichment (Westergaard and Munkenbeck-Fragaszy, 1985; Bayne et al., 1992; Byrne and Suomi, 1995). Straw, hay, wood-wool, shredded paper, wood chips, blankets, corncobs, and soil have been used. Species or individual animals can show preferences for and more effective use of some substrates than others (Ludes and Anderson, 1996). It is, however, important that gastrointestinal disorders caused by ingestion of substrate or of pathogens in substrate be minimized by care in selecting, storing, and manipulating these materials (Baer, 1998).

Wild Environment versus Captivity

In the wild, primate diets are diverse and include leaves, stems, flowers, fruits, seeds, gums, insects, spiders, lizards, eggs, and other animal matter. The items selected vary with the species, and the proportions selected can vary from month to month without a clear association of the selections with seasonality of the habitat (Chapman and Chapman, 1990). Precisely gathered information on natural dietary habits is scarce, and field studies that include quantitative nutrient-intake data are exceedingly rare. Data gathered at different sites over time to account for location and seasonal differences and in which food use has been quantified and food composition determined can provide guidance for the development of rational captive dietary systems.

To succeed in the wild, primates must learn by example to select foods that, in toto, provide nutrient requirements and that are not toxic. Acquisition of nutrient needs requires that wild primates spend 25–90% of their waking hours in foraging for and consuming food (Clutton-Brock and Harvey, 1977).

In contrast, conventionally fed primates in captivity can fulfill their nutrient and energy needs in just a few minutes. Thus, successful enrichment programs involving food are usually designed to extend foraging time by requiring primates to "work" for food and to spend more time in food processing. Nutritionally complete extrusions can be placed in covered plastic buckets and suspended by ropes from structures in primate enclosures. Primates can jump onto the buckets or slide down the ropes and reach through holes in the buckets to acquire food. Buckets with smaller holes allow access by small primates while ensuring that larger, dominant animals will not take more than their share. In this instance, environmental enhancement is accomplished through the means of providing the standard diet rather than through addition of treats that might be nutritionally incomplete.

Novel foods are often presented in the form of treats, although predictable presentations of treats are soon no longer novel. Treat feeding, in which the treat is handed to the primate, can foster trust and bonding with the caretaker and provide short-term sensory stimulation, but it differs greatly from natural foraging in occuping so little time (Fajzi et al., 1989). Furthermore, evidence of nutritional wisdom among nonhuman primates is not convincing. It is obvious that free-living primates have successfully evolved with their wild food supply and have learned which foods to choose and which to avoid. But there is ample evidence that captive primates given a selection of cultivated foods or treats of various nutrient densities do not consistently choose a complete diet (Ullrey, 1989; Oftedal and Allen, 1996). It also should be noted that the botanic classification of wild foods into categories, such as fruit, has commonly led to the misuse of cultivated fruits (for example, bananas, oranges, and apples) as though they were comparable with their wild equivalents in nutrient composition, color, texture, and proportions of inedible husks or shells. In fact, wild plants and their various parts are quite different from the cultivated plants used for human food (Edwards et al., 1990a, 1990b; Oftedal and Allen, 1996). In particular, wild foods tend to be higher in fiber, and that fiber is often of low digestibility. Nutrient bioavailability also varies with source (Ammerman et al., 1995) and can be different between wild foods and cultivated foods.

Nearly all captive primate species should be provided a nutritionally balanced dry food as the predominant item in their daily ration. If it is appropriately formulated, it will have a positive effect on oral health, and the addition of particular vegetables or fruits will not seriously distort nutrient balance until their proportion approaches 50% on a wet basis (Edwards, 1997). The main reasons for this are that such items as green beans, celery, carrots, and kale are all good sources of many nutrients and that they are also high in water (88–94%). Thus, even though they might make up a high proportion of dietary wet weight, they have a relatively small influence on the balance of nutrients supplied by pellets or extrusions that are typically 5–13% water.

However, if high-moisture vegetables or fruits are fed with a nutritionally balanced food that is high in moisture (canned or gel products) and the primates being fed are as small as marmosets and tamarins, it might be difficult for them to consume sufficient dry matter to meet nutrient and energy needs (Barnard et al., 1988).

If dry, very palatable foods that are nutritionally incomplete are offered, as is the case with many seeds and nuts (Ullrey et al., 1991), these preferred items might be con-

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sumed to the exclusion of nutritionally balanced foods, and nutrient distortion of the diet can be serious. The use of vitamin and mineral supplements is not a dependable way to correct these problems, because supplements might be inappropriately formulated for the purpose (not all supplements are alike), and they are often administered without measuring, so there are risks of overdosing or underdosing.

With respect to selecting foods to extend foraging time, novel colors, sizes, shapes, smells, and textures and the presence of shells or husks that require removal can be sensory stimulants (Schapiro et al., 1996; Noonan, 1998). If cognitive tasks are required to acquire food, the associated mental stimulation appears to be rewarding beyond the acquisition of calories (Reinhardt, 1997). Singly housed marmosets foraged for up to 6 h when food was mixed with sawdust (Scott, 1991). Juvenile patas monkeys have been reported to leap several feet in the air to reach fruit stuck on branches in a zoo, even when adequate amounts of fruit were available on the ground (McGovern, 1994). A comparative study found that cynomolgus monkeys preferred foraging activities more than other enrichment methods (Bryant et al., 1988). When various foraging enrichment devices were presented to squirrel monkeys, the devices that increased foraging times and that were manipulated the most were a capped polyvinyl chloride (PVC) pipe with food-dispenser holes and food dispensers made from 2-L plastic beverage containers (Boinski et al., 1994). Provision of a PVC feeding device and more frequent feeding reduced abnormal behaviors in singly housed baboons (Brent and Long, 1995). Puzzle feeders requiring manipulation to acquire treats were more effective than treats alone in reducing locomotor stereotypies in singly housed rhesus macaques. However, the effects lasted only as long as the manipulation time (about 1 h) that was required to acquire the treats. If puzzle difficulty was increased, the monkeys tended to give up (Novak et al., 1998). Thus, it might be important to distinguish between provision of treats with little or no foraging activity and promotion of foraging activity for acquisition of principal food sources.

Species Differences

Different species use different foraging techniques, and promotion of foraging activity in captivity should consider species differences. Are the primates principally frugivores, folivores, insectivores, gummivores, or omnivores? Are they principally terrestrial or arboreal foragers? Are they manually dextrous? Do they use their hands or tools? What is their relative cognitive ability? Those factors are all relevant in determining which foraging enhancements may be most effective.

Specialized foraging adaptations and food preferences of several species have been described. Ring-tailed lemurs have been reported to prefer fresh new leaves in the wild, whereas brown lemurs preferred mature leaves. Lemurs processed fruit very little and licked the open end of bananas rather than peel them (Jolly, 1985). Golden-lion tamarins forage for insects by manipulation; they sift through substrate, search for insect holes, remove bark, and break open wood in their quest for food. But cotton-top tamarins feed opportunistically on insects that they encounter as they move through dense tangles of branches and vines (Steen, 1995). Lorises are able to capture only slow-moving and often relatively unpalatable prey, whereas galagos capture more rapid and more palatable prey (Charles-Dominique, 1977). In captivity, patas monkeys preferred browse from poplar trees (*Populus* spp.) but used it more for bark-chewing than leaf-eating; for effective use, it was necessary to mount the browse in a metal sleeve to hold it in a natural, upright position (McGovern, 1994). Surfaces of novel devices containing food are inspected by sniffing, touching, and licking by captive squirrel monkeys but are more likely to be persistently manipulated by capuchins (Fragaszy and Adams-Curtis, 1991). Great apes, baboons, macaques, and capuchins explore the properties of objects and appear to have the cognitive ability to relate them to each other. These skills are basic to tool use, something that wild chimpanzees practice regularly in nut-cracking and in foraging for termites and ants. Although other apes and the monkey species mentioned above rarely use tools in the wild, they adapt readily to use of tools when they are provided in captivity (Tomasello and Call, 1997).

Manipulation of Foraging Opportunities

Food can be used to enrich a captive environment by manipulating foraging opportunities in time and space. If outdoor exhibit or holding areas are available, food can be placed on the ground or in trees, as it might be found in a wild environment. Foraging time also can be extended in inside areas by scattering food in a substrate, such as leaf litter, straw, hay, wood shavings, or shredded paper. Hidden foods can include the primary nutrient source, usually an extrusion, and low-density items, such as popcorn and some dry breakfast cereals. Whole fruits and vegetables that require husking or peeling before eating can also be useful. Time spent in feeding was increased when lion-tailed macaques were presented whole versus chopped foods (Lindburg and Smith, 1988). Stereotypies in singly caged baboons were reduced by offering corn on the cob (Bennett and Spector, 1989).

It is particularly important to place food in multiple locations in group enclosures so that aggression and food monopolization are minimized. Studies with Diana monkeys (*Cercopithecus diana*), Allen's swamp monkeys (*Cercopithecus nigroviridis*), lion-tailed macaques (*Macaca silenus*), and Hamlyn's monkeys (*Cercopithecus hamlyni*) in

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group enclosures found that food acquisition was equitable and foraging time greatest when cut-up apples and oranges were scattered in straw on the wire of enclosure roofs (Buchanan-Smith, 1995). Roof feeding promotes a variety of locomotor postures, muscle use, and physical fitness (Britt, 1993).

Environmental enhancement is particularly difficult, but still possible, with individually caged primates (NIH, 1991; Dean, 1999). Replacement of a standard hopper feeder with a foraging device that required manipulative and cognitive skills reduced self-directed behaviors in cynomolgus macaques. Periodic introduction of novel foods maintained interest in the device (Holmes et al., 1995). Moving extrusion feeders out of the cages of individually housed rhesus macaques and reattaching them to the outside of a 22 x 22-mm mesh cage front increased feeding time from 0.2 min to 18.3 min (Reinhardt, 1993). Placing extrusions on top of a chain-link ceiling enclosure also extended foraging time (Reinhardt, 1997). However, total foraging time was a small proportion of the day.

Raisins and seeds have been stuck in Astroturf® attached to hanging logs (Bollen, 1995). Acrylic food puzzles and various other devices that require manipulation with tools to acquire food have been attached to the outside of enclosures (Schapiro et al., 1991). Foraging devices hung from the ceiling are unpredictable in movement and stimulating when two primates attempt to use them simultaneously (Buchanan-Smith, 1997), and a free-spinning feeder log hung on a wire out of easy reach was particularly challenging to spot-nosed guenons and white-faced capuchins (Dorian, 1993). Pine cones stuffed with peanut butter and raisins, frozen juice cubes, frozen fruits and vegetables, and fruits and vegetables speared and hung on bamboo canes have been used for environmental enrichment with some success. Foraging devices are not all effective in a given situation (Lutz and Farrow, 1996), and different species, ages, and individuals may prefer different types (Watson, 1997).

Live Prey

Live prey can promote foraging activity, and some invertebrates can be important sources of nutrients for obligate insectivores. Beetles, caterpillars, moths, grasshoppers, locusts, ants, crickets, mealworms, wax moth larvae, butterflies, centipedes, millipedes, spiders, slugs, snails, lizards, mice, rats, and frogs have been offered. Mealworm feeders have been devised to reduce stereotyped behavior in common marmosets (Vignes et al., 2001). Goldfish in fishing pools have been used to stimulate foraging in squirrel monkeys (King and Norwood, 1989).

Because of limited commercial availability of most invertebrates, crickets from commercial suppliers have been used most often. Calcium concentrations in these insects (and many others, including mealworms and wax-moth larvae) are very low and not dependably corrected by dusting with calcium supplements. Variable amounts of the calcium dust are lost as the crickets move about or clean their body surfaces. A special high-calcium insect diet should be fed to crickets, mealworms, or wax-moth larvae for about 1–2 d before they are offered as food. Consumption of this high-calcium diet by these insects leaves a high-calcium gut residue that makes the whole insect a more nutritionally complete meal for the consuming vertebrate (Strzelewicz et al., 1985; Allen and Oftedal, 1989; Roberts and Kohn, 1993).

When insects were scattered among wood chips on the floor of their enclosure, cotton-top tamarins that are insectivorous (Rowe, 1996), but mostly arboreal, were enticed to forage on the floor (McKenzie et al., 1986). Passive dispensers hung from enclosure ceilings or walls will also allow slow dispersal of live prey. Active dispensers can be made from PVC or bamboo with holes of a size appropriate to admit a finger, hand, or arm for search and retrieval of prey mixed in a substrate, such as wheat bran. Such active dispensers also have been used with other foods (Banchero, 1995; Demlong, 1993; Glick-Bauer, 1997; Steen, 1995; Wassel and Race, 1994).

Consumption of live prey is not without risk. Laboratory mouse pups that have been proposed as food for prey-eating primates have been identified as a reservoir of a lymphocytic choriomeningitis virus that causes hepatitis in callitrichids (Montali and Bush, 1999); free-living cockroaches caught and eaten by callitrichids can be a source of pathogenic nematodes.

Exudates and Gums

Feeding on tree exudates or gums has been observed in 45 species of animals in the wild, including prosimians, marmosets, tamarins, and Old World monkeys (Kelly, 1993). Although gums do not appear to be obligatory ingredients in diets for these species, their use provides environmental enrichment and enhances the visitor viewing experience. Gum arabic (from *Acacia senegal*) is used in frozen desserts and in bakery, confectionery, and dairy products. As a consequence, it is commercially available, and gum mixtures can be presented in liquid dispensers or in holes drilled in trees, branches, or dowels (Brennan and Russel, 1986; LeBlanc, 1993).

Water

Water also can be used in environmental enrichment, particularly if presented in novel ways (Parks and Novak, 1993). Primates drink it directly from a water source, from their cupped hands, or by squeezing it into their mouths from water-soaked leaves, as from a sponge. Japanese

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macaques submerge potatoes and grains in water to remove dirt (Itani and Nishimura, 1973), and several macaque species dive and swim to retrieve food (Malik and Southwick, 1988; Suzuki, 1965).

Higher-Fiber Foods

Leafy vegetables, browse, and higher-fiber commercial extrusions have been used to provide environmental enhancement and may be important for physiologic reasons in highly folivorous species, such as howlers and the Colobinae. Lemurs and great apes also can benefit from appropriate sources and amounts of high-fiber foods (Gould and Bres, 1986; Edwards, 1995; Popovich et al., 1997). These foods tend to increase the time spent in feeding, can reduce aberrant behavior, favor the production of formed rather than liquid stools, and are useful in the control of obesity. The National Zoological Park in Washington, DC, has a list of East Coast browse species that were judged to be safe for primate feeding. They include alder, amaranths, arborvitae, aspen, bamboo, beech, birch, blackberry, bush honeysuckle, butterfly bush, cattails, chicory, clover, comfrey, cottoneaster, cottonwood, daylily, dogwood, elaeagnus, elm, fig, forsythia, grasses, greenbriers, hackberry, hawthorn, hazelnut, hibiscus, Japanese silver grass, kerria, kudzu, linden, maple (except red maple), mock orange, mulberry, nasturtium, Oregon grape holly, pear, pickerelweed, poplar (except tulip poplar), purslane, raspberry, redbud, rose, snowberry, violets, water hyacinth, and willow (Gross, 1990; Shumaker, 1995; McClung, 1999). Browse species that have been listed in peer-reviewed publications may be found in Chapter 10.

Studies at the Duke University Primate Center demonstrated that several local plants could be substituted for mango leaves in captive sifaka diets. Plant-species preferences were exhibited by both lemurs and sifakas, and there were seasonal preferences for particular plant parts (Pereira et al., 1989). Because some browses contain toxic chemicals or have a tendency to form indigestible phytobezoars, they must be selected and used with care (Ensley et al., 1982; Fowler, 1986; Knapka et al., 1995).

EPILOGUE

Nothing is more basic to the health and well-being of captive nonhuman primates than proper nutrition and dietary husbandry. Deficiencies or excesses of specific nutrients have been shown to produce specific signs of illness that reflect their metabolic roles (National Research Council, 1978; Machlin, 1990; Knapka et al., 1995; O'Dell and Sunde, 1997). Furthermore, there is a well-established relationship between nutritional status and susceptibility to infectious disease (Ullrey, 1993). Thus, the provision of a nutritionally balanced diet in amounts sufficient to meet daily energy and nutrient needs must not be subverted by well-intentioned but ill-advised uses of food in systems of environmental enhancement. A rational balance of the science of nutrition with knowledge of feeding behavior and of feeds appropriate to meet physiologic and psychological requirements is fundamental to the development of a successful feeding program. In turn, a successful feeding program is a vital part of animal well-being. The subject is very complex, and human perceptions of nonhuman-primate behaviors in response to changes in their environment might not be reliable guides to the perceptions of the nonhuman primates in question (Robinson, 1998). Attempts to resolve this complexity by using food in environmental enhancement must always consider physiologic, as well as psychological needs.

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Appendix

TABLE A-1 Taxonomic Relationships, Genera, and Partial List of Species in Order Primates, Based on Napier and Napier (1985), Oates et al. (1989), and Nowak (1999)[a]

Suborder Strepsirrhini		
Family Daubentoniidae		
	Daubentonia madagascariensis	Aye-aye
Family Cheirogaleidae		
	Allocebus trichotis	Hairy-eared dwarf lemur
	Cheirogaleus spp.	Dwarf lemurs
	Mirza coquereli	Coquerel's dwarf lemur
	Phaner furcifer	Fork-marked dwarf lemur
Family Indridae		
	Avahi laniger	Avahi or wooly lemur
	Indri indri	Indri
	Propithecus spp.	Sifakas
Family Lemuridae		
	Eulemur coronatus	Crowned lemur
	Eulemur fulvus	Brown lemur
	Eulemur macaco	Black lemur
	Eulemur mongoz	Mongoose lemur
	Eulemur rubriventer	Red-bellied lemur
	Hapalemur spp.	Gentle lemurs
	Lemur catta	Ring-tailed lemur
	Varecia variegata	Ruffed lemur
Family Megaladapidae		
	Lepilemur spp.	Sportive lemurs
Family Loridae		
Subfamily Lorinae		
	Arctocebus calabarensis	Angwantibo
	Loris tardigradus	Slender loris
	Nycticebus coucang	Slow loris
	Nycticebus pygmaeus	Pygmy slow loris
	Perodicticus potto	Potto
Family Galagonidae		
	Euoticus spp.	Needle-clawed bushbabies
	Galago spp.	Galagos, bushbabies
	Galagoides spp.	Dwarf galagos
	Otolemur spp.	Greater bushbabies

(continues)

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TABLE A-1 *(continued)*

Suborder Haplorrhini		
Family Tarsiidae		
	Tarsius spp.	Tarsiers
Family Callitrichidae		
	Callimico goeldii	Callimico or Goeldi's monkey
	Callithrix spp.	Marmosets
	Cebuella pygmaea	Pygmy marmoset
	Leontopithecus spp.	Lion tamarins
	Saguinus spp.	Long-tailed tamarins
Family Cebidae		
Subfamily Alouattinae		
	Alouatta spp.	Howler monkeys
Subfamily Aotinae		
	Aotus spp.	Douroucoulis or night monkeys
Subfamily Atelinae		
	Ateles spp.	Spider monkeys
	Brachyteles arachnoides	Wooly spider monkey
	Lagothrix spp.	Wooly monkeys
Subfamily Callicebinae		
	Callicebus spp.	Titi monkeys
Subfamily Cebinae		
	Cebus spp.	Capuchins
Subfamily Saimirinae		
	Saimiri spp.	Squirrel monkeys
Subfamily Pitheciinae		
	Cacajao spp.	Uakaris
	Chiropotes spp.	Bearded sakis
	Pithecia spp.	Sakis
Family Cercopithecidae		
Subfamily Cercopithecinae		
	Allenopithecus nigroviridis	Allen's monkey
	Cercocebus spp.	Mangabeys
	Cercopithecus spp.	Guenons
	Chlorocebus spp.	Savannah guenons
	Erythrocebus patas	Patas monkey
	Lophocebus spp.	Black mangabeys
	Macaca spp.	Macaques
	Mandrillus spp.	Drill, mandrill
	Miopithecus talapoin	Talapoin
	Papio spp.	Baboons
	Theropithecus gelada	Gelada
Subfamily Colobinae		
	Colobus spp.	Black and white colobus monkeys
	Nasalis larvatus	Proboscis monkey
	Presbytis spp.	Langurs, leaf monkeys
	Piliocolobus spp.	Red colobus monkeys
	Procolobus verus	Olive colobus monkey
	Pygathrix nemaeus	Douc langur
	Rhinopithecus spp.	Snub-nosed langurs
	Semnopithecus entellus	Hanuman langur
	Simias concolor	Pig-tailed langur
	Trachypithecus spp.	Brow-ridged langurs
Family Hylobatidae		
	Hylobates spp.	Gibbons, siamang
Family Pongidae		
	Gorilla gorilla	Gorilla
	Pan spp.	Chimpanzee, bonobo
	Pongo pygmaeus	Orangutan
Family Hominidae		
	Homo sapiens	Humans

[a] Groves (2001) has recently proposed revisions in primate taxonomy.

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TABLE A-2 Weight Equivalents

1 lb = 453.6 g = 0.4356 kg = 16 oz

1 oz = 28.35 g

1 kg = 1,000 g = 2.2046 lb

1 g = 1,000 mg

1 mg = 1,000 μg = 0.001 g

1 μg = 0.001 mg = 0.000001 g

1 $\mu g \cdot g^{-1}$ = 1 $mg \cdot kg^{-1}$ = 1 part per million (ppm)

TABLE A-3 Weight-unit Conversion Factors

Units given	Units wanted	For conversion multiply by
Lb	g	453.6
Lb	kg	0.4536
Oz	g	28.35
Kg	lb	2.2046
Kg	mg	1,000,000.0
Kg	g	1,000.0
G	mg	1,000.0
G	μg	1,000,000.0
Mg	μg	1,000.0
$Mg \cdot g^{-1}$	$mg \cdot lb^{-1}$	453.6
$Mg \cdot kg^{-1}$	$mg \cdot lb^{-1}$	0.4536
$\mu g \cdot kg^{-1}$	$\mu g \cdot lb^{-1}$	0.4536
Mcal	kcal	1,000.0
Kcal	kJ	4.184
KJ	kcal	0.239
$Kcal \cdot kg^{-1}$	$kcal \cdot lb^{-1}$	0.4536
$Kcal \cdot lb^{-1}$	$kcal \cdot kg^{-1}$	2.2046
Ppm	$\mu g \cdot g^{-1}$	1.0
Ppm	$mg \cdot kg^{-1}$	1.0
Ppm	$mg \cdot lb^{-1}$	0.4536
$Mg \cdot kg^{-1}$	%	0.0001
Ppm	%	0.0001
$Mg \cdot g^{-1}$	%	0.1
$g \cdot kg^{-1}$	%	0.1

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Nancy L. Conklin-Brittain, PhD, is a research associate at Harvard University and is working on a large chimpanzee and monkey dietary-comparison field project in Africa. She has consulted internationally for the Organization for Tropical Studies, the Food and Agriculture Organization of the United Nations, the US Agency for International Development, and other groups. Dr. Conklin-Brittain has evaluated the chemistry of dietary differences between monkeys and apes by analyzing the composition of natural foods selected by these animals in Kibale Forest, Uganda. In addition to teaching responsibilities, she studies primate plant-food samples from Costa Rica, Venezuela, and Indo-

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Index

A

Absorption
  carbohydrates, 60
  fats, 2, 90–91
  minerals, 97, 98–99, 101, 102, 104, 107, 191
  vitamins, 114, 123, 124, 134, 137
Acid-detergent fiber (ADF), 26, 27, 62, 63, 64–66, 68, 192, 193
  composition of food/feed ingredients, table, 197–212
  protein requirements, 75
Age factors, 1, 2, 159, 162–163, 167–171, 174
  see also Growth and development; Infants
  amino acid metabolism, 79
  body composition and weight, 168–170, 172–173, 174, 175
  bone, 95, 167, 168–169, 170
  energy requirements, 43, 44, 47, 48, 49, 50–53, 167, 168, 169
  fats, 87, 169, 171–172
  fiber, 68
  immune system, 170
  menopause, 167, 170
  minerals, 94, 98, 99, 100, 102, 167–169
  obesity, 172–173, 174, 175
  protein requirements, 77, 78, 80–83
  sex differences, 167, 168, 170
  vitamins, 125, 127, 133, 139, 167–168
  water, 150, 151, 153, 155
Aggressive behavior, 79, 116, 259, 261–262
Aging, 44, 167–171
Albumin, 75, 76, 77, 79–80, 81, 83, 100, 132, 153
  lactalbumin, 75, 76, 77, 79–80
Alopecia
  minerals, 101, 103, 105
  protein, 80, 82
  vitamins, 130, 131, 132, 134, 135
Amino acids, 2, 20–21, 75, 77, 78–79, 80, 82–83
  see also Proteins
  composition of food/feed ingredients, table, 242–255
  cysteine, 77, 98, 104, 105, 135
  cystine, 98, 134, 242–255
  dry matter, 83, 242–255
  lysine, 2, 78–79, 242–255
  methionine, 2, 77, 78–79, 98, 105, 135, 141, 242–255
  phenylalanine, 2, 79, 242–255
  selenium, 94, 104–106, 192, 193, 213–227, 256–257
  sulfur, 77
  taurine, 2, 79, 98, 166, 192, 242–255
  threonine, 78, 242–255
  tryptophan, 2, 79, 131, 132, 242–255
  valine, 137, 186, 242–255
  vitamins and, 124, 131
Anatomy, *vii*, 1, 2, 5, 20–26, 182
Anemia, 80, 81, 82–84, 99–100, 101, 124–125, 126, 129, 130, 134, 135, 136, 138
Animal and Plant Health Inspection Service, 259
Animal prey, *see* Carnivores; Insects
Arboreal species, general
  environmental enhancement, 259, 261
  feeding ecology, 6–18 (passim)
  water, 153
Arginine, composition of food/feed ingredients, table, 242–255
Arthritis, 96, 167, 170, 176
Ash, 64, 66, 94, 150–151, 171
  composition of food/feed ingredients, table, 197–212
Atherosclerosis, 66, 92, 132, 167, 171, 173–174

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B

Bamboo, 10, 187, 197, 213
Bark, 101, 188, 261
Bioavailability, 182, 188, 191
  amino acids, 78
  minerals, 97, 99–105 (passim), 107
  vitamins, 123, 124, 128–136 (passim)
Biotin, 133–134, 191, 192, 193
  composition of food/feed ingredients, table, 228–241
Blood, *see* Hematologic factors
Body composition and weight, 2, 92, 159–164, 171–176
  see also Growth and development
  age factors, 168–170, 172–173, 174, 175
  energy requirements, 43–49, 50–52
  feeding ecology, 6–13
  fiber, 66
  malnutrition, 2, 80–83, 91–96
  minerals, 106
  obesity, 2, 66, 151, 159, 172–176, 185
    age factors, 172–173, 174, 175
  proteins, 76, 77, 79, 80–81, 83, 102, 155
  sex differences, 159, 162–163, 171
  vitamins, 115, 119, 124, 127–141 (passim)
  water, 150–155 (passim)
Bone and bone marrow, 172
  aging, 95, 167, 168–169, 170
  arthritis, 96, 167, 170, 176
  fats, 90, 91
  minerals, 94, 95, 96, 97, 107, 127–128
    osteoporosis, 95, 167
  vitamins, 117, 118, 119, 121, 125, 127–128, 134, 137–138
  water, joint lubrication, 150
Brain
  carbohydrates, 58
  diabetes, 175–176
  fats, 89, 90
  protein, 79, 84
  vitamins, 113
  water, 152
Browse, general, 96, 186, 187, 261, 262

C

Cadmium, 94–95
Calcium, 27, 83, 94, 95–97, 98, 99, 104, 107, 192, 193
  aging, 170
  composition of food/feed ingredients, table, 213–227, 256–257
  vitamins and, 116, 117, 119, 121–122, 128, 131, 138
Caloric measures, 41, 43, 47, 50–54 (passim), 166, 171, 185, 192
  aging, 168
  fats, 89
  protein, 77, 80, 81–83
  restriction, 80, 171
Cancer, 83, 183
Canned foods, 3, 83, 184
Carbohydrates, 2, 58–66, 82, 106, 184
  see also Starch
  absorption, 58
  brain, 58
  cellulose, 59–60, 61, 62, 65–66
    composition of food/feed ingredients, table, 197–212
    energy requirements, 41, 42, 59–60
  digestion, 58, 59, 60
  energy requirements, 41, 42, 52, 58
  fermentation, 58, 59
  fruit, 58, 60, 62
  intestines, 58, 59
  pectin, 60, 62
  water, 154
Cardiovascular diseases, 2, 84, 91, 92, 98, 173
  see also Hematologic factors
  atherosclerosis, 66, 92, 132, 167, 171, 173–174
  fats, 91, 173
  minerals, 97, 99
  vitamins, 128–129, 132
  water, 151, 152
Carnitine, 141
Carnivores, general
  see also Fish; Insects
  digestion, 21
  environmental enhancement, 261, 262
  feeding ecology, 6–18 (passim)
  protein, 85
Carotenoids, *see* Vitamin A
Casein, 75, 76, 77, 80, 82, 83, 99, 136, 191
Cecum, 21, 24
Cellular biology
  see also Immune system
  aging, 170
  cholesterol, 91
  diabetes, 176
  fats, 88–89, 91, 174
  minerals, 94, 95, 97, 99, 102, 106
  proteins, 82
  vitamins, 111, 124, 131–132, 140–141
  water, 150, 151–152, 156
Cellulose, 59–60, 61, 62, 65–66
  composition of food/feed ingredients, table, 197–212
  energy requirements, 41, 42, 59–60
Chlorine, 94, 99, 192, 193
  composition of food/feed ingredients, table, 213–227, 256–257
Choline, 128, 130, 140, 141, 194
  composition of food/feed ingredients, table, 228–241

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Cholesterol, 88, 91–92, 101, 173
fiber, 66
infants, 166
metabolism, 2, 91, 123, 125
protein and, 83, 85
vitamins and, 123, 125, 126, 141
Choline, 140–141, 193
Chromium, 94, 99, 106–107, 192, 193
Cobalt, 2, 94, 106, 135–137
Cold, effects of, *see* Temperature and thermoregulation factors
Colon, 21, 24
Computer applications, 182
Internet, *vii*, 156
Copper, 2, 99, 100–101, 131, 191, 193
composition of food/feed ingredients, table, 213–227, 256–257
Corn, 50, 61, 77, 79, 90, 192, 258
Cost factors, 183
Cysteine, 77, 99, 104, 105, 135
Cystine, 99, 134
composition of food/feed ingredients, table, 242–255

D

Dental factors, *see* Oral cavity
Dermatitis, 79, 81, 103, 105, 130, 134
Detergent fiber, *see* Acid-detergent fiber; Neutral-detergent fiber
Dextrins, 59
Diabetes, 2, 151, 153, 167, 168, 169, 173–176
Diarrhea, 79, 81, 82, 103, 115, 130, 131, 132, 134, 135, 154, 188
Diet, 5–12, 14–21, 24, 26–27, 172–175, 185, 187–188, 260–263
carbohydrates, 58
energy, 42–48, 50–52
fat, 87, 89–92
fiber, 65–68, 70
formulation, 182
growth, 159, 164–167
minerals, 95–107
nutrient, 191–192
processing, 183
protein, 75–77, 78–84
restriction, 167–171
supplements, 186
vitamins, 113–116, 118–122, 124–128, 130–141
water, 153–155
Digestion, 2, 20–26, 129, 182, 186
see also Feces; Fermentation; Foregut; Hindgut; Intestines; Metabolic processes; Stomach
carbohydrates, 58, 59, 60
fiber, 61, 62, 66, 70
energy requirements, 41–42
environmental enhancement, 260
fats, 88
leaves, 24–26
minerals, 97
protein requirements, 75–77
starch, 62
time factors, 21, 24, 26, 41
water, 150
Disaccharides, 58–59
Diseases and disorders, *vii*, 2, 80–81, 91, 92, 167, 188
see also Cardiovascular disease; Immune system; Obesity; Toxicity
aging and, 167–171
alopecia, 80, 82, 101, 103, 105, 130, 131, 132, 134, 135
anemia, 80, 81, 82–83, 99–100, 101, 124–125, 126, 129, 138, 134, 135, 136, 138
arthritis, 96, 167, 170, 176
atherosclerosis, 66, 92, 132, 167, 171, 173–174
cancer, 83, 183
cardiovascular, 2, 84, 91, 92, 99
atherosclerosis, 66, 92, 132, 167, 171, 173–174
diabetes, 2, 151, 153, 167, 168, 169, 173–176
diarrhea, 79, 81, 82, 103, 115, 130, 131, 132, 134, 135, 154, 188
edema, 79, 80, 81, 82
fats and, 90–91; *see* Obesity
infant feeding, 166–167
infections, 81, 115, 135, 170
influenza, 170
malnutrition, 2, 80–83, 91–96
mineral deficiencies, 95, 96, 99–100, 101, 103–105, 107
mineral toxicity, 94–95, 97–98, 105–106, 107, 121–122, 155
phenylketonuria, 79
protein deficiencies, 75, 79, 80–84
vitamins,
deficiencies, 90–91, 115, 117–118, 119–120, 124–141 (passim)
hypervitaminosis, 2, 115–116, 121–122
water deficiencies, 151–152, 153, 154, 155
water pollution and, 155–156
wounds, 170–171
Diurnal species, general, feeding ecology, 6–20 (passim)
Dry matter, 3, 18, 49, 51, 83, 187, 188, 260–261
amino acids, 83, 242–255
carbohydrates, 58
composition of food/feed ingredients, tables, 197–257
extrusion, 60, 69, 96, 172, 182, 184, 185, 186, 260, 262, 263
minerals, 94, 95, 96, 97–98, 101, 102, 103, 104, 107

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composition of food/feed ingredients, table, 213–227, 256–257
pellets, 83, 121, 138, 167, 168, 183, 184, 185, 186
vitamins, 115, 118, 121, 126, 127, 128, 129, 131, 134, 135, 136, 139
composition of food/feed ingredients, tables, 228–241
Duodenum, 117

E

Ecology, *see* Environmental enhancement; Feeding ecology
Edema, 79, 80, 81, 82
Eggs
albumin, 75, 76, 77, 79–80, 81, 82, 101, 132, 153
protein requirements, 75, 76, 83
vitamins, 134
Endangered species, *vii*, 1
Energy, 1, 41–57, 186, 195
see also Caloric measures
age factors, 43, 44, 47, 48, 49, 50–53, 167, 168, 169
growth, 42, 48, 50, 52–54
body composition and weight, 43–49, 50–52
carbohydrates, 41, 42, 52, 58
cellulose, 41, 42, 59–60
composition of food/feed ingredients, tables, 197–241
digestion, 41–42
environmental enhancement, 259–260, 263
fats, 42, 43–44, 50, 52, 88–89, 91
feces, 41, 44
fiber, 41–42
infants, 43, 48, 50–51, 52–53
lactation, 41, 44, 51–52, 53–55
metabolic processes, 41, 42–43, 45–47, 49, 50, 58, 165–166, 169
milk, 42, 51–54
minerals, 95
obesity, 174, 185
pregnancy, 53
protein, 42, 50, 76, 77, 81
reproductive system, 41, 44, 48, 53
sex differences, other, 44, 47, 48, 49, 51, 52
thermoregulation, 41, 43, 44, 47, 50
water, 154
Environmental enhancement, 3, 186, 259–265
aggressive behavior, 79, 116, 259, 261–262
Environmental Protection Agency, 156
Enzymes
amino acids, 79
carbohydrates, 59, 60
digestion, general, 22, 26, 41
energy requirements, 41
fiber, 62
minerals, 94, 97, 98, 100, 101–102
vitamins, 124, 128, 129, 130, 132, 134, 135, 137
water, thermoregulation, 150
Ethical issues, 77
Excretion, *see also* Diarrhea; Feces; Urine
Exercise, *see* Physical activity
Extrusion, 60, 69, 96, 172, 182, 184, 185, 186, 260, 262, 263
Eyes
amino acids, 79
fats, 90
feeding, visual clues, 184, 185, 260, 261
minerals, 107
vitamins, 113, 116, 125, 130, 136
water, 150

F

Fats and oils, 2, 58, 87–93, 171–173, 176, 192, 193
see also Obesity
absorption, 2, 88–89
age factors, 87, 169, 171–172
growth and development, 87, 89, 90, 172
bone and, 90, 91
brain, 89, 90
cardiovascular disease, 91, 173
cellular biology, 88–89, 91, 172
composition of food/feed ingredients, tables, 197–241, 258
digestion, 2, 88
energy requirements, 42, 43–44, 50, 52, 88–89, 91
fiber and, 66
fish, 89, 258
hepatic system, 90, 141
infants, 89–90, 91
metabolic processes, 2, 88–89, 91, 97, 129, 141, 154
obesity, 2, 151, 167, 172–176, 185
age factors, 172–173, 174, 175
oilseeds, 91, 102, 107, 192, 258
protein and, 83
supplements, 90–91
vitamins and, 2, 123, 124, 125, 141
fat-soluble, 88, 89, 90–91, 113–128, 228–241
water, 150, 151, 153, 155
Feces, 262
see also Diarrhea
energy requirements, 41, 43
fats, 88
feeding ecology, 16, 19
minerals, 100
vitamins, 123, 136
water, 150, 154–155
Feeding ecology, *vii*, 2, 5–22, 184, 186–188
browse, 26, 96, 186, 187, 261, 262

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environmental enhancement, 3, 186, 259–265
feces, 16, 19
foraging, 2, 5, 6–13, 19, 53, 68, 184, 259–263
fruit, 6–20 (passim), 185
gums and exudates, 6, 9, 19, 20
insects, 6–13 (passim), 19, 20, 261
olfactory perception, 184, 185
seeds, 6–16 (passim), 19, 185
sex differences, 6–13 (passim)
tactile perception, 184, 185, 260, 261
taste, 103, 184, 185, 260–261
time factors, 5–13 (passim), 18, 19–20, 259, 260, 261–262
visual perception, 184, 185, 260, 261
water, 153–154
Feed processing, 183–184
canned foods, 3, 83, 184
composition of food/feed ingredients, tables, 195–258
extrusion, 60, 69, 96, 172, 182, 184, 185
foraging, 2, 53, 68, 184, 259–263
gelled foods, 3, 59, 60, 62, 83, 184
pellets, 83, 121, 138, 167, 168, 183, 184, 186
Females, *see* Lactation; Pregnancy; Sex differences
Fermentation, 22, 23, 26
carbohydrates, 58, 59
fiber, 61, 62, 68
energy requirements, 41–43
minerals, 98
protein, 78
water, 150–151
Fiber, 2, 20, 21, 26, 27, 61–64, 66–70, 191
acid-detergent fiber (ADF), 26, 27, 62, 63, 64–66, 68, 192, 193
composition of food/feed ingredients, table, 197–212
protein requirements, 75
carbohydrates, 60
composition of food/feed ingredients, table, 197–212
detergent fiber, 62, 63, 64–68
diet formulation, 183
digestion, 61, 62, 66, 70
energy requirements, 41–43
environmental enhancement, 263
fermentation, 61, 62, 68
lignin, 61, 62, 63, 64, 65–68, 75, 197–212
neutral-detergent fiber (NDF), 62–66, 67–70, 192, 193, 197–212
Fish
fats and oils, 89, 258
meal, 183
protein, 75, 82
vitamins, 129
water, 152
Flourine, 107
Flowers, 27, 187
feeding ecology, 6–19 (passim)
Folacin, 134–135, 136, 192, 228–241
Folivores
see also Leaves
digestion, 24–26
feeding ecology, 6–20 (passim), 261
fiber, 64, 65–66, 67
Foraging, 2, 5, 6–13, 19, 53, 68, 184, 259–263
see also Wild environment
Foregut, 20–21, 24, 26, 42
amino acids, 78
carbohydrates, 58, 59
fiber, 68
minerals, 98
water, 150–151
Fructose, 58, 59, 60, 67, 185
Fruit, 187, 188, 260, 261
see also Seeds
aging, 168
carbohydrates, 58, 60, 62
composition of food/feed ingredients, table, 197–212
digestion, 21, 24
feeding ecology, 6–20 (passim), 185
fiber, 69
minerals, 103–104
protein requirements, 75
vitamins, 121
water, 154, 155, 187, 194
Fungus, 8, 19

G

Galactose, 58–59
Gelled foods, 3, 59, 60, 62, 83, 184
Gender differences, *see* Sex differences
Genetic factors, 191
aging, 167
energy requirements, 52
minerals, 94, 102
vitamins, 116–117, 134
Glucose, 58, 66, 83, 137, 167, 175, 185
see also Cellulose
aging, 169–170
lactose, 52, 59
metabolic processes, 154, 171, 174
Glycogen, 59, 120
Grains and grain products, 75, 77, 78, 102, 107, 191, 192
rice, 83
wheat, 60, 77, 78, 79, 83, 102, 183
Group size, 261–262
feeding ecology, 6–18 (passim)
water, 156–157

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Growth and development, 1, 2, 159, 166, 170, 171, 172
see also Age factors; Infants
amino acids, 78–79
energy, 42, 48, 50, 52–54
environmental enhancement, 260
fats, 87, 89, 90, 172
minerals, 95, 99, 102, 104
protein, 77, 80–83, 171
standards, 159
vitamins, 118, 121, 130, 135
Gums, 21, 24, 60, 62, 94, 261, 262
feeding ecology, 6, 9, 19, 20

H

Heart disease, *see* Cardiovascular disease
Heat, *see* Temperature and thermoregulation factors
Hematologic factors, 66, 80, 168, 169–170, 172, 174, 175–176, 186
see also Cardiovascular disease
anemia, 80, 81, 82–83, 99–100, 101, 124–125, 126, 129, 130, 134, 135, 136, 138
atherosclerosis, 66, 92, 132, 167, 171, 173–174
carbohydrates, 58, 66
cholesterol, 66, 83, 84, 89, 91–93, 101, 166, 173
metabolism, 2, 91, 123, 125
vitamins and, 123, 125, 126, 141
fats, 88, 90, 92
insulin, 54, 66, 82, 106, 141, 151, 157, 168, 169, 172–176, 186
diabetes, 2, 151, 153, 167, 168, 169, 173–176
lipids, 61, 66, 81, 88–89, 91, 106, 166, 167, 171, 173–174 (passim), 176
vitamins and, 122, 123–124, 126, 128, 140
lipoproteins, 88, 89, 92, 123–124, 166, 171, 173
minerals, 98, 99, 100, 103, 105
protein, 75, 80, 81, 82
vitamins, 114, 118, 120–140 (passim)
water, 150, 151, 152, 153
Hemicelluloses, 60
Hepatic system, 22, 58, 79, 82, 100
fats, 90, 141
vitamins, 114, 123, 124, 128, 130, 131, 132, 136, 137, 141
Hindgut, 20–21, 26
fiber, 68
minerals, 106
Histidine, composition of food/feed ingredients, table, 242–255
Historical perspectives, *vii*
committee report at hand, *vii*, 1
energy requirements, 42
fiber, 61–62
minerals, 95, 96
protein requirements, 77, 79, 80
sampling methods, 5
Humidity, 152–153, 154
Homeostasis
see also Temperature and thermal regulation factors
minerals, 103, 105
vitamins, 114, 116, 120
water, 153, 156
Hormones
minerals and, 94, 97, 99, 104, 106
obesity and diabetes, 176
vitamins and, 119–120
water, 150, 156
Hypervitaminosis, 2, 115–116, 121–122

I

Immune system
aging, 170
minerals, 101, 105
vitamins, 119–120, 126, 131–132, 134, 135
water, 150
Infant formula, 51, 79, 97, 99–100, 102–103, 165–166
Infants, 159, 161, 164–167
see also Lactation; Pregnancy
amino acids, 79
carbohydrates, 59
energy requirements, 43, 48, 50–51, 52–53
fats, 89–90, 91
minerals, 96–97, 99–100, 101–103, 104
protein requirements, 77–82 (passim)
vitamins, 117–118, 128
water, 150, 151
weaning, 159, 161, 167
Infections, 81, 115, 135, 170
Influenza, 170
Inositol, 141–142
Insects
carnitine, 141
digestion, 21
feeding ecology, 6–13 (passim), 19, 20, 261
minerals, 96, 97
Insulin, 54, 66, 82, 106, 141, 151, 157, 168, 169, 172–176, 186
diabetes, 2, 151, 153, 167, 168, 169, 173–176
Intake, 9, 20–21, 42, 44–52, 58, 66, 68, 70, 76, 80–81, 83, 87, 90–91, 97–100, 102–104, 106–107, 113–115, 117–119, 121, 128, 130, 133, 137, 140, 152–156, 159, 164, 166–176, 184–186, 192–193, 259–260
Internet
number of laboratory primates, *vii*
water quality standards, 156
Intestines, 24

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carbohydrates, 58, 59
fats, 88
minerals, 99, 117
vitamins, 123
water, 154
Iodine, 106, 193, 213–227
Iron, 94, 95, 99–100, 104, 131, 138, 191, 192, 193
anemia, 80, 81, 82–83, 99–100, 101, 124–125, 126, 129, 130, 134, 135, 136, 138
composition of food/feed ingredients, table, 213–227, 256–257
Isoleucine, 186, 242–255
see also Leucine

K

Kidney, *see* Renal system
Kwashiorkor, 81

L

Lactalbumin, 75, 76, 77, 79–81
Lactation, 2, 161, 164, 165
energy requirements, 41, 43, 51–52, 53–54
mineral requirements, 96, 103
protein requirements, 75, 80
vitamin requirements, 117–118, 121, 128
Lactose, 52, 59, 81
Leaves, 187, 188, 261–262
carbohydrates, 58, 64
digestion, 24–26
feeding ecology, 6–20 (passim)
fiber, 64, 65–66, 67, 262
minerals, 94, 96, 98, 102
protein requirements, 75
water, 153
Leptin, 175–176
Leucine, 131, 186
see also Isoleucine
composition of food/feed ingredients, table, 242–255
Life stages, *see* Age factors
Light, 120
ultraviolet radiation, 96, 117, 118, 120, 121
water requirements, 150, 154
Lignin, 61, 62, 63, 64, 65–68, 75
composition of food/feed ingredients, table, 197–212
Linoleic acid, 87, 88, 89, 90–91
composition of food/feed ingredients, tables, 197–241
Linolenic acid, 87, 88, 89, 90, 91
composition of food/feed ingredients, tables, 197–241
Lipoproteins, 89, 89, 92, 123–124, 166, 171, 173
Lipids, 61, 66, 81, 88–89, 91, 106, 167, 171, 173–174 (passim), 176
infants, 166
vitamins and, 122, 123–124, 126, 128, 140
Liver, *see* Hepatic system
Lysine, 2, 78–79
composition of food/feed ingredients, table, 242–255

M

Magnesium, 94, 97–98, 191, 256–257
Maize, *see* Corn
Males, *see* Sex differences
Malnutrition, 2, 80–83, 91–96
Maltose, 59
Manganese, 94, 95, 99, 101–102, 192, 193
composition of food/feed ingredients, table, 213–227, 256–257
Marasmus, 81
Menopause, 167, 170
Metabolic processes, 2, 22, 166
see also Digestion; Enzymes; *terms beginning "Vitamin"*
aging, 169, 171
amino acids, 79
body weight, 159, 165–166
carbohydrates, 58, 97, 129, 154
cholesterol, 2, 91, 123, 125
energy, 41, 42–43, 45–47, 49, 50, 58, 165–166, 169
fats, 2, 88–89, 91, 97, 129, 141, 154
glucose, 154, 171, 174
insulin, 54, 66, 82, 106, 141, 151, 157, 168, 169, 172–176, 186
minerals, 66, 95, 96–97, 99, 104, 105, 106, 117
proteins, 83, 97, 129, 154, 165–166
vitamins, 2, 114, 115, 117, 118–120, 123–133 (passim), 135, 137, 138, 140, 141
water, 150–157 (passim)
Methionine, 2, 77, 78–79, 98, 105, 135, 141
composition of food/feed ingredients, table, 242–255
Methodology, *see* Research methodology
Milk, 2, 9, 89, 159, 161, 164–167
see also Lactation
carbohydrates, 52, 58
casein, 75, 76, 77, 80, 82, 83, 99, 136, 191
energy requirements, 42, 51–54
lactalbumin, 75, 76, 77, 79–80
lactose, 52, 59, 81
minerals, 98, 99, 100, 102
protein requirements, 75, 76, 81, 83
replacers, 52, 59, 159, 161, 164–167
vitamins, 117–118, 128
Mineral Tolerances of Domestic Animals, 95
Minerals, 2, 63, 94–112, 185
see also Calcium; Phosphorus
absorption, 95, 96–97, 99, 100, 102, 105, 191

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age factors, 96, 98, 99, 100, 102, 167–169
growth and development, 95, 99, 102, 104
bioavailability, 97, 99–105 (passim), 107
body composition and weight, 106
bone, 94, 95, 96, 97, 107, 127–128
osteoporosis, 95, 167
teeth, 95, 107
cadmium, 94–95
cellular biology, 94, 95, 98, 99, 102, 106
chromium, 94, 99, 106–107, 192, 193
cobalt, 2, 94, 106, 135–137
composition of food/feed ingredients, table, 213–227
copper, 2, 99, 100–101, 131, 191, 193, 213–227, 256–257
deficiencies, diseases caused by, 95, 96, 99–100, 101, 103–104, 107
dry matter, 94, 95, 96, 97–98, 101, 102, 103, 104, 107, 213–227
composition of food/feed ingredients, table, 213–227, 256–257
enzymes and, 94, 97, 98, 100, 101–102
fiber, 64, 66
genetic factors, 94, 102
homeostasis, 103, 105
hormones and, 94, 97, 99, 104, 106
immune system, 99, 103
infants, 96–97, 99–100, 101–103, 104
iron, 94, 95, 98–100, 102, 131, 138, 191, 192, 193
anemia, 80, 81, 82–83, 99–100, 101, 124–125, 126, 129, 130, 134, 135, 136, 138
composition of food/feed ingredients, table, 213–227, 256–257
insects, 96, 97
intestines, 99, 117
lactation, 96, 103
magnesium, 94, 97–98, 191, 256–257
manganese, 95, 99, 101–102, 192, 193, 213–227, 256–257
metabolism, 66, 95, 96–97, 99, 104, 105, 106, 117
muscles, 95, 97, 105
milk, 98, 99, 100, 102
nervous system, 95, 99, 102
potassium, 94, 99, 104, 192, 193, 213–227, 256–257
reproductive system, 96, 99–100, 104–105
pregnancy, 102–103, 104, 105, 106, 115
selenium, 2, 94, 104–106, 192, 193, 213–227, 256–257
sex differences, 98, 103, 104–105, 107
skin, 102, 103, 105
sodium, 94, 96, 98, 105, 153, 192, 193, 213–227, 256–257
sulfur, 2, 77, 94, 96, 98, 213–227, 256–257
supplements, 96, 98, 101, 102, 103, 256–257, 261
teeth, 95, 109
toxicity, 94–95, 97–98, 105–106, 110, 121–122, 155
trace minerals, 94, 98–107, 192, 193, 213–227, 256–257
water, contents of, 155–156
wild environment, 94, 96–97, 100
zinc, 94, 99, 102, 102–104, 115, 166–167, 191, 193, 213–227, 256–257
Monosaccharides, 58
Muscles and muscular activity, 171, 172
see also Physical activity
energy requirements, 41
environmental enhancement, 260
fats, 92
minerals, 95, 97, 105
vitamins, 124, 137–138
water, 150, 152

N

National Institutes of Health, 183
Nervous system
see also Brain
aging, 167
carbohydrates, 58
diabetes, 176
fats, 89
minerals, 95, 99, 105
proteins, 79, 82, 84
vitamins, 113, 116, 118, 119–120, 129, 132, 136, 137
water, 150, 152, 155, 156
Neutral-detergent fiber (NDF), 62–66, 67–70, 192, 193
composition of food/feed ingredients, table, 197–212
Niacin, 131–132, 191–192, 193
composition of food/feed ingredients, table, 228–241
Nitrogen, 138
energy requirements, 42, 61
fecal loss, 77
feeding ecology, 21
protein requirements, 75, 77, 80
Nocturnal species, general
environmental enhancement, 259
feeding ecology, 6–13 (passim)
Nutrient composition, 26, 164, 182, 184, 188, 195, 260
Nutritional Energetics of Domestic Animals, 42

O

Obesity, 2, 151, 167, 172–176, 185
age factors, 172–173, 174, 175
sex differences, 173, 174
Oils, *see* Fats and oils
Oilseeds, 91, 102, 107, 192, 258
Olfactory factors, 184, 185
Oligosaccharides, 58, 59, 62

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Oral cavity, 3, 185
fiber, 62
minerals, 95, 107
vitamins, 125, 132, 135, 138, 140
Osteoporosis, 95, 167

P

Pancreas, 59, 82, 84, 123, 168, 191
diabetes, 2, 151, 153, 167, 168, 169, 173–176
Pantothenic acid, 130–131, 192, 193
composition of food/feed ingredients, table, 228–241
Pectin, 60, 62
Pellets, 83, 121, 138, 167, 168, 183, 184, 185, 186
Perception, *see* Eyes; Olfactory factors; Tactile perception; Taste
Phenylalanine, 2, 79
composition of food/feed ingredients, table, 242–255
Phosphorus, 94, 95–97, 99, 107, 170, 191, 192, 193
composition of food/feed ingredients, table, 213–227, 256–257
vitamins and, 116, 117, 119, 122, 124, 128, 132, 140
Physical activity, 159
see also Muscles and muscular activity; Obesity
energy requirements, 44, 47
water, 152
Plant feeding, 64, 65–66, 67, 75, 135, 185, 187, 188, 260, 263
see also Carbohydrates; Fiber; Fruit; Leaves; Seeds; *specific fruits and vegetables*
bamboo, 10, 187, 197, 213
bark, 101, 188, 261
browse, general, 26, 96, 186, 187
composition of food/feed ingredients, tables, 197–258
digestion, 23, 26, 28–29
feeding ecology, 5–21 (passim)
foraging, 2, 5, 21, 26, 53, 68, 184, 259–263
water, 154, 187, 194
Polysaccharides, 58, 59–60, 63
Potassium, 94, 98, 104, 192, 193
composition of food/feed ingredients, table, 213–227, 256–257
Pregnancy, 2, 161
energy requirements, 53
minerals, 102–103, 104, 105, 106, 115
protein, 75, 80, 104
vitamins, 115, 121, 124, 128, 134–135
water, 150, 151
Proteins, 2, 61, 62, 75–86, 166, 171, 186, 191, 192, 193
see also Amino acids
age factors, 77, 78, 80–83
growth and development, 77, 80–83, 171
albumin, 75, 76, 77, 79–80, 81, 83, 102, 132, 153
lactalbumin, 75, 76, 77, 79–80
body composition and weight, 76, 77, 79, 80–81, 83, 102, 155
brain, 79, 84
caloric measures, 77, 80, 80–83
composition of food/feed ingredients, tables, 197–255
diet formulation, 183
diseases, deficiencies caused by, 75, 79, 80–84
eggs, 75, 76, 83
energy requirements, 42, 50, 76, 77, 81
feeding ecology, 22
fats and, 88
infants, 77, 78, 79, 80, 81, 82
lactalbumin, 75, 76, 77, 79–80
lactation, 75, 80
lipoproteins, 88, 89, 92, 123–124, 166, 171, 173
metabolic processes, 83, 97, 129, 154, 165–166
milk, 75, 76, 81, 83
minerals and, 83, 95, 96, 98, 100, 104–105, 107
nervous system, 79, 81, 84
pregnancy, 75, 80, 104
sex differences, 78, 82–83
skin, 79, 81
soya, 75, 77, 79, 83–84, 97, 99, 191
supplements, 78, 79, 82, 105, 107, 129
vitamins and, 123–124, 127, 128, 141
water, 83, 153, 154, 155
Psychological well-being, 3, 186, 259–265
aggressive behavior, 79, 116, 259, 261–262

R

Renal system, 58, 83, 96, 98
vitamins, 119, 120, 124
water, 153, 154, 156
Reproductive system and reproduction, 159
see also Lactation; Pregnancy
diet formulation, 183
energy requirements, 41, 43, 49, 53
minerals, 96, 99–100, 104–105
vitamins, 134–135
water, 150
Requirements
energy, 41, 43, 49, 53, 60, 83, 186, 191
mineral, 95
protein, 43–48, 75–77, 80
vitamin, 58
water, 156–157
Respiratory system, 150, 152, 154
Retina, *see* Eyes
Research methodology
see also Caloric measures; Standards
aging, 167–170
birth to weaning, 159, 161, 167
body composition, 171–172

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carbohydrates and fiber, 61–64, 66
committee report at hand, 1
diet formulation, 182–183
energy requirements, 41–43, 47–48, 50–54
ethical issues, 77
feeding ecology, 5, 13, 16, 18, 20
minerals, 94, 99
obesity, 172–175
proteins, 75–82
sampling, 5, 13
taxonomy, *vii*, 2, 3, 266–267
vitamins, 113, 116, 122–123, 125, 126, 127, 133, 139
water requirements, 151, 156–157
weight equivalents/conversion factors, tables, 268
Riboflavin, 129–130, 131, 192, 193
composition of food/feed ingredients, table, 228–241
Rice, 83

S

Sampling, 5, 13
Seasonal factors, 65–66
see also Temperature and thermoregulation factors
carbohydrates, 60, 64
feeding ecology, 6–20 (passim)
water, 153–154
humidity, 152–153, 154
Seeds, 11, 12, 262
carbohydrates, 58
digestion, 23
feeding ecology, 6–16 (passim), 19, 185
minerals, 102
oilseeds, 91, 102
protein requirements, 75
water, 154
Selenium, 2, 94, 104–106, 192, 193
composition of food/feed ingredients, table, 213–227, 256–257
Sensory perception, *see* Eyes; Olfactory factors; Tactile perception; Taste
Sex differences
see also Lactation; Pregnancy; Reproductive system and reproduction
aging, 167, 168, 170
amino acids, 79
body composition and weight, general, 159, 162–163, 171
energy requirements, 44, 47, 48, 49, 51, 52
feeding ecology, 6–13 (passim)
menopause, 167, 170
minerals, 98, 103, 104–105, 107
obesity, 173, 174
protein, 78, 82–83
vitamins, 115, 119, 122, 134
water, 150–155 (passim)
Skin
dermatitis, 79, 81, 103, 105, 130, 134
fats, 90
fold thickness, 172
minerals, 102, 103, 105
protein, 79, 81
vitamins, 116, 117–118, 120, 130
water, 152, 154
Social factors, 173
see also Environmental enhancement; Group size
Sodium, 94, 96, 99, 105, 153, 192, 193
composition of food/feed ingredients, table, 213–227, 256–257
Soya, 75, 77, 79, 83–84, 97, 99, 191
Species (Tables of), 6–18
Stages of life, *see* Age factors
Standards
composition of food/feed ingredients, tables, 197–241
energy requirements, 41
environmental enhancement, 259
growth, 159
vitamin measures, 113, 115, 117, 123, 126
water quality, 156
Starch, 59, 62, 82, 184, 185
Stomach, 191–192
carbohydrates, 60
digestion, general, 21, 24
feeding ecology, 13, 19
energy requirements, 50
minerals, 94, 106
Stress
see also Environmental enhancement
energy requirements, 52
protein, 76
Sucrose, 58, 59, 82, 174, 185
Sulfur, 2, 94, 96, 98
amino acids, 77
composition of food/feed ingredients, table, 213–227, 256–257
Supplements, 161, 167, 174, 186–187
fat, 90–91
mineral, 96, 98, 101, 102, 103, 256–257, 261
protein, 78, 79, 82, 105, 107, 129
vitamin, 105, 114, 122, 125, 129–136 (passim), 140, 141, 183, 184, 261

T

Tactile perception, 184, 185, 260, 261
Taste, 103, 184, 185, 260–261
Taxonomy, *vii*, 2, 3, 266–267

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Taurine, 2, 79, 98, 166, 192
composition of food/feed ingredients, table, 242–255
Temperature and thermoregulation factors
aging, 169
cold, 44, 47, 152
energy requirements, general, 41, 43, 44, 47, 50
feed processing, 183–184
heat, 47, 150, 152–153, 154
soy, 83–84
starch, 62
water, 150, 152–153, 154
Terrestrial species, general
environmental enhancement, 259, 261
feeding ecology, 5–22 (passim)
Thermoregulation, *see* Temperature and thermoregulation factors
Thiamin, 128–129, 184, 192, 193
composition of food/feed ingredients, table, 228–241
Threonine, 78, 242–255
Thyroid gland, 104, 106
Time factors
see also Diurnal species; Nocturnal species
clotting, vitamin K, 128
digestion, 21, 24, 26, 41
feeding ecology, 5–13 (passim), 18, 19–20, 259, 260, 261–262
foraging, 259, 260, 261
minerals, 101
vitamin deficiencies, 129
water deprivation, 153
Toxicity, *vii*, 188
minerals, 94–95, 97–98, 105–106, 107, 121–122, 155
vitamins, 2, 115–116, 121–122
Trace minerals, 94, 98–107, 192
chromium, 96, 101, 108–109, 192, 193
cobalt, 2, 94, 106, 135–137
copper, 2, 99, 100–101, 131, 191, 193, 213–227, 256–257
iodine, 104, 193, 213–227
iron, 94, 95, 98–100, 102, 131, 138, 191, 192, 193, 213–227, 256–257
manganese, 94, 95, 99, 101–102, 192, 193, 213–227, 256–257
selenium, 2, 94, 104–106, 192, 193, 213–227, 256–257
zinc, 94, 99, 101, 102–104, 115, 166–167, 191, 193, 213–227, 256–257
Treat feeding, 186, 260
Tryptophan, 2, 79, 131, 132
composition of food/feed ingredients, table, 242–255

U

Ultraviolet radiation, 96, 117, 118, 120, 121
Urine
energy requirements, 43
protein, excessive, 83
vitamins, 124
water, 150, 152, 155

V

Valine, 137, 186
composition of food/feed ingredients, table, 242–255
Vegetation, *see* Plant feeding
Visual perception, *see* Eyes
Vitamin A, 113–116, 118, 184, 192, 193
composition of food/feed ingredients, tables, 228–241
Vitamin B, 60, 94, 106, 131, 132–133, 135–137, 192, 193
choline, 128, 130, 140, 141, 194, 228–241
composition of food/feed ingredients, table, 228–241
Vitamin C, 101, 129, 137–140, 183, 184, 185, 192, 193
composition of food/feed ingredients, table, 228–241
Vitamin D, 96, 97, 116–122, 128, 166, 184, 192, 193
aging, 170
composition of food/feed ingredients, table, 228–241
Vitamin E, 1–2, 90–91, 105, 120–121, 122–126, 127, 184, 192, 193
composition of food/feed ingredients, table, 228–241
Vitamin K, 116, 126–128, 192, 193
composition of food/feed ingredients, table, 228–241
Vitamins, general, 20–21, 83, 98, 113–151, 183, 184, 185, 191, 192
absorption, 114, 123, 124, 134, 137
age factors, 125, 127, 133, 139, 167–168
growth and development, 118, 121, 130, 135
amino acids and, 124, 131
bioavailability, 123, 124, 128–136 (passim)
body composition and weight, 115, 119, 124, 127–141 (passim)
bone, 117, 118, 119, 121, 125, 127–128, 134, 137–138
cardiovascular disease, 128–129, 132
calcium and, 116, 117, 119, 121–122, 128, 131, 138
cellular biology, 113, 124, 131–132, 140–141
composition of food/feed ingredients, tables, 228–241
cholesterol and, 123, 125, 126, 141
deficiencies, diseases caused by, 90–91, 115, 117–118, 119–120, 124–141 (passim)
dry matter, 115, 118, 121, 126, 127, 128, 129, 131, 134, 135, 136, 139
composition of food/feed ingredients, tables, 228–241
enzymes and, 124, 128, 129, 130, 132, 134, 135, 137
eyes, 113, 116, 125, 130, 136
fats and, 2, 123, 124, 125, 141
fat-soluble, 88, 89, 90–91, 113–128, 228–241
feces, 123, 136
feed processing, 184, 185

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genetic factors, 116–117, 134
hepatic system, 114, 123, 124, 128, 130, 131, 132, 136, 137, 141
homeostasis, 114, 116, 120
hormones and, 119–120
immune system, 119–120, 126, 131–132, 134, 135
infants, 117–118, 128
lactation, 117–118, 121, 128
metabolic processes, 2, 114, 115, 117, 118–120, 123–133 (passim), 135, 137, 138, 140, 141
milk, 117–118, 128
muscles, 124, 137–138
nervous system, 113, 116, 118, 119–120, 129, 132, 136, 137
oral cavity, 125, 132, 135, 138, 140
phosphorus and, 116, 117, 119, 122, 124, 128, 132, 140
pregnancy, 115, 121, 124, 128, 134–135
proteins and, 123–124, 127, 128, 141
renal system, 119, 120, 124
reproductive system, 134–135
sex differences, 115, 119, 122, 134
skin, 116, 117–118, 120, 130
standard measures, 113, 115, 117, 123, 126
supplements, 105, 114, 122, 125, 129–136 (passim), 140, 141, 183, 184, 261
toxicity, 2, 115–116, 121–122
water-soluble, 2, 128–142, 228–241
Vitamins, other specific
biotin, 133–134, 191, 192, 193, 228–241
carnitine, 141
choline, 128, 130, 140–141, 194, 228–241
composition of food/feed ingredients, table, 228–241
folacin, 134–135, 136, 192, 228–241
inositol, 141–142
niacin, 131–132, 191–192, 193, 228–241
pantothenic acid, 130–131, 192, 193, 228–241
riboflavin, 129–130, 131, 192, 193, 228–241
thiamin, 128–129, 184, 192, 193, 228–241
wild environment, 119, 121, 122

W

Water, 2, 150–158, 185
age factors, 150, 151, 153, 155
body composition and weight, 150–155 (passim)
bone, joint lubrication, 150
cardiovascular disease, 151, 152
cellular biology, 150, 151–152, 156
cobalt, 107
digestion, 150
diseases,
deficiencies caused by, 151–152, 153, 154, 155
pollution caused by, 155–156
environmental enhancement, 262–263
fats and, 150, 151, 153, 155
feces, 150, 154–155
fluorine, 107
homeostasis, 153, 156
hormones and, 150, 156
humidity, 152–153, 154
infants, 150, 151
metabolic processes, 150–157 (passim)
minerals, 155–156
muscles, 150, 152
nervous system, 150, 152, 155, 156
pregnancy, 150, 151
proteins, 83, 153, 154, 155
quality of, 155–156
renal system, 153, 154, 156
respiratory system, 150, 152, 154
riboflavin, 129–130
sex differences, 150–155 (passim); *see also "pregnancy" supra*
skin, 152, 154
sodium, 99
thermoregulation, 150, 152–153, 154
urine, 150, 152, 155
Weaning, 159, 161, 167
Weight, *see* Body composition and weight
Wheat, 60, 77, 78, 79, 84, 102, 183
Wild environment, 182, 184, 185, 260–261
see also Endangered species
body weight, 159
browse, general, 26, 96, 186, 187, 261, 262
carbohydrates, 64–66
digestion, 26, 27
endangered species, *vii*, 1
energy requirements, 47, 52
fiber, 64–66, 67–68, 69
foraging 2, 5, 53, 68, 184, 259–263
minerals, 94, 96–97, 100
obesity, 172
protein requirements, 75
vitamins, 119, 121, 122
World Health Organization, 117
World Wide Web, *see* Internet
Wound healing, 170–171

Z

Zinc, 94, 99, 101, 102–104, 115, 166–167, 191, 193
composition of food/feed ingredients, table, 213–227, 256–257
Zoo animals, *vii*, 27, 48, 94

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