John M. Fryxell, Anthony R. E. Sinclair and Graeme Caughley

Wildlife Ecology, Conservation, and Management

THIRD EDITION

Companion Website

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To our colleagues Graeme Caughley, Jamie Smith, and Peter Yodzis, who have influenced both our approach to wildlife biology and the writing of this book.

Wildlife Ecology, Conservation, and Management

Third Edition

John M. Fryxell PhD
Department of Integrative Biology, University of Guelph, Guelph, Canada

Anthony R. E. Sinclair PhD
Biodiversity Research Centre, University of British Columbia, Vancouver, Canada

The late Graeme Caughley PhD
CSIRO, Canberra, Australia

WILEY Blackwell

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Preface

Modern principles of sustainable management and conservation of wildlife species require a clear understanding of demography, animal behavior, and ecosystem dynamics. Our book weaves together these disparate elements in a single coherent text intended for senior undergraduate and graduate students. The first half provides a solid background in key ecological concepts such as demography, population growth and regulation, competition within and among species, and predator–prey interactions. The second half uses these key ecological concepts to develop a deeper understanding of the principles underlying wildlife management and conservation, including population viability assessment, sustainable harvesting, landscape planning, and ecosystem management.

New quantitative methods, developed over the last 10 years, are now so fundamental to management that we have included them at the most basic levels. Several chapters of the book will be useful to practicing wildlife managers. For example, we have included modern approaches to estimating animal abundance and habitat selectivity, the use of age- and stage-structured data in demography studies, and the use of models as efficient methods for making conservation and management decisions. As a study aid, we have included a wide variety of downloadable computer programs in R and Mathcad on an accompanying website. These are intended to help readers develop a solid understanding of key statistical procedures and population models commonly used in wildlife ecology and management.

In this edition we have arranged the sequence of chapters to reflect the progression from individuals to populations, communities, and ecosystems. Four new chapters have been added to cover rapidly developing topics: effects of climate change on wildlife, the evolutionary response by wildlife populations to rapidly changing conditions, home range use and habitat selection as a consequence of patterns of individual movement, and the importance of corridor use and metapopulation dynamics for wildlife populations living in the highly fragmented landscapes that increasingly characterize the modern world.

Anne Gunn and David Grice were invaluable in bringing together the first edition of this book after Graeme Caughley fell ill. Fleur Sheard prepared the line drawings for that edition. Since then we have continued to benefit from the helpful contributions of a number of people, including Tal Avgar, Andrew McAdam, Cort Griswold, David Grice, Sue Briggs, Andrea Byrom, Steve Cork, Charles Krebs, Graham Nugent, John Parkes, Roger Pech, Laura Prugh, Wendy Ruscoe, Dolph Schluter, Julian Seddon, Grant Singleton, David Spratt, Eric Spurr, Vernon Thomas, and Bruce Warburton. We also thank the Natural Sciences and Engineering Research Council of Canada for continuing support over the years.

Our close friend and colleague, Graeme Caughley, died in 1994. We have retained the substance and spirit of his scholarship, expanding the fields where advances have occurred since the first edition. For this new edition we are indebted to Sue Pennant and Anne Sinclair, who are always willing (if not necessarily eager) to provide a fresh set of eyes for proofreading of the new material.

About the companion website

This book is accompanied by a companion website:

www.wiley.com/go/Fryxell/Wildlife

The website includes:

- Additional resources
- Powerpoints of all figures from the book for downloading
- PDFs of all tables from the book for downloading

1 Introduction: goals and decisions

1.1 How to use this book

This book is structured as two interlocking parts. The first provides an overview of wildlife ecology, as distinct from that portion of applied ecology that is called wildlife management and conservation. The chapters on wildlife ecology (Chapters 2–11) cover such topics as growth and regulation of wildlife populations, spatial patterns of population distribution, and interactions among plants, herbivores, carnivores, and disease pathogens. While these topics are often covered in introductory biology or ecology courses, they rarely focus on the issues of most concern to a wildlife specialist. A solid understanding of ecological concepts is vital in formulating successful wildlife conservation and management policy. In particular, you will need an understanding of the theory of population dynamics and of the relationship between populations, their predators, and their resources if you are to make sensible judgments on the likely consequences of one management action versus another.

The second section deals with wildlife conservation and management (Chapters 12–22). These chapters cover census techniques, how to test hypotheses experimentally, how to evaluate alternative models as tools for conservation and management, and the three major aspects of wildlife management: conservation, sustained yield, and control. In closing, Chapter 22 places the problems of wildlife management into the context of the ecosystem. Species populations cannot be managed in isolation because they are influenced by, and they themselves influence, many other components of the ecosystem. In the long run, wildlife management becomes ecosystem management.

Many of the key issues in wildlife ecology are of a quantitative nature: processes of population growth, spatial distribution, or interactions with the physical environment or other organisms. Coping with these topics demands conceptual understanding of quantitative ecology. Mathematical models are also an essential component of decision-making in both wildlife conservation and management, for the simple reason that we can rarely rely on previous experience to identify the most appropriate choices. Every problem is unique: new species, new sets of challenges and constraints, all taking place in a continually changing physical environment. Mathematical models provide a useful tool for dealing appropriately with these uncertainties. Moreover, mathematical models help to clarify the logic that guides our thinking.

To assist in developing the requisite skills, many of the models and statistical analyses covered in the book can be obtained via a link at Fryxell's departmental Web page (http://www.uoguelph.ca/ib/people/faculty/fryxell.shtml). This provides a set of text files suitable for application using "R," a nonproprietary (i.e. free) software package that has been developed by a hard-working and highly committed group

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of professional scientists and statisticians from all around the world. By learning to perform the examples used to illustrate this book, you will both expand your familiarity with useful mathematical principles and hone the problem-solving skills involved in modern wildlife ecology, conservation, and management. This can prove invaluable in future professional endeavors.

The R package provides a powerful set of integrated tools for numerical computation, statistical analysis, and graphical depiction of data and results. More information about R can be found at the R project homepage, www.r-project.org, while instructions on how to download R can be found at the CRAN repository for R materials, http://cran.r-project.org.

1.2 What is wildlife conservation and management?

The remainder of this chapter explains what wildlife management is, how it relates to conservation, and how it should operate. We discuss the difference between value judgments and technical judgments and how these relate to goals and policies compared to options and actions; we enumerate the various steps involved in deciding what to do and how to do it; and we describe decision analyses and matrices and how they help in evaluating feasible management options.

Wildlife is a word whose meaning expands and contracts according to the viewpoint of the user. Sometimes it is used to include all wild animals and plants. More often it is restricted to terrestrial vertebrates. In the discipline of wildlife management it designates free-ranging birds and mammals, and that is the way it is used here. Until about 25 years ago, "wildlife" was synonymous with *game*: those birds and mammals that were hunted for sport. The management of such species is still an integral part of wildlife management, but increasingly it embraces other aspects too, such as conservation of endangered species.

Wildlife management may be defined for present purposes as the *management of wildlife populations in the context of the ecosystem*. That may be too restrictive for some, who would argue that many of the problems of management deal with people and, therefore, that education, extension, park management, law enforcement, economics, and land evaluation are legitimate aspects of wildlife management and ought to be included within its definition. They have a point, but the expansion of the definition to take in all these aspects diverts attention from the core around which management activities are organized: the manipulation or protection of a population to achieve a goal. Obviously, people must be informed as to what is being done; they must be given an understanding of why it is necessary, their opinions must be canvassed, and their behavior may have to be regulated with respect to that goal. However, the most important task is to choose the right goal and to know enough about the animals and their habitat to ensure its attainment. Hence, wildlife management is restricted here to its literal meaning, thereby emphasizing the core at the expense of the periphery of the field. The broader extension and outreach aspects of wildlife management are dealt with thoroughly in other texts devoted to those subjects (Lyster 1985; Geist and McTaggert-Cowan 1995; Moulton and Sanderson 1999; Vásárhelyi and Thomas 2003).

1.2.1 *Kinds of management*

Wildlife management implies stewardship; that is, the looking after of a population. A population is a group of coexisting individuals of the same species. When stewardship fails, conservation becomes imperative. Under these circumstances, wildlife management shifts to remedial or restoration activities.

Wildlife management may be either *manipulative* or *custodial*. Manipulative management does something to a population, either changing its numbers by direct means or influencing them by the indirect means of altering food supply, habitat, density of predators, or prevalence of disease. Manipulative management is appropriate when a population is to be harvested, when it slides to an unacceptably low density, or when it increases to an unacceptably high level.

Custodial management, on the other hand, is preventative or protective. It is aimed at minimizing external influences on the population and its habitat. It is not aimed necessarily at stabilizing the system but rather at allowing free rein to the ecological processes that determine the dynamics of the system. Such management may be appropriate in a national park where one of the stated goals is to protect ecological processes, and it may be appropriate for the conservation of a threatened species where the threat is of external origin rather than being intrinsic to the system.

Regardless of whether manipulative or custodial management is called for, it is vital that (i) the management problem is identified correctly, (ii) the goals of management explicitly address the solution to the problem, and (iii) criteria for assessing the success of the management are clearly identified.

1.3 Goals of management

A wildlife population may be managed in one of four ways:

1 make it increase;
2 make it decrease;
3 harvest it for a continuing yield;
4 leave it alone but keep an eye on it.

These are the only options available to the manager.

Three decisions are needed: (i) What is the desired goal? (ii) Which management option is therefore appropriate? (iii) By what action is this best achieved? The first decision requires a value judgment, the others technical judgments.

1.3.1 *Who makes the decisions?*

It is not the function of the wildlife manager to make the necessary value judgments in determining the goal, any more than it is within the competence of a general to declare war. Managers may have strong personal feelings as to what they would like, but so might many others in the community at large. Managers are not necessarily provided with heightened aesthetic judgment just because they work on wildlife. They should have no more influence on the decision than does any other interested person.

However, when it comes to deciding which management options are feasible (once the goal is set) and how goals can best be attained, wildlife managers have the advantage of their professional knowledge. Now they are dealing with testable facts. They should know whether current knowledge is sufficient to allow an immediate technical decision or whether research is needed first. They can advise that a stated goal is unattainable, or that it will cost too much, or that it will cause unintended side effects. They can consider alternative routes and advise on the time, money, and effort each would require. These are all technical judgments, not value judgments. It is the task of the wildlife manager to make them and then to carry them through.

Since value judgments and technical judgments tend to get confused with each other, it is important to distinguish between them. By its essence, a value judgment is neither right nor wrong. Let us take a hypothetical example. The black rat (*Rattus rattus*) is generally unloved. It destroys stored food, it is implicated in the spread of bubonic plague and several other diseases, it contributes to the demise of endangered species, and it has been known to bite babies. Suppose a potent poison specific to this species were discovered, thereby opening up the option of removing this species from the face of the earth. Many would argue for doing just that, and swiftly. Others would argue that there are strong ethical objections to exterminating a species, however repugnant or inconvenient that species might be. Most of us would have a strong opinion one way or the other but there is no way of characterizing either competing opinion as right or wrong. That dichotomy is meaningless. A value judgment can be characterized as hardheaded or sentimental (these are also value judgments), or it may be demonstrated as inconsistent with other values a person holds, but it cannot be declared right or wrong. In contrast, technical judgments can be classified as right or wrong according to whether they succeed in achieving the stated goal.

1.3.2 *Decision analysis*

In deciding what objective (goal) is appropriate, we consider a range of influences, some dealing with the benefits of getting it right and others with the penalties of getting it wrong. Social, political, biological, and economic considerations are each examined and given due weight. Some people are good at this and others less so. In all cases, however, there is a real advantage, both to those making the final decision and to those tendering advice, to having the steps of reasoning laid out before them as the decision is approached.

At its simplest, this need mean no more than the people helping to make the decision spelling out the reasons underpinning their advice. However, with more complex problems it helps to be more formal and organized, mapping out on paper the path to the decision through the facts, influences, and values that shape it. This process should be explicit and systematic. Different people will assign different values (weights) to various possible outcomes, and, particularly if mediation by a third party is required, an explicit statement of those weights will allow a more informed decision. It helps also to determine which disagreements are arguments about facts and which are arguments about judgments of value.

Table 1.1 is an objective/action matrix in which possible objectives are ranged against feasible actions. The objectives are not mutually exclusive. It comes from the response of the Department of Agriculture of Malaysia to the attack of an insect pest on rice (Norton 1988). It allows the departmental entomologists and administrators to view the full context within which a decision must be made. Each of the listed objectives is of some importance to the department. The next step would be to rank these objectives and score the management actions most appropriate to each. The final outcome is the choice of one or more management actions that best meet the most important objective or objectives. Such very simple aids to organizing our thoughts are often the difference between success and failure.

Another such aid is the feasibility/action matrix. Table 1.2 is Bomford's (1988) analysis of management actions to reduce the damage wrought by ducks on the rice crops of the Riverina region of Australia. The feasibility criteria are here ranked so that if a management action fails according to one criterion there is no point in considering it against further ones. Note how this example effortlessly identifies areas of ignorance that would have to be attended to before a rational decision could be possible.

Our third example of decision aids is the pay-off matrix (Table 1.3). This expresses the state of nature (level of pest damage, in this example) as rows and the options for management action as columns (Norton 1988). The problem is to assess the probable outcome of each combination of the level of damage and the action mounted

Table 1.1 Possible objectives and management actions for public pest management. The initial problem is to assess how each action is likely to meet each objective. (After Norton 1988.)

	Objectives					
Actions	Improve farmers' ability to control pest	Improve farmers' incentives	Strengthen political support	Keep Dept.'s costs low	Reduce damage	Reduce future pest outbreaks
Short Term						
1 Warn and advise farmers						
2 Advise and provide credit						
3 Advise and subsidize pesticides						
4 Advise, subsidize, and supervise spraying						
5 Mass treat and charge farmers						
6 Mass treat at Dept.'s cost						
Medium Term						
7 Intensive pest surveillance						
8 Implement area wide biological control						
9 Training courses for farmers						

Table 1.2 Matrix for examining possible management actions against criteria of feasibility. (After Bomford 1988.)

	Feasibility Criteria					
Control Options	Technically possible	Practically feasible	Economically desirable	Environmentally acceptable	Politically advantageous	Socially acceptable
1 Grow another crop	1	0				
2 Grow decoy crop	1	1	?	1	1	1
3 Predators and diseases	0					
4 Sowing date	1	1	?	1	1	1
5 Sowing technique	1	1	?	1	1	1
6 Field modifications	1	1	?	1	1	1
7 Drain or clear daytime refuges	?	0				
8 Shoot	1	1	?	1	?	1
9 Prevent access, netting	1	1	0	1	1	1
10 Decoy birds or free feeding	?	1	?	1	1	
11 Repellants	1	0				
12 Deterrents	1	1	?	1	1	1
13 Poisons	1	1	?	0		
14 Resowing or transplanting seedlings	1	?	1	?	1	1

1, yes; 0, no; ?, no information.

to alleviate it. Note that the column associated with doing nothing gives the level of damage that will be sustained in the absence of action. It is the control against which the net benefit of management must be assessed. The cells of this matrix are best filled in with net revenue values (benefit minus cost) rather than with benefit/cost ratios, because it is the absolute rather than the relative gain that shapes the decision.

Table 1.3 Pay-off matrix for pest control. (Adapted from Norton 1988.)

State of Nature	Actions: Do nothing (0)	Pest Control Strategies (1)	(2)	(3)
Level of Pest Attack				
Low (L)	Outcome L, 0	Outcome L, 1	Outcome L, 2	Outcome L, 3
Medium (M)	Outcome M, 0	Outcome M, 1	Outcome M, 2	Outcome M, 3
High (H)	Outcome H, 0	Outcome H, 1	Outcome H, 2	Outcome H, 3

1.4 Hierarchies of decision

Before we begin manipulating a wildlife population and its environment, we must ask ourselves why we are doing so and what is it supposed to achieve. In management theory, that decision is usually divided into hierarchical components.

At the bottom, but here addressed first, is the management action. This might be to eliminate feral pigs (*Sus scrofa*) on Lord Howe Island off the coast of Australia. The management action must be legitimized by a technical objective; for example, to halt the decline of the Lord Howe Island woodhen (*Tricholimnas sylvestris*). Above this is the policy goal, a statement of the desired end-point of the exercise, which in this example might be to secure the continued viability of all indigenous species within the nation's National Park system.

In theory, the decisions flow from the general (the policy goal) to the specific (the management action), but in practice this does not work because each is dependent on the others, in both directions. Nothing is achieved by specifying "halt a species decline" as a technical objective unless a set of management actions is available that will secure this Obviously, a management action cannot be specified to cure a problem of unknown cause. All three levels of decision must be considered together, such that the end product is a feasible option.

A feasible option is identified by answering these questions:

1 Where do we want to go?
2 Can we get there?
3 Will we know when we have arrived?
4 How do we get there?
5 What disadvantages or penalties accrue?
6 What benefits are gained?
7 Will the benefits exceed the penalties?

The process is iterative. There is no point in persevering with the policy goal thrown up by the first question if the answer to the second is negative. The first choice of destination should instead be replaced by another, and the process repeated.

Question 3 is particularly important. It requires the formulation of stopping rules. This does not necessarily mean that management action ceases on attainment of the objective, but rather that management action is altered at this point. The initial action is designed to move the system towards the state specified by the technical objective; the subsequent action is designed to hold the system in that state. If we cannot determine when the objective has been attained, either for reasons of logic (ambiguous or abstract statement of the objective) or for technical reasons (inability to measure the state of the system), the option is not feasible.

1.5 Policy goals

Policies are usually couched in broad terms that provide no more than a general guide for the manager. The specific decisions are made when the technical objectives are formulated. However, there are two types of policy goal that the manager must know about in case they clash with the choosing of those objectives.

1.5.1 *The non-policy*

Non-policies stipulate goals that are not clearly defined. They are usually formulated in this way on purpose so that the administering agency is not tied down to a rigidly dictated course of action. Policies are usually formulated by the administering agency whether or not they are given legislative sanction. If the agency has not developed a policy, it may fill the gap with a non-policy that commits it to no specified action. Take for example the goal of "protecting intrinsic natural values." This reads well but is entirely devoid of objective meaning.

1.5.2 *The non-feasible policy*

In contrast to the relatively benign non-policy, the nonfeasible policy can be damaging. Although it may give each interest group at least something of what they desire, sometimes the logical consequence is that two or more technical objectives are mutually incompatible.

An example is provided by the International Convention for the Regulation of Whaling of 1946, which had as its goal "to provide for the proper conservation of whale stocks" and "thus make possible the orderly development of the whaling industry." This pleased both those concerned with conservation of whales and those wishing to harvest whales. Unfortunately, the goal is a nonsense, because, for reasons that are elaborated in Chapter 18, species with a low intrinsic rate of increase are not suitable for sustainable harvesting. The two halves of the policy goal contradict each other. The history of whaling since 1948, in which the blue (*Balaenoptera musculus*), the fin (*B.physalus*), the sei (*B.borealis*), the Brydes (*B.edeni*), the humpback (*Megaptera novaeangliae*), and the sperm (*Physeter macrocephalus*) were reduced to the level of economic extinction, is a direct consequence of the choice of a policy goal that was not feasible.

Another form of the nonfeasible policy is one that is so specific that it actually determines technical objectives and sometimes even management actions. If these are unattainable in practice, the policy goal itself is also unattainable. An example is provided by the now defunct policy to exterminate deer in New Zealand. It was always an impossibility.

1.6 Feasible options

Objectives must be attainable. It is the wildlife manager's task to produce the attainable technical objectives by which the policy goal is defined. In contrast to the goal, which may be described in somewhat abstract terms, a technical objective must be stated in concrete terms and rooted in geographic and ecological fact. It must be attainable in fact, and it should be attainable within a specified time. A technical objective should, therefore, be accompanied by a schedule.

1.6.1 *Criteria of failure*

It follows as a corollary that there must be an easy way of recognizing the failure to attain an objective. The most common method is to measure the outcome against that specified by the technical objective. Another is to compare the outcome with a set of *criteria of failure*, set before the management action is begun. These two methods are not the same. Comparison of outcome with objective can produce assessments such as "not quite" or "not yet." Criteria of failure cannot; they take the form, "the operation will be judged unsuccessful, and will therefore be terminated, if outcome *x* has not been attained by time *t*."

1.7 Summary

We view wildlife management as simply the management of wildlife populations. Three important points underlie any management: (i) the management problem is identified correctly; (ii) the goals of management explicitly address the solution to the problem; and (iii) criteria for assessing the success of the management are clearly identified.

Four management options are available: (i) to make the population increase; (ii) to make it decrease; (iii) to take from it a sustained yield; or (iv) to do nothing but keep an eye on it. We have first to decide our goal for the population, which will be largely a value judgment. To help us steer through social, political, and economical influences, we use a decision analysis to reveal these influences and their effects on goals and policies. A series of questions about the selected option must be posed and answered to ensure that it is feasible and that its success or failure can be determined.

Part 1

Wildlife ecology

2 Food and nutrition

2.1 Introduction

The three main areas of wildlife management (conservation, sustained yield, and control) require knowledge of the food and nutrition of animal populations. Some of the important questions are:

1 Is there enough food to support and conserve a particular rare or endangered species?
2 What is the food supply needed to support a particular sustained yield?
3 Can we alter the food supply so as to provide more effective control of pest populations?

The field of animal nutrition covers subjects such as anatomy, physiology, and ecology, and there are several good reviews of these areas; for example, Hofmann (1973) deals with the anatomy of ruminants, Robbins (1983) addresses the physiology of wildlife nutrition, and Chivers and Langer (1994) review the form, function, and evolution of the digestive system in mammals. From the point of view of wildlife management, however, we are interested in two main types of information if we are to answer the preceding questions: we need to know (i) the availability of the food and (ii) the requirements of the animals. By matching the two sets of information, we can answer these questions. Sections 2.2–2.4 deal with availability, while Sections 2.5–2.9 address animal requirements.

2.2 Constituents of food

2.2.1 *Energy*

Energy is measured in units of calories or joules (1 cal = 4.184 joules). The energy contents of foods can be found by oxidizing a sample in a bomb calorimeter. Differences in the energy contents of different plant and animal materials result from the differences in their constituents. The energy contents of some common food components are given in Table 2.1. We can see that fats and oils have the highest content (over 9 kcal/g), followed by proteins (around 5 kcal/g) and then sugars and starches (carbohydrates; close to 4 kcal/g). The gross energy of a tissue depends on the combination of these basic constituents, particularly in animals. In plant tissues, energy content remains relatively uniform, in the region of 4.0–4.2 kcal/g. Plant parts with a high oil content, such as seeds (over 5 kcal/g), and evergreen plants with waxes and resins, such as conifers and alpine plants (4.7 kcal/g), are the exceptions (Golley 1961; Robbins 1983).

Energy flow through animals can be measured with isotopes of hydrogen (^{3}H) and oxygen (^{18}O) by the *doubly labelled water method* (Nagy 1983; Bryant 1989). First, water labeled with ^{3}H and ^{18}O is injected and allowed to equilibrate in the animal, this taking 2–8 hours depending on body size. A blood sample is then collected to establish the starting concentrations of the two isotopes. Analysis of ^{3}H is carried out by liquid

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Table 2.1 Approximate energy contents of food components.
(Source: Robbins, 1983. Reproduced with permission of Elsevier.)

Food Component	Energy (kcal/g)
Fat	9.45
Protein	5.65
Starch	4.23
Cellulose	4.18
Sucrose	3.96
Urea	2.53
Leaves	4.23
Stems	4.27
Seeds	5.07

scintillation spectrophotometry and that of ^{18}O by proton activation of ^{18}O to ^{18}F (the isotope of fluoride), with subsequent counting of γ-emitting F in a γ-counter. A second blood sample is collected several days later. The timing of the second collection does not need to be exact, but it should occur when approximately half of the isotope has been flushed from the body. Thus, timing depends on body size and the flow rates of the isotopes. Oxygen leaves the body via CO_2 and water, at a rate measured by dilution of the ^{18}O. Rate of water loss is measured from the dilution of ^3H. Thus, the difference between the total oxygen loss and the oxygen loss in water gives the rate of CO_2 production, which is a measure of energy expenditure. The method and its validation are described by Nagy (1980, 1989).

2.2.2 *Protein*

The term *protein* covers a varied group of high-molecular-weight compounds; these are major components in cell walls, enzymes, hormones, and lipoproteins and are made up of about 25 amino acids linked together through nitrogen–carbon peptide bonds. Most animal species have a relatively similar gross composition of amino acids.

Animals with simple stomachs require 10 *essential amino acids*, these being the forms that cannot be synthesized by the animal and must be obtained in the diet: arginine, histidine, isoleucine, leucine, threonine, lysine, methionine, phenylalanine, tryptophan, and valine. *Nonessential amino acids*, therefore, are ones which can be synthesized in the body. Ruminants, as well as other species that rely on fermentation through the use of microorganisms, synthesize many of the amino acids themselves and so have a shorter list of essential amino acids.

Although there is some variability in the nitrogen content of amino acids (ranging from 8 to 19%), the average is 16%. Thus, in analyzing tissues for *crude protein*, the proportion composed of nitrogen is multiplied by the constant 4.25 (i.e. 100/16). The crude protein content of plant material tends to vary inversely with the proportion of fiber. Since one of the major constituents of fiber is the indigestible compound lignin, fiber content can be used as an index of the nutritive value of the plant food. In many plant tissues, such as leaves and stems, protein and digestible energy content (i.e. the non-fiber component) tend to vary together. However, some plant parts, such as seeds, are high in energy but quite low in protein.

2.2.3 *Water*

The water content of birds and mammals is a function of body weight (W) to the power of 0.98 when comparing across species, but more restricted groups vary in the exponent. Robbins (1983) found the water content of white-tailed deer and several rodents varied as a function of $W^{0.9}$.

Water is obtained from three sources:

1 *Free water* From external sources such as streams and ponds.
2 *Preformed water* Found in the food.
3 *Metabolic water* Produced in the body from the oxidation of organic compounds.

Preformed water is high in animal tissues such as muscle (72%) and in succulent plants, roots, and tubers. Because of this, carnivores may not have to drink often; herbivores such as the desert-adapted antelope, oryx, which eat fleshy leaves and dig up roots, can also live without free water (Taylor 1969; Root 1972).

The highest rate of production of metabolic water in animals comes from the oxidation (catabolism) of proteins, due to their initially high water content. Catabolism of fats produces 107% of the original fat weight as water, but the low preformed water content (3–7%) means that the absolute amount produced is less than that from protein (Robbins 1983).

Measures of free water intake from drinking underestimate total water turnover. More accurate methods use the ^{3}H or deuterium oxide isotopes of water: a known sample of isotopic water is injected into an animal, and after a period of 2–8 hours (depending on size of animal) for equilibration, a blood sample is collected; the concentration of isotope in the blood is then measured using a liquid scintillation spectrometer. A second blood sample is collected a few days to a few weeks later, again depending on body size, providing a new value of isotope concentration. Because water is lost through feces, urine, and evaporation, the isotope is diluted by incoming water. Therefore, the rate of dilution is a measure of water turnover. These techniques are described by Nagy and Peterson (1988) and have been used on a wide range of animals, including eutherian mammals, marsupials, birds, reptiles, and fishes.

2.2.4 *Minerals*

Minerals make up only 5% of body composition but are essential to body function. Some minerals (roughly in order of abundance: calcium, phosphorus, potassium, sodium, magnesium, chlorine, sulfur) are present or required in relatively large amounts (mg/g) and are called *macroelements*. Those that are required in small amounts (μg/g) are called trace elements (iron, zinc, manganese, copper, molybdenum, iodine, selenium, cobalt, fluoride, chromium). So far, very little is known about the mineral requirements of wildlife species, but Robbins (1983) has provided a summary of available information. It is assumed that most native species are adapted to their environment and so can tolerate the levels of minerals found there (Fielder 1986). However, some mineral deficiencies have been observed. Selenium deficiency increases the mortality of juvenile, preweaned mammals (Keen and Graham 1989). Flueck (1994) supplemented wild black-tailed deer in California and increased preweaning fawn survival threefold.

Calcium and phosphorus are essential for bones and eggshells. Cervids have a very high demand for these minerals during antler growth. Calcium is also needed during lactation, for blood clotting, and for muscle contraction. Phosphorus is present in most organic compounds. Deficiencies of calcium result in osteoporosis, rickets, hemorrhaging, thin eggshells, and reduced feather growth. Carnivores that normally eat the flesh of large mammals need to chew bone in order to obtain their calcium. Mundy and Ledger (1976) found that the chicks of Cape vultures (*Gyps coprotheres*) in South Africa developed rickets when they were unable to eat small bone fragments. This has an important management consequence: bone fragments from large carcasses are made available to vultures by large carnivores, in this case lions and hyenas; where carnivores are exterminated on ranch land, carcasses are not dismembered and bones are too large for the chicks to swallow. This is a good example of how the interaction of species should be considered in the management and conservation of habitats.

Sodium is required for the regulation of body fluids, muscle contraction, and nerve impulse transmission. Sodium is usually found in low concentrations in plants, so herbivores face a potential sodium deficiency. In areas of low sodium availability, herbivores consume soil or water from mineral licks (Weir 1972; Fraser and Reardon 1980). Carnivores can easily obtain sodium from their food, and so are unlikely to experience sodium deficiency. Isotopic sodium has been used as a measure of the food intake rates of carnivores such as lions (Green *et al*. 1984), seals (Tedman and Green 1987), crocodiles (Grigg *et al*. 1986), and birds (Green and Brothers 1989). This approach is possible because sodium remains at a relatively constant concentration in the food supply. The technique is similar to that for isotopic water described in Section 2.2.3.

Both potassium and magnesium are abundant in plants, and deficiencies in free-living wildlife are therefore unlikely. The same is true for chloride ions and for sulfur. Trace element deficiencies are unusual under normal free-ranging conditions but they occur locally from low concentrations in the soil: there are some reports of iodine and copper deficiencies and of toxicity from too much copper and selenium (Robbins 1983).

2.2.5 *Vitamins*

Vitamins are essential organic compounds that occur in minute amounts in food and cannot normally be synthesized by animals. There are two types of vitamin: fat-soluble (vitamins A, D, E, and K) and water-soluble (vitamin B complex, vitamin C, and several others). Fat-soluble vitamins can be stored in the body. Water-soluble vitamins cannot be stored and hence must be constantly available. Overdose toxicities can arise only from the fat-soluble vitamins.

Vitamin A, a major constituent of visual pigments, can be obtained from β-carotene in plants. Vitamin D is needed for calcium transport and the prevention of rickets. Vitamin E is an antioxidant needed in many metabolic pathways; it is high in green plants and seeds, but decreases as the plants mature. Vitamin K is needed to make proteins for blood clotting. Deficiencies are unlikely to occur because it is common in all foods. The vitamin K antagonist, warfarin, causes hemorrhaging. It is used as a rodenticide.

Little is known about the B-complex vitamins and whether deficiencies occur in free-living wildlife species, although cases of thiamin (B1) deficiency have been reported for captive animals (Robbins 1983). Vitamin C differs from the others in that most species can synthesize it in either the kidneys or liver. Exceptions include primates, bats, guinea pigs, and possibly whales. Vitamin C is not as commonly available as the B vitamins but is found in green plants and fruit. It is absent in seeds, bacteria, and protozoa.

Other physiological constraints that may not be called vitamins nevertheless provide limits to animal nutrition. For example, old-world starlings and flycatchers cannot digest sucrose (Martinez del Rio 1990).

2.3 Variation in food supply

2.3.1 *Seasonality*

Food supply varies with season. To some degree, all environments are seasonal, including those of the tropics. Food supply is greatest for herbivores when plants are growing: during the summer at higher latitudes (temperate and polar regions) and during the rainy season in lower ones (tropics and subtropics). Protein in grass and leaves declines from high levels of 15–20% in young growth to as little as 3% in mature flowering grass,