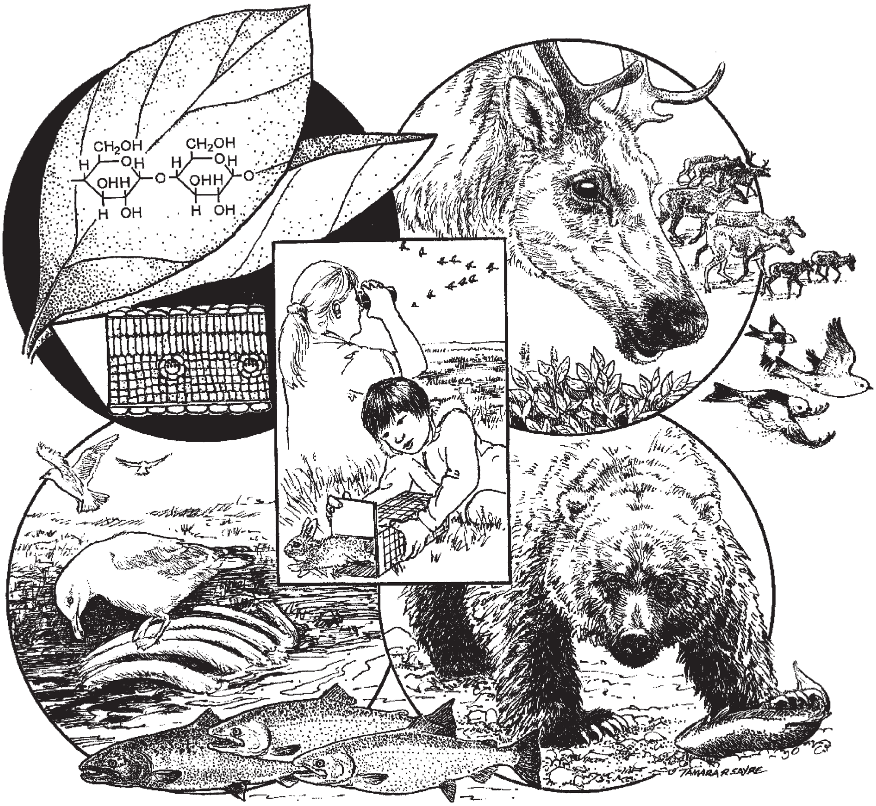
Integrative Wildlife Nutrition



Food flows through a web of wildlife. In the arctic, willows provide nutrients for herbivores such as migrating caribou and habitat for songbirds such as snow buntings. Grizzly bears prey on salmon while herring gulls scavenge the salmon carcasses. Animal tissues decompose and return their nutrients to soils and plants as the cycle of nutrition continues. We observe changes in populations that reflect changes in food and habitat for wildlife such as geese and snowshoe hares. Our ability to effectively conserve and manage wildlife species depends on understanding their needs in changing habitats with changing food supplies. (Illustrator: T. Sayre)

Perry S. Barboza • Katherine L. Parker
Ian D. Hume

Integrative Wildlife Nutrition

Springer

Dr. Perry S. Barboza
Department of Biology and Wildlife
Institute of Arctic Biology
University of Alaska
PO Box 75000
Fairbanks, Alaska 99775-7000;
USA
e-mail: ffpsb@uaf.edu

Dr. Katherine L. Parker
Natural Resources and Environmental Studies
University of Northern British Columbia
Prince George, British Columbia V2N 4Z9
Canada
e-mail: parker@unbc.ca

Dr. Ian D. Hume
School of Biological Sciences A08
University of Sydney
New South Wales 2006, Australia
e-mail: ianhume@bio.usyd.edu.au

ISBN: 978-3-540-87884-1 e-ISBN: 978-3-540-87885-8
DOI: 10.1007/978-3-540-87885-8

Library of Congress Control Number: 2008938180

Cover design: WMX Design GmbH, Heidelberg, Germany

Cover illustration by Tamara Sayre

Printed on acid-free paper

9 8 7 6 5 4 3 2 1

springer.com

Contributors

Perry Barboza teaches undergraduate and graduate courses in physiology and nutrition of wildlife. He has also taught courses in human nutrition, biochemistry, histology and introductory biology. The principal focus of his research is the consequences of life history and environmental change on nutrition. He and his students study ungulates (reindeer, caribou and muskoxen) and waterfowl (ducks and geese) as well as non-game species in both wild and captive populations.

Katherine Parker teaches courses in wildlife ecology, animal physiology and wildlife nutrition. Her current interests incorporate nutritional ecology within extensive field studies of northern ungulates, bears and wolves. She and her students research the energetic strategies of wildlife for survival and reproduction; plant–herbivore and predator–prey interactions; and the role of individual animal requirements within large-scale ecosystems.

Ian Hume has taught courses in wildlife nutrition, eco-physiology and biochemistry in the USA and Australia. He has written over 150 research publications on the digestive physiology and nutrition of mammals and birds in international journals, and is the author of *Marsupial Nutrition* (1999) and co-author with C.E. Stevens of *Comparative Physiology of the Vertebrate Digestive System* (1995).

Edible. Good to eat and wholesome to digest, as a worm to a toad, a toad to a snake, a snake to a pig, a pig to a man, and a man to a worm.

Ambrose Bierce (1910) The Devil's Dictionary.

Preface

Nutrition spans a wide range of mechanisms from acquisition of food to digestion, absorption and retention of energy substrates, water and other nutrients. Nutritional principles have been applied to improving individual health, athletic performance and longevity of humans and of their companion animals, and to maximizing agricultural efficiency by manipulating reproduction or growth of tissues such as muscle, hair or milk in livestock. Comparative nutrition borrows from these traditional approaches by applying similar techniques to studies of ecology and physiology of wildlife. Comparative approaches to nutrition integrate several levels of organization because the acquisition and flow of energy and nutrients connect individuals to populations, populations to communities, and communities to ecosystems. *Integrative Wildlife Nutrition* connects behavioral, morphological and biochemical traits of animals to the life history of species and thus the dynamics of populations. An integrated approach to nutrition provides a practical framework for understanding the interactions between food resources and wildlife populations and for managing the harvest of abundant species and the conservation of threatened populations.

This book is for students and professionals in animal physiology and ecology, conservation biology and wildlife management. It is based on our lectures, demonstrations and practical classes taught in the USA, Canada and Australia over the last three decades. Instructors can use *Integrative Wildlife Nutrition* as a text in wildlife and conservation biology programs, and as a reference source for related courses in wildlife ecology. Each chapter introduces basic concepts such as units of measurement and allometric scaling, but we assume that the reader has completed introductory courses in biology, chemistry, ecology and animal physiology in the first or second year of undergraduate programs in the biological sciences. We describe a series of basic mechanisms in behavioral ecology, morphology and biochemistry involved in foraging, processing of foods and retention of energy and nutrients in animals. We focus on mammals, birds, reptiles and fish because most efforts in conservation and management concern those taxa. However, we also use examples from invertebrates to illustrate diversity of form and function such as chitin in the exoskeleton of insects and digestion of cellulose in crabs and termites. The broad diversity of species covered in the book may be considered in the groups listed in Table 1.1 and in the Index.

Integrative Wildlife Nutrition emphasizes the general features of vertebrates that pertain to the ecology and adaptations of wildlife. This approach builds on comprehensive descriptions of the digestive physiology (Van Soest 1994; Stevens and Hume 1995; Hume 1999) and nutritional biochemistry (Linder 1991; Groff et al. 1995; Brody 1999) of animals; including humans. It integrates cellular responses with function of the animal body and with the ecological requirements of wild animals. Our approach extends previous texts in wildlife nutrition (Robbins 1993; Klasing 1998; Hume 1999) by discussing the ecology of foraging and the evolution of structures and mechanisms. Our intent is not to overwhelm the reader with numerous details or specialization in any of the chapters, but rather to present aspects of a nutritional hierarchy in the context of ecological implications. This integrative approach emphasizes the importance of wildlife nutrition, from molecules and cells to ecosystems. Key concepts are illustrated with flow diagrams of biochemical pathways and with practical examples for monitoring the nutritional status of wild animals. We begin with a discussion of food resources for populations (Part I) and end with responses to variable environments (Part III). Part II describes the nutrients and their functions in the metabolism and structure of animals.

We use only common names of plants and animals in the text, figures and tables, but the ‘List of Common and Scientific Names of Animals and Plants’ at the end of the book contains a complete list of the common and scientific names of all species mentioned in the book.

October 2008 Perry Barboza, Katherine Parker and Ian Hume

Acknowledgments

This book attempts to answer some of the many questions posed by our students and our colleagues. We are most grateful for those questions and for the discussions that have prompted us to search the literature and our own work to prepare this text. We have enjoyed stimulating discussions with R.G. White, R.T. Bowyer, F.S. Chapin, D.G. Jorde, K. Klasing, M.P. Gillingham and others while preparing this perspective. The libraries and librarians at the Universities of Alaska, Northern British Columbia and Sydney provided the many documents we required. K.A. Kenyon advised and assisted in assembling the bibliography and index of the book. T. Sayre enthusiastically designed a cover illustration that encapsulated the scope of the book. We thank D. Czeschlik and A. Schlitzberger at Springer for their support during the preparation of the book. We are grateful to our families, friends and coworkers for tolerating our distraction during this project and for accepting the term 'almost done' without a precise definition. Most importantly we thank the animals we have observed because without them we would know very little about wildlife nutrition.

Contents

Abbreviations

AA	arachadonic acid
ADF	acid-detergent fiber
ADH	anti-diuretic hormone
ALT	alanine amino transferase
ANH	atrial naturetic hormone
AP	alkaline phosphate
AVP	arginine vasopressin
AVT	arginine vasotocin
BIA	bioelectrical impedance analysis
BMR	basal metabolic rate
BSA	bovine serum albumen
CCK	cholecystokinin
CLA	conjugated linoleic acid
CNS	central nervous system
CSTR	continuous-flow stirred-tank reactor
D_2	ergocalciferol
D_3	cholecalciferol
DAPA	2,6-diaminopimelic acid
DBP	vitamin D binding protein
DE	digestible energy
DEXA	dual emission x-ray absorptiometry
DHA	docosohexanoic acid
DIT	diet-induced thermogenesis
DM	dry matter or dry mass
ENSO	El Nino Southern Oscillation
EPA	eicosopentanoic acid
EUN	endogenous urinary nitrogen
FSH	follicle stimulating hormone

GC	gas chromatography
GCORT	glucocorticoid hormone
GE	gross energy
GFR	glomerular filtration rate
GLO	glucono-lactone oxidase
HDL	high density lipoprotein
LDL	low density lipoprotein
LH	luteinizing hormone
ME	metabolizable energy
MFN	metabolic fecal N
MPFR	modified plug-flow reactor
MRT	mean retention time
NAG	N-acetyl glucosamine
NAO	North Atlantic Oscillation
NDF	neutral-detergent fiber
NE	net energy
OM	organic matter or organic mass
PFR	plug-flow reactor
PSM	plant secondary metabolite
PTH	parathyroid hormone
PUFA	polyunsaturated fatty acid
QFASA	quantitative fatty acid signature analysis
RMR	resting metabolic rate
RMT	relative medullary thickness
RQ	respiratory quotient
SCFA	short-chain fatty acid
SMR	standard metabolic rate
T_3	tri-iodo-thyronine
T_4	thyroxine
TCA	tricarboxcylic acid
TDS	total dissolved solids
TOBEC	total body electrical conductivity
TT	turnover time
UV	ultraviolet
VLDL	very low density lipoprotein

Chapter 1
Introduction: Common Themes Across Diverse Taxa

Concerns about animal populations by various audiences, from elected officials and policy boards to the general public, often result in two disarmingly simple questions for wildlife biologists:

- What does a population need?
- Will that population grow or decline, and why?

The ability to answer these questions rests on a synthesis of nutritional ecology and physiology.

Nutritional ecology and physiology track the dynamic supply and demand of energy and nutrients in wildlife and their habitats. Our integrative approach to wildlife nutrition attempts to answer two general questions:

- How do animals contend with variations in the supply of resources and the environmental challenges in their habitat?
- What structures, metabolic pathways and life history parameters constrain or limit animal responses?

This first chapter introduces the topics of nutrient composition and nutrient requirements of wildlife. Table 1.1 lists the general groups of animals that are managed for control or conservation of populations. Functional relationships between food resources and animals are discussed in Part I from the scale of the population down to the individual digestive system (Chapters 2 to 5). Chemical components that provide energy substrates or tissue constituents are discussed in Part II (Chapters 6–9). Part III (Chapters 10 and 11) discusses energy flow and the adaptations of animals to changing environments and supplies of food.

1.1 Resource Supply and Organismal Demand

Supply and demand are features of both the environment and wildlife. The environment supplies food but also exerts demands on the animal. For example, low ambient temperatures increase the demand for energy to heat the body whereas

P.S. Barboza et al., *Integrative Wildlife Nutrition*,

Table 1.1 General groups of animals

Taxa	Group	Energy demand	Trophic level	Typical application[1]
Fish	Marine: reef fish	Ectotherm	Carnivore	Conservation
Fish	Marine: salmon, bream, tuna, shark, herring, halibut, pollock	Ectotherm	Carnivore	Control
Fish	Freshwater: catfish, cichlids, trout, barramundi	Ectotherm	Omnivore	Control
Amphibian	Frogs, salamanders	Ectotherm	Carnivore	Conservation
Reptile	Snakes, lizards, crocodiles	Ectotherm	Carnivore	Conservation
Reptile	Iguanine lizards, chelonians	Ectotherm	Herbivore	Conservation
Bird	Passerines: songbirds	Endotherm	Omnivore	Conservation
Bird	Ratites: emus, ostrich, rhea	Endotherm	Omnivore	Control
Bird	Upland game birds: grouse, ptarmigan, pheasants	Endotherm	Herbivore	Control
Bird	Waterfowl: geese, ducks	Endotherm	Herbivore	Control
Bird	Seabirds: waders, albatross, gulls	Endotherm	Carnivore	Conservation
Bird	Cranes, raptors	Endotherm	Carnivore	Conservation
Mammal	Marine: seals, whales	Endotherm	Carnivore	Conservation
Mammal	Marsupials: grazing kangaroos	Endotherm	Herbivore	Control
Mammal	Marsupials: wallabies, wombats, possums	Endotherm	Herbivore	Conservation
Mammal	Marsupials: bandicoots, quolls	Endotherm	Carnivore	Conservation
Mammal	Rodents	Endotherm	Omnivore	Control
Mammal	Hares, rabbits	Endotherm	Herbivore	Control
Mammal	Ruminants: deer, sheep, bison, giraffes	Endotherm	Herbivore	Control
Mammal	Horses, rhinos, elephants	Endotherm	Herbivore	Control
Mammal	Primates, lemurs	Endotherm	Omnivore	Conservation
Mammal	Cats: lions, lynx	Endotherm	Carnivore	Conservation
Mammal	Bears, wolves, hyena	Endotherm	Carnivore	Control

[1] Control = monitored and often manipulated to control a population for maximum sustainable harvest or minimal adverse effects of overabundance. Conservation = monitored and often manipulated to conserve minimal viable population size.

high ambient temperatures increase the need for water to cool the animal. The patterns of energy and nutrient availability in an ecosystem provide the context for environmental supply and demand for wildlife. These patterns may be defined by the average abundance of the resource (high to low), the range of variation (broad to narrow), spatial distribution (uniform to patchy) and timing of resource availability (frequent to infrequent; constant to erratic). Wildlife diversity and abundance are high in rainforest ecosystems that are characterized by moderate temperature and high availability of water and nutrients, conditions that promote continuous plant production. Conversely, hot deserts typically support smaller populations of fewer species of wildlife because temperature and precipitation are highly variable and less conducive to plant production (Fig. 1.1)

Fig. 1.1 Primary production of plants varies widely with patterns of temperature, water availability and soils. **a** Mild temperatures and rich soils support diverse communities of plants and animals in wetlands when weather patterns are relatively stable. **b** Extreme temperatures of cold or heat combined with low and infrequent rains limit plant and animal communities in montane and desert habitats

The demands of the animal are ultimately met with food from the environment. These demands include the maintenance of body tissues that follows the genetic program of the species throughout the life of each individual. Life-history patterns reflect the allocation of energy and nutrients to the tissues and the activities and time required for survival, growth and reproduction. For example, among northern elephant seals, adult males awaiting the arrival of females at the breeding beach appear to expend little energy or nutrients but are nonetheless maintaining their muscles and organs even as they lie motionless. Female seals incur additional costs of energy and nutrients for production of milk soon after they arrive at the beach and deliver their pups (Boness et al. 2002). The costs of growth in seal pups are likewise a programmed productive demand that will continue until they in turn begin reproduction at adulthood. The ability to support maintenance or production of tissues when environmental supplies are inadequate depends on the supply of energy and nutrients from internal stores. Female seals use body fat and protein to produce milk when fasting or eating very little.

The ability of wildlife to contend with environmental variations depends on behavioral and physiological flexibility. Estuarine species of fish contend with daily tidal flows by tolerating a wide range of salinity (Spicer and Gaston 1999). Desert reptiles contend with infrequent rainfall by tolerating a wide range of internal fluid concentrations and by accumulating water stores in the urinary bladder after each rain (Bradshaw 2003). Environmental conditions that alter the abundance and timing of food and water select for an operational range that varies both among and within species. Variation within species is often associated with phenotypic plasticity, such as the amount of body fat in songbirds at the start of winter (Rogers et al. 1994). Persistent environmental change over multiple generations may favor one phenotype over another, resulting in population drift. For example, a population of birds may increase body fat or begin migration earlier as winters become colder and the period of snow cover lengthens for each generation. The combination of demography and genetics may ultimately result in speciation. In the austere and erratic environment of the Galapagos islands, beak size within a population of finches varies with the availability and form of their diet of seeds (Grant 1999). Similarly, energy expended at rest in wild mice can vary with primary plant production in their environment (Mueller and Diamond 2001). Phenotypic and genotypic differences among animals therefore alter their demands for energy and nutrients as well as their vulnerability to environmental changes.

1.2 Principal Components of Animals and Plants

The transfer of nutrients and energy from the environment to wildlife is reflected in the chemical composition of materials from soils through plants to herbivores, omnivores and predators. The elements of food are ultimately returned to the environment in excreta and tissues lost by animals throughout their lives. Tissues synthesized at one level of this trophic hierarchy are the food for the next level. The chemical composition of ingested animals and plants reflects the costs of depositing tissues as well as their value to a consumer. This section introduces the components of water, nutrients and energy in plants and animals.

Water is the principal interface between animals and their environment because organisms absorb and excrete matter across a wet interface. Removal of water (moisture) from living tissue preserves the nutrients contained in the remaining dry material (dry matter or dry mass; DM). In human agriculture, desiccation of plant seeds and stems in late summer and autumn produces grain and hay for winter storage. Similarly, the natural desiccation of seeds allows many birds and rodents to cache a stable source of food for winter. Moisture may be the largest fraction of plant and animal tissues, and is typically measured in grams per hundred grams ($g \cdot 100\,g^{-1}$) whole mass or percent (%). Water content is greatest for aquatic plants such as algae (Fig. 1.2), and for some parts of terrestrial plants such as nectar, flowers, fruits and budding leaves. Dietary sources of water may be important for hydration of animals, but excess moisture in food can dilute the nutrients and energy in a diet. Nectarivores such as hummingbirds must therefore consume large volumes of

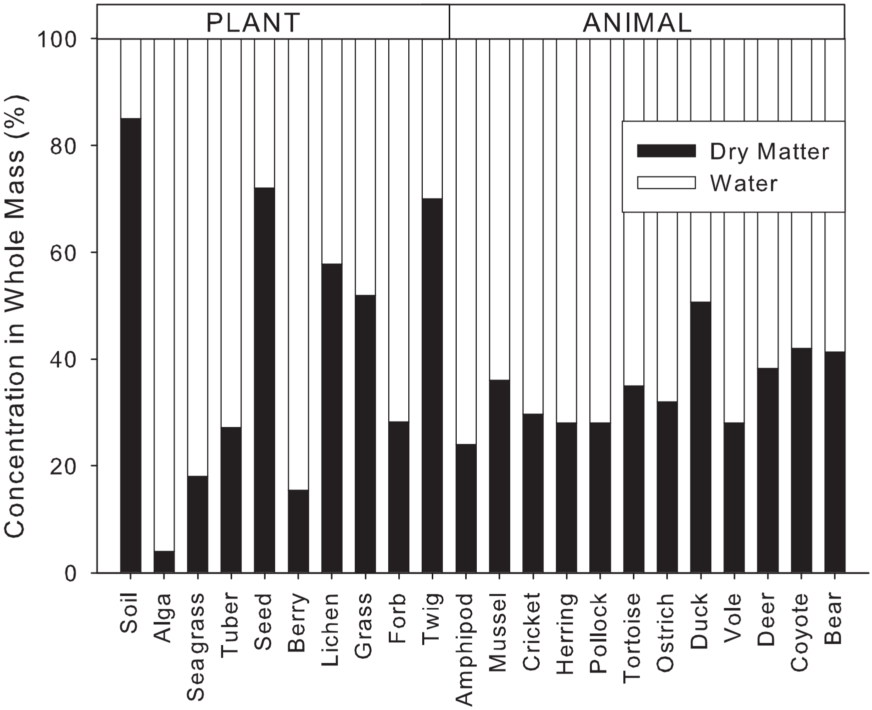


Fig. 1.2 Content of water (moisture) and dry matter in selected plants and animals in comparison with rich terrestrial soils (Chapin et al. 2002). Plants: blue-green alga (National Research Council 1983); leaves of sea grass (Mason et al. 2006); tubers of sweet potato (National Research Council 2003); seeds of corn (National Research Council 1996); blueberries (National Research Council 2003); terricolous lichen (Barboza, unpublished); aerial parts of *Schismus* grass and the leaves of the forb globemallow in spring (Barboza 1996); twigs of Barclay willow in winter (Spaeth et al. 2002). Animals: aquatic and terrestrial invertebrates (an amphipod, blue mussel and the mormon cricket) (Jorde and Owen 1990; National Research Council 2003); marine fish (herring and pollock) (Trumble et al. 2003); a reptile (the desert tortoise) (Barboza, unpublished); birds (ostrich and black duck) (Swart et al. 1993b; Barboza and Jorde 2002); and mammals (northern red-backed vole, white-tailed deer, coyote, black and brown bears) (Robbins et al. 1974; Farley and Robbins 1994; Huot et al. 1995; Zuercher et al. 1999)

water to extract sufficient nutrients from their dilute diet (Karasov et al. 1986). The water content of animal tissues is less variable than that of plants because hydration is tightly controlled in relation to exchanges of electrolytes such as sodium (Na) and potassium (K) (Chapter 9).

The dry matter of plants and animals may be divided between organic matter and minerals that are usually measured in grams per hundred grams ($g \cdot 100\,g^{-1}$) dry mass or percent (%). Organic matter (OM) includes all the combustible material that is primarily based on carbon (C), nitrogen (N), hydrogen (H) and oxygen (O). Biochemical oxidation is the process of combining substances with oxygen to yield energy and chemical byproducts. The oxidation of C in organic matter is the principal source of energy for animals. Organic matter therefore reflects the potential energy in the tissue. The non-combustible residue or ash includes most of the minerals. Minerals comprise the majority of the dry matter in soils (Fig. 1.3) whereas organic matter predominates in organisms. The distinction between organic matter and ash in organisms allows for the calculation of a crude measure of the content of structural minerals. Mineral concentrations are increased by the shell in mussels and by the bony carapace of tortoises (Fig. 1.3).

Unlike the minerals in soils, minerals in organisms are deposited in an organic matrix of protein in bone, or carbohydrate in plant cell walls. That is, much of the mineral is inert in soils, but in organisms, minerals are continuously turned over with the organic components. The most active fraction of tissue minerals is the trace minerals in enzymes of metabolic pathways. As the name suggests, ‘trace

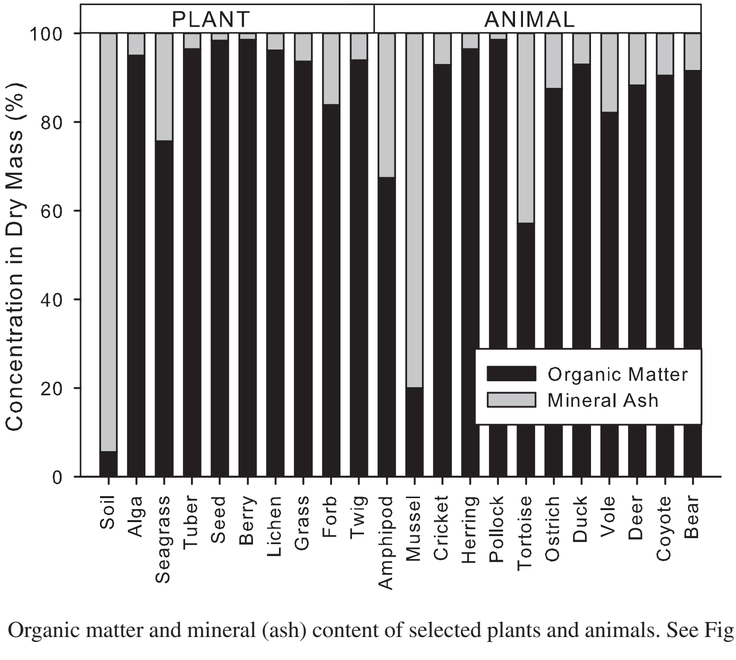


Fig. 1.3 Organic matter and mineral (ash) content of selected plants and animals. See Fig. 1.2 for details

minerals' and other nutrients such as vitamins are only a tiny fraction of the body mass and are typically measured in milligrams per kilogram (mg·kg^{-1}) or micrograms per kilogram (μg·kg^{-1}) of whole or dry mass of tissue. These units are also referred to as parts per million (ppm = mg·kg^{-1}) or parts per billion (ppb = μg·kg^{-1}). The activities of trace minerals and vitamins are discussed in Chapter 9.

The organic matrix can be divided into protein, carbohydrate and fat in a similar fashion to the labels on foods for humans and domestic animals. These three components define the relative value of foods consumed by wild animals. The units for these components are usually expressed as grams per hundred grams (g·100 g^{-1}) whole mass or dry mass, but may be presented as the percentage of the organic mass (Fig. 1.4). We use the term 'crude' to indicate that precise chemical definitions are relaxed for this division: crude protein includes most compounds containing N, such as protein and nucleic acids; total carbohydrate includes sugars as well as fiber; and crude fat includes triglycerides as well as the components of cell membranes. The bulk of organic matter in plants is comprised of carbohydrate, but in animals crude protein is the principal organic component. Herbivorous animals consume foods that are quite different from their own tissues in contrast to carnivores, which digest materials that are similar to their own bodies. The consequences of this simple difference in food chemistry are discussed in relation to the functional anatomy of the digestive system in Chapter 5. The compositional difference between plants and animals partly reflects the structural roles of carbohydrates in plants and protein in animals, but components of both fractions are also involved in the intermediary

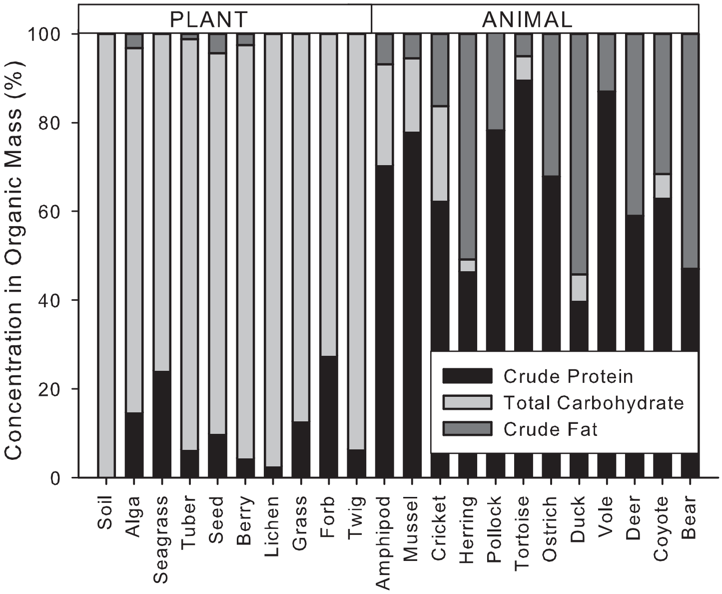


Fig. 1.4 Crude protein, total carbohydrate and crude fat in the organic mass of selected plants and animals. See Fig. 1.2 for details

metabolism of all organisms. The importance of carbohydrates and organic N in the structure and function of animals and their foods is discussed in Chapters 6 and 8.

Dietary organic matter can be oxidized as fuel or deposited in tissue for later use. Crude fat is the most energy-dense component of tissue because fat contains more C than either protein or carbohydrate, and because the C in fat is the most reduced and therefore yields the highest amount of oxidizable energy. Fat content varies widely among fish, reptiles, birds and mammals depending on the role of fat as an energy depot (Fig. 1.4). The energy available in crude fat, crude protein and total carbohydrate of tissue can be approximated from Atwater's physiological fuel values: $9\,\mathrm{kcal\cdot g^{-1}}$ fat, $4\,\mathrm{kcal\cdot g^{-1}}$ protein, $4\,\mathrm{kcal\cdot g^{-1}}$ carbohydrate (Atwater and Bryant 1900) (Fig. 1.5). The kilocalorie (kcal) is the principal unit used in public health and agriculture in the United States of America, but the kilojoule (kJ) is more commonly used throughout the world and in the scientific literature on wildlife. We use the units of the Système Internationale throughout this book. Energy contents are presented in kilojoules by using the conversion of 4.184 kJ for each kilocalorie.

Energy contents can be calculated on the basis of dry or organic mass of food since water and ash have no 'fuel value' to animals. Large fractions of ash reduce the overall energy density on the basis of dry tissue. For example, the energy density of soil, mussels and the tortoise in Fig. 1.5 are low due to the high ash content of the dry matter. Although fuel values are used to estimate the energy content of foods for humans and companion animals such as cats and dogs, the values are best used only as a general guide for the maximum energetic content of foods for wildlife.

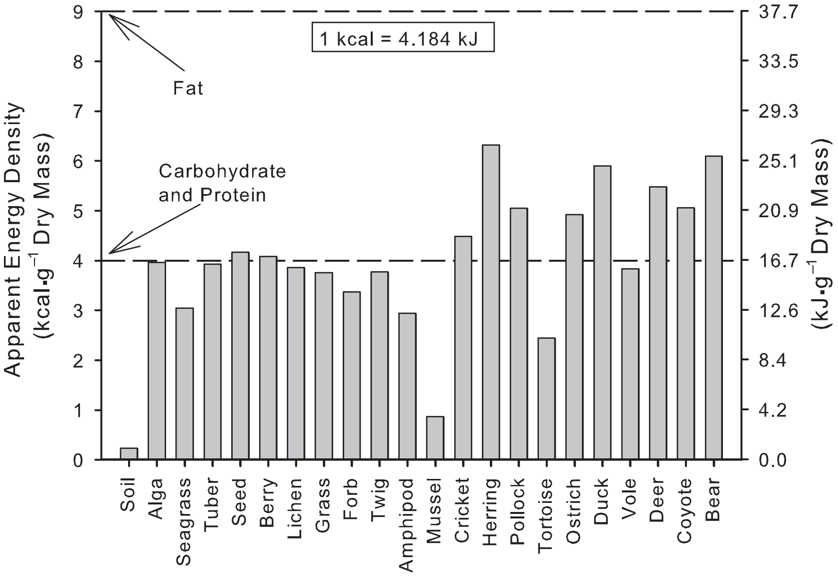


Fig. 1.5 Estimated energy content in dry mass based on Atwater's physiological fuel values (*broken lines*) (Atwater and Bryant 1900) for carbohydrate, crude protein and crude fat. See Fig. 1.2 for details

Table 1.2 The potential yield of energy is calculated with Atwater's fuel values for the corresponding amounts of fat, protein and carbohydrate in a diet. In this example we use the composition of blueberries (*Vaccinium* sp.)

Parameter	Calculation	Result
Whole mass (g)	A	2000
Dry matter (g)	B	315.8
Fat (g)	C	7.7
Protein (g)	D	13.6
Carbohydrate[1] (g)	E	241
Energy[2] from fat (kJ)	F = C × 9 × 4.184	290
Energy[2] from protein (kJ)	G = D × 4 × 4.184	227
Energy[2] from carbohydrate (kJ)	H = E × 4 × 4.184	4,041
Total 'fuel' value (kJ)	I = F + G + H	4,558
Energy density ($kJ \cdot g^{-1}$ DM)	J = I ÷ B	14.8
Energy density ($kJ \cdot g^{-1}$ whole mass)	K = I ÷ A	2.28

[1] Carbohydrate content is based on the non-structural components such as starch for calculations of available energy. We discuss the energy yields from fiber, starch and sugar in Chapters 6 and 10.

[2] Energy equivalents from Atwater's fuel values of 9 $kcal \cdot g^{-1}$ fat and 4 $kcal \cdot g^{-1}$ protein and carbohydrate. Kilocalories are converted to kilojoules with the factor 4.184 ($kcal \cdot kJ^{-1}$).

For example, the energy available to a bear (Family Ursidae) consuming 2,000 g of berries is calculated as 4,558 kJ in Table 1.2. The bear can therefore extract up to 1.92 kJ of energy from each gram of fresh berries. Such fuel values are then used to assess the energy yield from a food item in relation to the cost of finding and processing the food (Chapter 3). The assumptions of fuel values and the conversion of dietary substrates to energy for herbivores and carnivores are discussed in Chapters 6 through 10.

1.3 Scaling Body Size and Demands for Energy and Nutrients

The relationship between body size and resource demands is critical to wildlife science, especially when applying nutritional requirements across wide ranges of body size both among and within species. Body mass varies by over 50% among populations of Canada geese (Bellrose 1976) and white-tailed deer, as well as between sexes of dimorphic species such as caribou (Wilson and Ruff 1999). The nutrient demand of a large animal is not always a simple multiplication of the demand for a small animal because the requirement of each unit of body mass (grams or kilojoules per day per kilogram; $g \cdot d^{-1} \cdot kg^{-1}$ or $kJ \cdot d^{-1} \cdot kg^{-1}$) can vary with body size. In Canada geese the energy requirements of the smallest races in Alaska are probably higher per unit body mass than the largest races in the Mississippi flyway.

Relationships between body mass or size (M) and a dependent variable (Y) such as home range area, daily energy expenditure or capacity of the digestive tract are called allometric relationships. These relationships are of the form:

$$Y= a\bullet M^b \tag{1.1}$$

where ‘a’ is a constant and ‘b’ is a scalar for body mass. If the scalar differs from 1.00, then the relationship is curvilinear, that is, Y changes disproportionately to body mass (Fig. 1.6). Curvilinear relationships may be plotted on logarithmic axes to provide straight lines with different slopes (b) that intersect when M = 1 ($\log_{10}1 = 0$) at Y = $\log_{10}a$ (Fig. 1.6).

Scalars greater than one predict that Y increases more quickly than body mass whereas scalars less than one predict slower changes in Y as body size is gained. For example, scalars for ungulates are greater than one for home range area, equal to one for digestive tract capacity and less than one for energy demand (Reiss 1989). Large ungulates may therefore require much greater areas but use less food than the same total mass of smaller animals. The interactions between scalars for dependent variables such as food quality, energy demand and digestive tract capacity are discussed in Chapters 2 to 5.

The utility of allometric relationships can be illustrated with an example of the use of a hypothetical nutrient by Canada geese (Table 1.3). In this example, A = 100 $mg\cdot d^{-1}$ and B = 0.75. Increasing the body mass of geese by 50% from 1 kg to 1.5 kg only increases the daily demand by 36% because the scalar is less than 1. A total biomass of 1000 geese at 1000 kg will therefore use 100,000 mg each day. The same resource of 100,000 mg of the nutrient will support only 738 birds, each weighing 1.5 kg body mass (Table 1.3) because the scalar is 0.75 rather than 1.0. Only 667 birds would be supported by this resource if B was 1.0. Increasing the scalar to 1.25 further reduces the nutritional carrying capacity to 602 birds. Failure to account for body size when applying an estimate determined with one size class

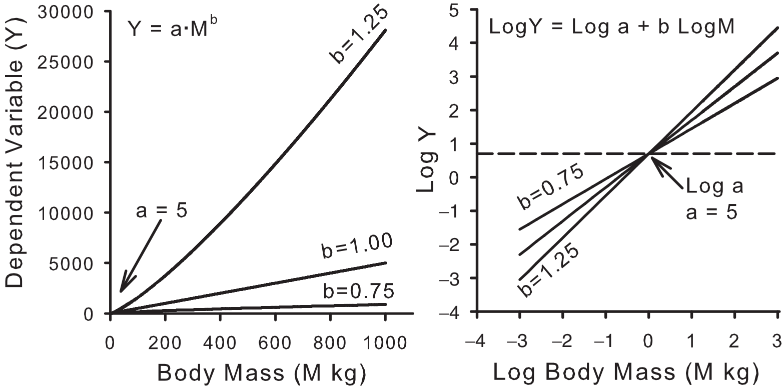


Fig. 1.6 Representative allometric relationships between a dependent variable (Y) and body mass (kg)

Table 1.3 Estimates of the number of geese that can meet their demands from a common resource when body size is increased with different scalars for the rate of nutrient use

Parameter	Calculation	Small geese	|——— Large geese		———|
Rate of use ($mg \cdot d^{-1}$)	A	100	100	100	100
Scalar	B	0.75	0.75	1	1.25
Body mass (kg)	C	1	1.5	1.5	1.5
Individual demand ($mg \cdot d^{-1}$)	$D = A \times C^B$	100[1]	136	150	166
Resource available (mg)	E	100,000	100,000	100,000	100,000
Carrying capacity (number of animals)	$F = E \div D$	1,000	738	667	602

[1] D = A when C = 1 because 1 to any scalar is still 1.

to animals of a different body size may underestimate or overestimate the resources needed for a population and contribute to starvation or overabundance. We further discuss allometry and resource use by populations in Chapters 2 and 3.

1.4 Dietary Requirements and Nutritional Niche

We use the term ‘requirement’ to refer to the amount of water, nutrients or energy needed by an animal from its diet. Animals can temporarily use their body tissues to maintain body function during a fast, but those demands are usually referred to as minimal or fasting rates of metabolism or expenditure (Chapter 10). Food intakes ultimately support the return of body tissues after a fast, maintenance of body tissue during regular feeding, and the synthesis of new tissue during growth or reproduction. The amount of a nutrient required by an animal, therefore, increases with metabolic demands from maintenance of body mass (zero gain or loss of nutrient) to net gains of nutrients during seasonal mass gain, growth or reproduction. (Fig. 1.7).

All animals require a source of oxidizable C for energy. Intermediary metabolic pathways allow animals to derive that energy from dietary carbohydrate, protein and fat (Chapters 6 to 10). The source of nutrients for maintaining and growing body tissues may vary with intermediary metabolism, but a preformed dietary source can be essential for some species. Dietary vitamin C, for example, is required by some birds and some rodents, humans, other primates and bony fish. Essentiality of a nutrient varies among species because intermediary pathways of metabolism vary with genotype. There are two levels of essentiality: complete and conditional. Complete essentiality indicates that the animal cannot synthesize a nutrient from common precursors due to the absence of an enzyme or the production of an inactive enzyme in a pathway (Chapters 8 and 9). Vitamin C is essential for species that lack one enzyme for conversion of glucose to ascorbic acid. Conditional essentiality means that the nutrient is required in the diet when demands are elevated by growth or reproduction. The enzyme pathways are present, but they are not sufficiently active to meet the demands of a particular condition. The amino acid

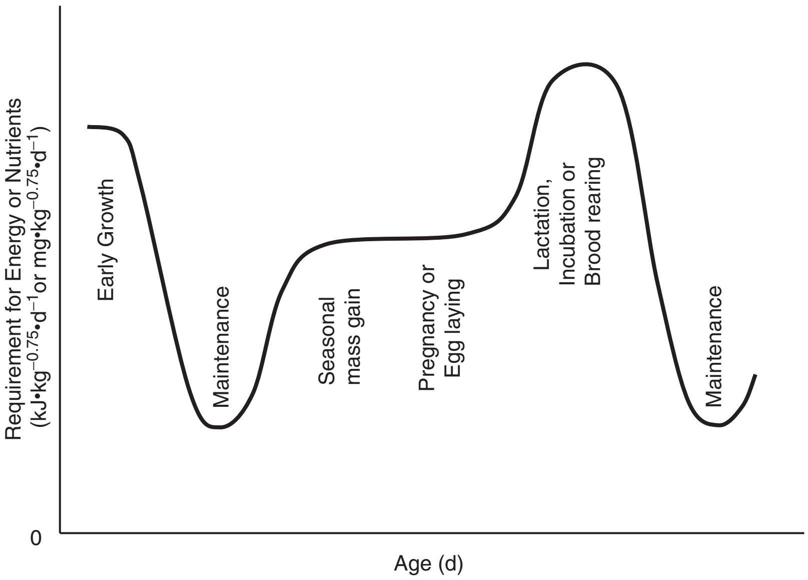


Fig. 1.7 Mass-specific requirements for energy (kJ·kg$^{-0.75}$·d^{-1}) and nutrients (mg·kg$^{-0.75}$·d^{-1}) change with metabolic demands during the life of an animal. Requirements are lowest for maintenance of body mass when animals are neither growing nor reproducing. Deposition of tissues increases requirements above maintenance during growth, seasonal mass gain or maturation, and during each phase of reproduction. This general pattern varies among species because absolute requirements and the duration of each stage vary with life history. (Adapted from Hume 1999; see Chapters 2 and 10.)

histidine is not required for rodents and humans for adult maintenance, but is required in the diet during growth. Requirements for completely and conditionally essential nutrients may be increased by interactions between nutrients and by disease. Dietary requirements for copper (Cu), for example, can be increased in young animals when rates of bacterial infection are high (Linder 1991).

Intakes of essential nutrients range from deficiency through sufficiency to toxicity. Intakes below a requirement are deficient and are accompanied by specific symptoms that directly or indirectly reflect the metabolic role of the nutrient. Night-blindness in mammals is symptomatic of vitamin A deficiency because vitamin A metabolites are required for light transmission at the retina of the eye (Chapter 9). High intakes of essential nutrients that are stored in the body may be potentially toxic. Overconsumption (toxicity) of vitamin A can lead to bone remodeling and skin loss because vitamin A metabolites also signal cellular division which is disrupted during toxicity.

Nutritional pathologies can be complex and difficult to resolve because more than one toxicity and/or deficiency may be involved. The presence of a single anomaly is usually referred to as a primary toxicity or deficiency, whereas interactions between nutrients are secondary toxicities or deficiencies. Excess intakes of zinc (Zn) in primates produce a primary toxicity with secondary effects on Cu that are symptomatic of a Cu deficiency. Normal health is only restored by treating the primary problem, in this case, the source of excess Zn consumption; the addition of Cu to the diet would only remedy some but not all pathologies. We further discuss nutritional deficiencies and toxicities for wildlife in Chapter 9.

Although the absence of toxic or deficient symptoms suggests adequate intakes, a quantitative measure of adequacy is most useful in determining the range of dietary solutions available to wildlife populations. Adequacy of diets is usually measured in relation to the requirements of an animal. Requirements may be measured through two different approaches: minimal and optimal.

A minimal requirement is commonly estimated from the relationship between nutrient balance and nutrient intake (Fig. 1.8). In this relationship, the Y axis is a measure of the nutrient retained in the body so that values above zero indicate net gains and values below zero indicate net losses. Nutrient intake (amount per time) or nutrient density (amount per mass of food) is plotted on the X axis. Minimal requirement is estimated as the nutrient intake or dietary content at zero balance. This approach is often used to define the requirement for maintenance of the body. Total requirements for activity, thermoregulation, growth or reproduction can be subsequently estimated by adding the costs of energy or nutrients for these demands to the maintenance costs (Table 1.4). We further discuss this factorial approach to estimating N and energy requirements in Chapters 8 and 10.

Requirements for growth and production are also measured with an optimal approach (Fig. 1.9) that is an extension of the minimal approach (Fig. 1.8). A productive response by the animal, such as mass gain or number of eggs, on the Y axis is plotted against the broad range of possible nutrient intakes or dietary content on the X axis (Fig. 1.9). The optimal intake or dietary content of a specific nutrient is

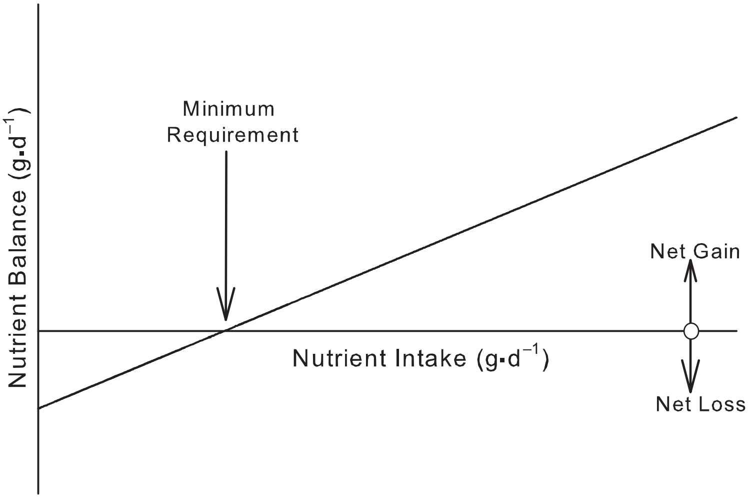


Fig. 1.8 The minimal requirement for a nutrient is estimated as the nutrient intake at zero balance (no net gain or loss)

Table 1.4 The factorial approach to estimating the total requirement for energy (kJ) in female cervids at two body sizes. Mass-specific rates for maintenance are derived from a relationship between energy intake and balance similar to that shown in Fig. 1.8

Parameter	Calculation	Small size	Large size
Body mass (kg)	A	100	150
Scalar	B	0.75	0.75
Mass-specific rate for maintenance ($kJ \cdot kg^{-0.75} \cdot d^{-1}$)	C	293	293
Maintenance cost ($kJ \cdot d^{-1}$)	$D = C \times A^B$	9,265	12,558
Activity (× maintenance)	E	0.5	0.5
Reproduction (× maintenance)	F	1.0	1.0
Additional costs ($kJ \cdot d^{-1}$)	$G = D \times (E + F)$	13,898	18,838
Requirement ($kJ \cdot d^{-1}$)	$H = D + G$	23,164	31,396

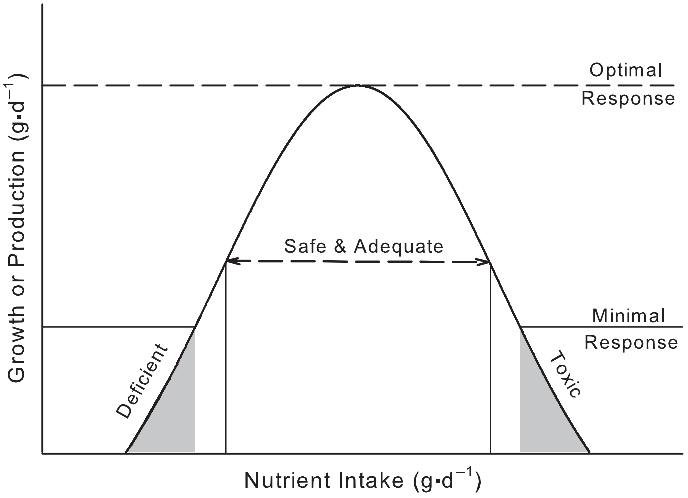


Fig. 1.9 The optimal nutrient requirement is estimated as the nutrient intake at maximum response for growth or reproduction. Intakes in the *shaded regions* are deficient or toxic because they fail to support minimum growth or production for the species. Safe and adequate intakes of the nutrient support growth or production above the minimum response

estimated at the maximum response. A range of optimal intakes is usually defined for species of domestic animals depending on environmental conditions (e.g., temperature) and genetics (e.g., race, breed). The shape of this relationship may vary with the potential for nutrient accumulation in the body. If the nutrient does not accumulate and is rapidly excreted, then the relationship reaches a plateau at the optimal response. For example, animals do not retain increasing amounts of dietary N once they reach the maximum rate of depositing N in proteins, but rather excrete the excess N to avoid toxic accumulations of ammonia (Chapter 8). Nutrients that accumulate in the body may be toxic if production is impaired when high intakes deposit large loads in the body (Fig. 1.9) (Moriarty 1999). In desert ungulates, overconsumption of milk vetch may cause toxic accumulation of selenium (Se), which impairs movement and cell function.