

# Analysis and Management of Animal Populations

*Modeling, Estimation, and Decision Making*

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# Introduction to Population Ecology

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In this chapter we introduce the concept of a population that changes over time, in response to primary biological processes that influence population dynamics. We discuss the concepts of density dependence and density independence in these processes, and their roles in regulating and limiting population growth. We incorporate these concepts into a biological context of conservation and management of animal populations. The framework of population dynamics as influenced by primary biological processes and their vital rates will be seen to be useful across ecological scales, and in particular will be seen to contribute to a unified frame of reference for investigations at the scale of individuals (evolutionary ecology), populations, and communities.

## 1.1. SOME DEFINITIONS

A *population* often is defined as a group of organisms of the same species occupying a particular space at a

particular time (e.g., Krebs, 1972), with the potential to breed with each other. Because they tend to prefer the same habitats and utilize the same resources, individuals in a population may interact with each other directly, for example, via territorial and reproductive behaviors, or indirectly through their use of common resources or occupation of common habitat. Spatial boundaries defining populations sometimes are easily identified (e.g., organisms inhabiting small islands or isolated habitat patches) but more typically are vague and difficult to determine. Spatial and temporal boundaries often are defined by an investigator; however, this arbitrariness does not detract from the utility of the population concept.

A key quantity in population biology is population size, which refers to the number of individual organisms in a population at a particular time. In this book, the terms *abundance* and *population size* are used synonymously. We reserve the term *density* for the number of organisms relative to some critical resource. Typically the critical resource is space, so that density represents, e.g., the number of organisms per unit land area for terrestrial species, or the number of organisms per unit water volume for aquatic species. However, the concept of density is sufficiently general that it need not involve space. For example, a meaningful use of the term would be the number of organisms per unit food resource, or in the case of discrete habitat patches, the number of organisms per patch (e.g., the number of ducks per pond on prairie breeding areas).

The structure of a population often can be described in terms of the number of individual organisms characterized by specific attributes of interest. For example, the age structure of a population refers to the respective

proportions of individuals in discrete age classes. A population also may be described by its stage structure, with discrete stages defined by variables such as size (the proportions of animals in discrete size classes) (e.g., see Sauer and Slade, 1987a,b), reproductive behavior (e.g., breeders or nonbreeders), or physiological development. In fact, the structure of a population can be described in terms of any attribute thought to be relevant to population dynamics. A common example utilizes the sex ratio of a population, which expresses the proportionate sex composition of a population.

## 1.2. POPULATION DYNAMICS

Population ecology can be viewed as the study of the distribution of the individuals in a population over time and space. Population ecologists often focus on temporal change in abundance or population dynamics, asking how and why a population changes over time. Temporal population change can be expressed via a simple balance equation that incorporates gains and losses:

$$N(t + 1) = N(t) + B(t) + I(t) - D(t) - E(t), \quad (1.1)$$

where  $N(t + 1)$ , the population size at time  $t + 1$ , is written as a function of population size  $N(t)$  at time  $t$ , with increases to  $N(t)$  during the interval  $t$  to  $t + 1$  as a result of reproduction  $B(t)$  and immigration  $I(t)$ , and losses during the interval from mortality  $D(t)$  and emigration  $E(t)$ . The four variables,  $B(t)$ ,  $I(t)$ ,  $D(t)$ , and  $E(t)$ , reflect the primary population processes responsible for changes in population size. If an environmental factor or a management action is to influence population size, its influence must be registered through one of these processes.

The primary population processes in Eq. (1.1) describe gains and losses in terms of numbers of individual organisms. But births and deaths during the interval  $(t, t + 1)$  are likely to depend on the number  $N(t)$  of animals in the population at the beginning of the interval. For this reason, it often is useful to rewrite  $B(t)$  as  $B(t) = b(t)N(t)$ , where  $b(t)$  is defined as a per capita reproductive rate, or the number of new individuals in the population at time  $t + 1$  resulting from reproduction during  $(t, t + 1)$ , per individual alive in the population at time  $t$ . Similarly, the number of deaths often is rewritten as  $D(t) = [1 - S(t)]N(t)$ , where  $S(t)$  is an interval survival rate, reflecting the proportion of animals alive at time  $t$  that are still alive at time  $t + 1$ . For populations that are geographically closed (i.e., there are no gains or losses resulting from movement), Eq. (1.1) can be rewritten as

$$N(t + 1) = N(t)[b(t) + S(t)]. \quad (1.2)$$

For populations that are not geographically closed, it is tempting to write immigration and emigration as functions of  $N(t)$ . This often is reasonable for emigration, and we can write  $E(t)$  as  $E(t) = e(t)N(t)$ , where  $e(t)$  is the proportion of animals in a population at time  $t$  that emigrate out of the population by time  $t + 1$ . But it is less reasonable for immigration, given that the number of individuals immigrating into the population between  $t$  and  $t + 1$  is more likely a function of abundance or density in the source population of immigrants, rather than the size of the recipient population. Immigration thus is treated differently than the other primary population processes, in that it usually is not modeled as a per capita rate based on the recipient population size.

Equations (1.1) and (1.2) constitute simple mathematical models of population change, to be discussed in more detail in later chapters. For present purposes, models can be viewed generally as abstractions and simplifications of reality, and in particular, Eqs. (1.1) and (1.2) can be thought of as simple hypotheses about population change. In later chapters we expand and enhance these models, to incorporate a number of biologically relevant factors that influence population change. For example, single-species population models frequently incorporate information about the attributes of individuals in the population, with individuals grouped into classes as defined by variables such as age, size, and sex (e.g., Lefkovich, 1965; Streifer, 1974; Caswell, 2001). The population then is characterized by a vector specifying the number of individuals in each class or stage.

Model enhancements also can include spatial structure, as in Levins' (1970) description of a metapopulation as a "population of populations." Metapopulation models often include different habitat patches that may or may not contain individuals, with reproduction occurring among individuals within a patch and movement of individuals occurring between patches (Levins, 1969, 1970; Hanski and Gilpin, 1997; Hanski, 1999). Metapopulation dynamics are thus a function of both within-patch (reproduction, survival) and between-patch (emigration, immigration) processes. Finally, both single-location and multiple-location models can be extended to include multiple species and their potential interactions.

## 1.3. FACTORS AFFECTING POPULATIONS

Equation (1.1) provides a framework for population change, but carries little information about why populations change. Many questions of ecological and man-

agement relevance involve factors that potentially influence the four primary processes driving population change. These can be categorized in many ways, but it often is convenient to think in terms of abiotic and biotic factors. Abiotic factors include physical and chemical characteristics of an organism's environment such as soil type, water availability, temperature, and fire frequency for terrestrial organisms, and water salinity, pH, currents, light penetration, and dissolved oxygen for aquatic organisms. Factors such as these commonly influence population dynamics via multiple rather than single population processes. For example, water and wetland availability on prairie breeding areas in North America can influence duck populations (Johnson *et al.*, 1992) by affecting reproduction (lower probabilities of breeding and increased duckling mortality when conditions are dry), survival of adults (higher mortality of hens associated with predation when nesting during wet years), and movement (increased movement away from relatively dry areas and to relatively wet areas).

On the other hand, biotic factors are understood in terms of interactions among members of the same species (intraspecific), or interactions involving species other than that of the population of interest (interspecific). Interspecific factors include vegetative components of the habitat as well as processes such as predation, interspecific competition, parasitism, and disease. Like abiotic influences, they also can affect more than one of the primary population processes. For example, predation clearly influences mortality, but may also influence movement (increased emigration from areas with large numbers of predators) and reproduction (decreased probability of reproducing in response to increased predation risk).

Intraspecific factors involve interactions among the individuals in a population, with potential influences on all of the primary population processes. They often involve direct behavioral interactions, in which some individuals in the population actively exclude other members of the population from habitat patches or deny access to food resources or even to members of the opposite sex. But they also can involve indirect interactions, through the possible depletion of common resources and the occupation of common habitat. Indirect interactions such as these almost always involve other biotic and abiotic factors.

### 1.3.1. Population Regulation

Because population processes are influenced simultaneously by abiotic and biotic factors, there may be only limited value in trying to ascertain which class of factors is most relevant to population change. Never-

theless, the history of population ecology has been characterized by repeated arguments about the relative importance of abiotic vs. biotic factors in controlling population dynamics, and the importance of interspecific vs. intraspecific factors (e.g., see Nicholson, 1933; Andrewartha and Birch, 1954; Lack, 1954; Slobodkin, 1961; Reddingius, 1971; Murdoch, 1994). Much of this debate has focused on explanations for the simple observation that populations do not increase indefinitely (Malthus, 1798). The terms population regulation and population limitation refer to concepts that emerge from the impossibility of indefinite population increase.

Population regulation refers to the process by which a population returns to an equilibrium size (e.g., Sinclair, 1989). A glance at Eq. (1.1) indicates that in order for a population to grow [i.e.,  $N(t + 1) > N(t)$ ], gains must exceed losses, or  $B(t) + I(t) > M(t) + E(t)$ . On the other hand, the equilibrium condition  $N(t + 1) = N(t)$  is attained when additions to the population equal losses, that is, when  $B(t) + I(t) = M(t) + E(t)$ . A growing population eventually must reach a state in which the primary population processes change in the direction of equilibrium, that is, births and immigration decrease and/or deaths and emigration increase until gains equal losses. Population ecologists have expended considerable effort in attempting to identify factors that can influence the primary processes of growing populations and thereby produce equilibrium. In reality, such an equilibrium is not likely to be a single fixed population size. Instead, regulation can be viewed as producing a "long-term stationary probability distribution of population densities" (Dennis and Taper, 1994; Turchin, 1995). Murdoch (1994) identified regulation with "boundedness," noting that some cyclic and chaotic populations can also be viewed as regulated.

### 1.3.2. Density Dependence and Density Independence

The debate about population regulation often is framed in terms of density dependence and density independence. Sometimes these concepts are defined in terms of the rate of population change  $\lambda_t = N(t + 1)/N(t)$ , although such definitions can become relatively complicated (Royama, 1977, 1981, 1992). Our preference is to define density dependence and density independence in terms of the vital rates associated with the primary population processes. For example, the vital rates associated with a geographically closed population are the survival rate  $S(t)$  and reproductive rate  $b(t)$  in Eq. (1.2). Though the absolute numbers of births  $b(t)N(t)$  and deaths  $[1 - S(t)]N(t)$  occurring during the interval  $(t, t + 1)$  obviously depend on the population

size at the beginning of the interval [see Eq. (1.2)], density dependence is defined by the functional dependence of a vital rate on abundance or density [i.e.,  $S(t) = f[N(t)]$  and/or  $b(t) = g[N(t)]$ ]. Density independence refers to the absence of such a functional dependence. Examples of density dependence might include survival and reproductive rates, which typically decrease as abundance or density increases. The relevance of this concept to population regulation is that regulation requires negative feedback between  $\lambda_t$  (and thus the vital rates that produce  $\lambda_t$ ) and population size at  $t$  or some previous period. Finally, we note the possibility of Allee effects, in which survival and reproductive rates may decrease in populations at very low density (e.g., Allee *et al.*, 1949; Courchamp *et al.*, 1999; Stephens and Sutherland, 1999).

The concepts of density dependence and density independence provide another means of classifying factors affecting animal populations. Some factors operate as functions of density or abundance (i.e., in a density-dependent manner) and represent dynamic feedbacks. For example, in some rodent populations, intraspecific aggressive behavior among individuals appears to increase as density increases, leading to decreased rates of survival and reproduction (Christian 1950, 1961). Interspecific factors also can act in a density-dependent manner, as when rates of predation or parasitism depend on the abundance of the prey or host population (e.g., Holling, 1959, 1965).

On the other hand, some factors act in a density-independent manner, absent dynamic feedback. When flooding reduces alligator reproductive rates by destroying nests, the magnitude of the reduction in reproductive rate depends on the proportion of nests that are constructed in susceptible locations (e.g., Hines *et al.*, 1968), but not on alligator density. Similarly, severe grassland fires may cause direct mortality of insect and small mammal inhabitants, but the increase in mortality associated with fire events typically is independent of the density of the affected population. In some situations, factors acting in density-dependent and density-independent manners interact, as when density-dependent decreases in reproductive rate occur because of increases in numbers of cavity-nesting birds using a fixed supply of cavities (Haramis and Thompson, 1985).

### 1.3.3. Population Limitation

Every population is restricted in its growth potential, with a range of conditions beyond which the population tends to decrease because of reductions in survival rates, reproduction rates, or both. Consider a population at equilibrium, such that gains equal losses

over time and population size does not deviate greatly from some average or expected value. *Limitation* refers to "the process which sets the equilibrium point" (Sinclair, 1989) or, more generally, that determines the stationary probability distribution of population densities. Limitation can involve factors that act in a density-dependent manner as well as factors that are density independent.

A limiting factor can be defined as one in which changes in the factor result in a new equilibrium level (Fretwell, 1972) or, more generally, a new stationary distribution of population densities. For example, if predation is a limiting factor for a prey population, then a sustained decrease in predation should bring about an increase in equilibrium abundance of the prey. This new equilibrium level would itself be determined by the action of other factors on the primary population processes. Consistent with this definition of a limiting factor is the recognition that populations potentially have multiple equilibria, and a given population may move among equilibria as conditions and limiting factors change (e.g., Hestbeck, 1986).

## 1.4. MANAGEMENT OF ANIMAL POPULATIONS

Interest in certain animal populations has led to management efforts to try to achieve population goals. These goals frequently involve a desired abundance and, for harvested species, a desired level of harvest. Some animal species exist at abundances thought to be too great, and management efforts are directed at reducing abundance. These include pest species associated with human health problems [e.g., Norway rats (*Rattus norvegicus*); see Davis, 1953] and economic problems such as crop depredation [e.g., the use of cereal crops by the red-billed quelea (*Quelea quelea*) in Africa; see Feare, 1991]. Other species are viewed as desirable, yet are declining in number or persist at low abundance. Relevant management goals for the latter typically involve increases in abundance, in an effort to reduce the probability of extinction in the near future. Such a goal is appropriate for most threatened and endangered species, and methods for its achievement dominate the field of conservation biology (e.g., Caughley, 1994; Caughley and Gunn, 1996). Still other species are judged to be at desirable abundances, and management efforts involve maintenance of population size. Finally, for harvested species, an abundance-oriented goal must be considered in the context of maintaining harvest yield that is consistent with recreational and/or commercial interests (e.g., Hilborn and Walters, 1992; Nichols *et al.*, 1995a).

If management is to influence animal abundance, then it must do so by influencing at least one of the four primary population processes in Eq. (1.1). For example, white-tailed deer are judged to be overabundant in portions of eastern North America, and management efforts to reduce abundance have been directed at both increasing mortality (via hunting and culling operations) and decreasing reproduction (via sterilization and chemical contraception) (McShea *et al.*, 1997; Warren, 1997). Management efforts directed at endangered species frequently involve attempts to decrease mortality via predator control, or attempts to influence reproduction, emigration, and mortality by setting aside or maintaining good habitat. For harvested species, the regulation of harvests focuses on both harvest yield (harvest regulations should influence yield directly) and abundance (harvest regulations influence abundance by changing rates of mortality and, sometimes, movement).

The concepts of population limitation and regulation underlie population management, especially as they factor into the roles of density dependence and independence. For example, the manager of a threatened or endangered species can utilize an understanding of limiting factors to effect management actions to improve the species status. Many endangered species are habitat specialists that are thought to be limited by the amount of suitable habitat available to them. Thus, the purchase or creation of additional habitat represents an effort to remove a limiting factor and to permit the population to increase to a new equilibrium level commensurate with the expanded habitat. Of course, a population increase occurs because of changes in the primary population processes corresponding to the increase in habitat, and it often is useful to focus on the processes as well as the limiting factors.

The concept of density dependence is especially important in management of harvested populations. As a direct mortality source, harvest acts to reduce abundance. However, reduced abundance may lead to increases in reproductive rate or to decreases in nonharvest mortality or emigration, depending on which vital rates behave in a density-dependent manner. For example, much fisheries management is based on stock-recruitment models that incorporate density-dependent reproductive rates (e.g., Beverton and Holt, 1957; Ricker, 1975; Hilborn and Walters, 1992). Management of North American mallard (*Anas platyrhynchos*) populations is based on competing models that represent different sets of assumptions about the density dependence of survival and reproductive rates (Johnson *et al.*, 1997). Because our definitions of density dependence and independence involve the population-level vital rates of survival, reproduction, and move-

ment, density dependence again directs the manager's attention to the primary population processes.

### 1.5. INDIVIDUALS, FITNESS, AND LIFE HISTORY CHARACTERISTICS

The comments above, and indeed most chapters in this book, focus on the population level of biological organization. However, it is important to remember that the constituents of populations are individual organisms, and the characteristics of these organisms are shaped by natural selection. Characteristics associated with relatively high survival or reproductive rates are favored by natural selection, in that organisms possessing them tend to be represented by more descendants in future generations than do other organisms. Individuals with greater potential for genetic representation in future generations are said to have relatively high fitness.

Though they typically are thought to deal with different levels of biological organization, fitness and population growth are closely related. Thus, the growth rate of a geographically closed population is determined by survival rate and reproductive rate, whereas the fitness of an individual organism is determined by its underlying probabilities of surviving from year to year and of producing 0, 1, 2, . . . offspring each reproductive season. Indeed, fitness associated with a particular genotype can be defined operationally as the growth rate of a population of organisms of that genotype (see Fisher, 1930; Stearns, 1976, 1992; Charlesworth, 1980). An important consequence of the close relationship between population growth and individual fitness is that evolutionary ecologists, population ecologists, and population managers are often interested in the same population processes and their vital rates.

Nevertheless, a subtle difference can exist between definitions of survival and reproductive rates at the population and individual levels of organization. We defined the interval survival rate  $S(t)$  as the proportion of animals in the population at time  $t$  that survives until time  $t + 1$ . This quantity is not so useful at the level of the individual organism, because an organism either survives or it does not; however, it can be thought of as having some underlying probability of surviving the interval between times  $t$  and  $t + 1$ . These two distinct quantities, the probability that an individual survives and the proportion of animals in a population that survive, are closely related. Consider a population of individuals with identical underlying survival probabilities for some interval of interest. The

proportion of individuals that survives the interval likely is not identical with the underlying individual survival probability. On the other hand, the proportion that survives is expected to deviate little from the individual survival probability. More precisely, multiple realizations of population dynamics over comparable time intervals would produce an average proportion of survivors approaching the individual survival probability. In Chapter 8 we define the terms needed to specify the relationship between population-level survival rate and individual probability of survival. The important point for now is that these quantities are closely related. Throughout most of this book, we will use the terms *survival rate* and *survival probability* interchangeably to refer to the underlying individual survival probability. When discussing survival at the population level we will use the term *survival rate* to denote the surviving proportion of a population or group. Of course, the latter quantity is of interest regardless of whether all individuals in the population have the same survival probability.

A similar situation exists for reproductive rate. An individual can produce some integer number of offspring {0, 1, 2, . . .} during a single reproductive season, but a reproductive rate refers to the number of offspring produced per adult in the population. In essence, this offspring/adult ratio is a population-level attribute. The term *reproductive rate* could refer in concept to (1) the average number of young produced if we could observe an individual over many replicate time intervals or (2) the average number of young produced per adult in the population if we could observe the population over many replicate time intervals. Our intention here is not to dwell on subtle differences in the terms used for individuals and populations, but instead to emphasize the role of vital rates in determining both fitness and population growth.

In the discussion above we suggested that the concepts of population limitation and regulation follow naturally from the simple observation that populations do not increase indefinitely. Similarly, evolutionary ecology is based on the observation that neither species nor populations of genotypes can increase indefinitely, though temporary increases are possible. Species and populations of genotypes must eventually reach a state in which temporary increases and declines in numbers of individuals fluctuate about some equilibrium over time. The necessary balance between average survival and reproductive rates has led to various classification schemes [e.g., *r*- and *K*-selected species, "fast" versus "slow" species (Cody, 1966; MacArthur and Wilson, 1967; Boyce, 1984; Stearns, 1992)] for species based on these average values. A basic idea underlying all of

these schemes is that species with high reproductive rates must also be characterized by high mortality rates, whereas species with low reproductive rates must also have low mortality rates.

The underlying survival and reproductive rates that apply at each age throughout an organism's lifetime are frequently referred to as *life history characteristics* (Cole, 1954; Stearns, 1976, 1992). Most discussions of life history characteristics also include features such as age at first reproduction, individual growth rate, body size, and age at which individuals can no longer reproduce (see Chapter 8). However, the relevance of these features to life history evolution involves their relationship to the age-specific schedule of survival and reproductive rates. The magnitudes of survival and reproductive rates throughout the organism's lifetime often are viewed as species-specific characteristics, allowing for variation in survival and reproduction rates among individuals. The expectation is that variation among individuals within a species typically is much smaller than variation among individuals of different species.

The suite of life history characteristics is important not only for understanding and predicting population dynamics, but also for managing populations. Consider, for example, the management of two harvested species, one with high mortality and reproductive rates (e.g., several commercially harvested fish species) and one with low reproductive and mortality rates (e.g., harvested whales). Imposition of a fixed harvest rate (proportion of animals in the population harvested) typically has a larger influence on the population dynamics of the species with the otherwise low mortality and the low reproductive rate. In addition to low per capita reproductive rates, such species tend to exhibit delayed sexual maturity, with the consequence that they take longer to recover from decreases in abundance.

In summary, there is a close relationship between fitness and population change, despite the fact that these quantities apply to different levels of biological organization. One consequence of this relationship is that even though population ecologists, population managers, and evolutionary ecologists address different kinds of questions and have different objectives, they are all concerned with population vital rates. Thus, the methods presented in this book for estimating vital rates should be relevant to scientists in these different disciplines. Another consequence is that life history characteristics molded by natural selection are relevant to population dynamics and population management. Knowledge of a species' life history characteristics is of key importance in predicting population

responses to management, and thus should play an important role in management decisions.

## 1.6. COMMUNITY DYNAMICS

In this book, our focus occasionally shifts to the community level of biological organization, where the term *community* refers to a group of populations of different species occupying a particular space at a particular time. A community may include all the different plant and animal species represented in the space, or, more commonly, may refer to a subset of species defined by taxonomy (e.g., the bird community of an area), functional relationships (e.g., vegetative or herbivore community), or other criteria that are relevant to a question of interest.

One way to model community-level dynamics is to model the population for each species, perhaps linking the models via the sharing of resources to induce interactions. For example, consider a simple model of a single predator species and a single prey species. The survival and reproductive rates of the predator species might be modeled as functions of prey species abundance, such that larger numbers of prey lead to higher survival and reproductive rates of the predator species. In the same model, the survival rate for the prey species could be written as a function of predator abundance, with more predators leading to reduced survival for the prey species. A similar approach frequently is taken for the modeling of interspecific competition. The importance of population-level vital rates is again emphasized in this modeling approach, as the interactions between populations are specified as functional relationships involving the vital rates (or composite quantities that combine vital rates).

A less mechanistic and more descriptive approach for community-level modeling does not focus on interspecific interactions. This modeling approach has been used by community ecologists (e.g., MacArthur and Wilson, 1967; Simberloff, 1969, 1972) and by paleobiologists (Raup *et al.*, 1973; Raup, 1977) and simply involves models such as those of Eqs. (1.1) and (1.2) shifted to the community level. Thus, instead of projecting changes in numbers of individual organisms within a population, the models specify change in the numbers of different species in the community. The primary population processes and their corresponding vital rates are replaced by analogous processes and vital rates at the community level.

To see how, let  $N(t)$  denote the number of species in the community at time  $t$ , with  $S(t)$  the species-level survival rate (the complement of local extinction rate) for the interval  $t$  to  $t + 1$ , and  $I(t)$  the number of colonists during the interval (species absent from the community at  $t$ , but present at  $t + 1$ ). Using notation similar to that of Eqs. (1.1) and (1.2), the natural expression for change in the number of species in the community is

$$N(t + 1) = N(t)S(t) + I(t).$$

Consideration of the processes determining  $S(t)$  and  $I(t)$  again leads back to the primary population processes and associated vital rates. Local extinction rate for a species-population is a function of population-level rates of survival, reproduction, immigration, and emigration, and the number of colonizing species is a function of immigration at the population level.

The approach of representing a "population" of species via a model for which local extinction plays the role of mortality, and immigration/colonization plays the role of reproduction, is a natural extension of the biological framework portrayed in Eq. (1.1). This analogy has been used in biogeography for many years (MacArthur and Wilson, 1967) and is used frequently in other fields such as conservation biology (e.g., Rosenzweig and Clark, 1994; Russell *et al.*, 1995; Boulmier *et al.*, 1998, 2001; Cam *et al.*, 2000).

## 1.7. DISCUSSION

In this chapter we have introduced the biology of animal populations in terms of the fundamental processes of survival, reproduction, and migration, along with their associated vital rates. These quantities define the balance equation [Eq. (1.1)] by which population dynamics can be investigated, and they also provide a basis for understanding the factors that influence population dynamics. In the chapters to follow we make liberal use of this framework, as we focus on the modeling of populations and the estimation of population attributes. We will see that quantities such as population size, harvest numbers and rates, recruitment levels, and migration patterns are key to an understanding of population dynamics. We focus much of what follows on the use of field data to estimate these and other population parameters. A careful accounting of the statistical properties of these estimates will be seen to be an essential component in the informed conservation of animal populations.