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principles of  
**population**

**dynamics**

and their application



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# Dynamics: theoretical ecology and the rules of change

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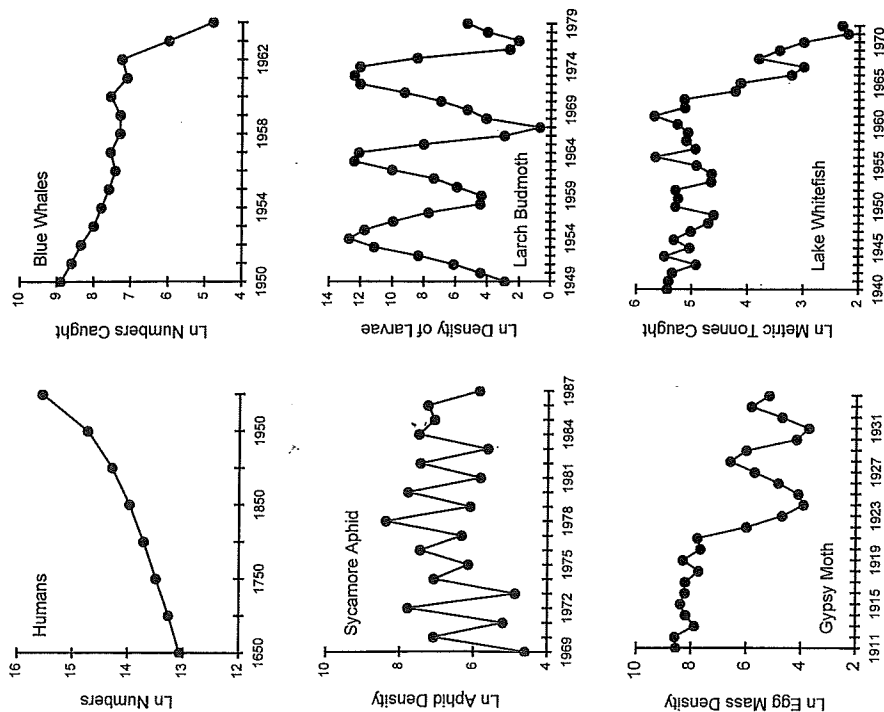
*Populations of organisms can meaningfully be analyzed as feedback systems of a rather complex kind, showing both positive and negative feedback loops. (L. B. Slobodkin, 1968)*

Numbers of organisms change in interesting and mysterious ways (Figure 1.1). Some, like the human population, seem to be growing continuously, while others, like the blue whale, seem to be on their way to extinction. Growth patterns such as these have important implications for the species in question, for those utilizing them as resources, and for the persistence of life on this planet. Obviously, the human population cannot grow forever, but when will it stop growing and what will stop it? Are blue whales becoming extinct and, if so, what should be done to aid their recovery?

Other species, like the sycamore aphid in England, appear to remain remarkably constant for long periods of time, even though they may fluctuate considerably from one year to the next. What keeps these populations from increasing like humans or decreasing like whales, and why do they exhibit the sharp, short, 2-year fluctuations called, in this book, high-frequency or "saw-toothed" oscillations?

Yet other populations, like the larch budmoth in the Swiss Alps, go through dramatic and very regular multi-annual oscillations which often take around 10 years to repeat themselves. Although ecologists have been fascinated by these so-called "population cycles" for more than 50 years, there is still no general agreement about their causes.

Other species have much more variable dynamics. Gypsy moth egg mass counts in New England, for example, declined suddenly and, at the same time, switched from a saw-toothed to a cyclical pattern of fluctuation, while whitefish in Lake Ontario remained relatively constant for a long time but recently entered a period of decline.



**Figure 1.1** Dynamics of various animal populations with numbers, expressed as natural logarithms, plotted against time (see reference 3 for data sources).

## 1.1 THEORETICAL ECOLOGY

Why do some populations of living organisms grow and decline, while others oscillate around a relatively constant average density? Why do some oscillate rapidly while others cycle slowly? Theoretical population ecology attempts to answer these and other similar questions, to make sense out of the complexity and confusion we see in nature, to uncover the general rules or principles that all populations of living organisms must obey.

Students sometimes ask why they have to learn abstract theoretical concepts when what we are really interested in is solving real practical

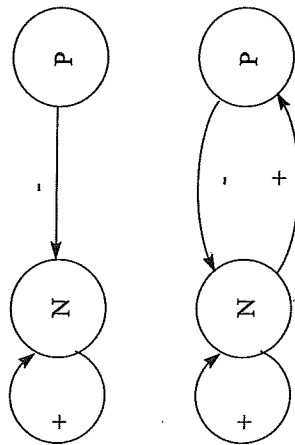
problems, such as how to harvest renewable resources, reduce the ravages of pests, or save endangered species. The best answer to this question may well lie in a quote borrowed from a forgotten writer: "*theory without fact is fantasy, fact without theory is chaos*". What this statement means is that theories should be based on factual information and that, once established, the theory should be used as a framework, or a set of guidelines, for organizing facts and actions. A good example is the space programme: although it was modern engineers who designed and built the vehicle that put men on the Moon, it was the theories of gravity and planetary motion, laid down more than 300 years earlier by Kepler and Newton, that showed how it could be done. Without theory, putting a human on the Moon would have been impossible.

Resource and pest managers sometimes seem reluctant to pay the same attention to theory as space engineers, and have occasionally reaped the dire consequences. A good example is the use (or misuse) of the chemical DDT to control insects. After its rediscovery in 1939, DDT was hailed as a miracle insecticide and was widely used against all kinds of insects without regard to the theoretical consequences of such actions. Those scientists who warned that insects would become resistant to the chemical, as predicted by the theory of evolution, were ignored or ridiculed. Yet they were right, for DDT became more or less useless against the many insect pests that evolved resistance to it. Theory, therefore, should be considered an essential ingredient of pest and resource management policy<sup>2</sup>.

A theory can be defined as a systematic statement of the principles, processes and relationships that underlie a particular natural phenomenon. Thus, theories attempt to explain observed events by reference to known principles, relationships and causal processes. For example, the theory of evolution attempts to explain the complexity and diversity of life on this planet from the basic principles of heredity, variability, and natural selection. Similarly, population theory attempts to explain the complexity and diversity we observe in the fluctuations of natural populations, such as those illustrated in Figure 1.1, by appeal to the basic principles of dynamic systems and to the ecological processes that evoke those principles. Thus, in order to develop a theory of population dynamics, it is first necessary to understand something about the general rules of change, rules that apply to all dynamic systems; automobiles, rocket ships, television sets and ecosystems.

## 1.2 THE RULES OF CHANGE

Changes in a dynamic system can be caused by either *exogenous* or *endogenous* processes. For example, the predator population in the top diagram of Figure 1.2 acts as an exogenous effect on the prey population



**Figure 1.2** Flow diagram for the effects of a population of predators  $P$  on the numbers of its prey  $N$ : top, predators act as a negative exogenous factor on the prey population (i.e. negative arrow from  $P$  to  $N$ ), and the prey have a positive effect on their own numbers (i.e. the arrow from the prey to itself has a positive sign); bottom, prey now have a positive effect on the predators so that the interaction forms an endogenous feedback loop [Note that the feedback is negative because the product of the signs in the loop is negative; i.e.  $(+) \times (-) = (-)$ ].

because it causes changes in prey numbers without being affected itself by those changes. This is shown as an arrow with a negative sign going from the predator to the prey population (ignore the positive arrow from the prey to itself for the moment). The arrow is negative because changes in the prey population are inversely related to the number of predators; for example, an increase in the number of predators causes a reduction in the prey population because more are eaten. Notice that the prey population has no influence on the predator (no arrow from prey to predator). In this sense, the predator population is external to and independent of prey numbers and, because of this, is considered to be an *exogenous* influence on prey dynamics.

Endogenous effects, on the other hand, cause changes in a dynamic variable and are also affected in return by those changes. For example, in the bottom diagram of Figure 1.2, the prey population is now assumed to have a positive effect on the predator population (e.g. an increase in prey numbers leads to more predators because, given more food, they produce more offspring). The addition of this arrow links the prey and predator populations together in a mutually causal *feedback loop*, and the two populations are now considered to be parts of the same closed system. In this sense, predators are now an *endogenous* influence on prey dynamics.

### 1.2.1 Endogenous dynamics

Feedback loops are created whenever a variable influences itself, either directly or through another variable (Figure 1.2). Feedback loops are identified by the sign of the feedback (+ or -) and by the number of components that are involved in the loop (*order* or *dimension*). For example, a *first-order* feedback loop possesses only one component (e.g. the positive loop from the prey population to itself in Figure 1.2), while a *second-order* feedback loop possesses two components (e.g. the feedback loop involving both prey and predator populations in Figure 1.2, bottom). As we will see below, the sign and dimension of the feedback have important effects on the *stability* of dynamic systems.

Dynamic systems are said to be *stable* if their variables return to, or towards, their original states following disturbances. For example, the temperature of a room is stable if, when a door is opened (= exogenous effect), the thermostatic control system brings the room back to, or at least towards, its previous temperature (= endogenous process). This does not mean that the temperature will be exactly the same as that set by the thermostat, but it will not deviate very far from that setting. Here the thermostat set point is also called an *equilibrium point*. Hence, stable systems tend to remain in the vicinity of an equilibrium point and to persist in a state of balance, even though the environments in which they exist may be quite variable. They are said to be *homeostatic* or *regulated*. Notice that, although an equilibrium or set point always exists in a stable dynamic system, this point may never actually be observed if the system is subjected to continuous exogenous disturbance.

Stability in dynamic systems is brought about by the action of *negative feedback* processes (in shorthand notation 'feedback'). Hence, it is 'feedback' that acts to oppose changes in the state of a dynamic variable, just as the thermostat opposes changes in room temperature. The thermostat is, in fact, part of a mechanical 'feedback' mechanism. Natural ecosystems can also create 'feedback' processes. For example, consider the second-order feedback loop created by the interaction between populations of predators and prey (Figure 1.2, bottom). Here an increase in the number of prey leads to more predators and this larger population of predators then reduces the prey population back towards its previous level of abundance. As a result, the prey population tends to be stabilized or regulated by the interaction with its predators. Notice that the sign of the feedback loop is determined by multiplying the signs of the individual interactions within the loop. In the case of the predator-prey interaction we have a positive effect of the prey population on the predator population and a negative effect of the predator on the prey, or  $(+) \times (-) = (-)$ .

Although 'feedback' is a *necessary* condition for stability in dynamic systems, it is not a *sufficient* condition, for in order to have a high degree

of temporal stability, the feedback must also occur rapidly. It is fairly obvious that the operation of a second-order feedback loop, such as that in Figure 1.2 (bottom), must take some time, because time is needed for the predators to react to an increase in their food supply and to turn that food into offspring. This is called the time *delay* or time *lag* in the feedback loop. In general the greater the order or dimension of the feedback loop, the longer the time delay. Time delays in feedback loops tend to introduce oscillatory instability into the system, with longer time delays causing oscillations of longer period and greater amplitude. For example, one explanation for the 10-year cycles observed in larch budmoth populations (Figure 1.1) is that defoliation of larch in 1 year reduces the quality of the foliage in the following year. As a result, the reproductive rate of the insect in that year is affected by the density of the population in the previous year, giving rise to a time delay of 1 year in the feedback loop. Note that the feedback between insect and foliage has a dimension of two (or second order) because two components are linked together in a mutually causal feedback loop (e.g. in a similar way to Figure 1.2, bottom). In general then, the higher the order or dimension of the feedback loop, the longer it takes for the effects to be transmitted through the loop, and the less stable the dynamics of the system. For this reason, high-dimensional feedback processes are likely to be involved in many of the periodic rhythms observed in nature.

Dynamic systems are said to be *unstable* if their variables continue to move away from their original states following an exogenous disturbance. The human population, for instance, is currently exhibiting unstable dynamics because it is continuously increasing. The blue whale population may also be unstable because it seems to be continuously decreasing. Unstable dynamics are usually caused by the action of positive feedback (\*feedback) processes. For example, the first-order \*feedback loop in Figure 1.2 informs us that a change in prey numbers is positively, or directly, related to prey numbers; i.e. the more prey there are the more there will be in the future, and vice versa. As long as this condition holds, the prey population will continue to change in the same direction, like the human or blue whale populations. Hence, \*feedback is the general process underlying the inflation spiral, the arms race, the population explosion, the extinction of species, and organic evolution.

### 1.2.2 Exogenous dynamics

Although the feedback structure of a dynamic system determines its properties of stability and instability, exogenous factors like temperature, rainfall, soil type, topography, etc. set the stage on which these dynamic interactions occur. For example, gradual increases in temperature due to global warming can change the interaction structure of ecological systems,

say by making plants more susceptible to disease, and this can lead to instability due to outbreaks of disease. In contrast, normal variations in climate (weather) merely disturb the system temporarily from its stable state. Thus, we recognize two major kinds of exogenous effects: (1) those that cause changes in the stability properties of the ecosystem, which we call exogenous *forcing* processes; and (2) those that merely displace variables from their steady states and do not affect their stability, which we call exogenous *disturbances*. The latter are often considered to be *random* processes.

Because the feedback structure determines the stability properties of dynamic systems and, through this, the patterns and regularities that we observe in nature, it is important to understand how feedback loops are created in ecological systems, and how to detect and manipulate these feedback loops to produce stable, self-sustaining ecosystems. For this reason, the general principles of population dynamics developed in Part One of this book are built around these fundamental ideas. Then, in Part Two, methods are developed for detecting the feedback structure of real population systems, and for modelling these feedback processes. Finally, in Part Three, the methods are applied to a number of specific examples. In taking this approach we must accept the fact that ecological systems are extremely complex and, because of this, will never be completely understood nor precisely modelled. Each ecosystem is, to some extent, unique. Yet the fact that each person is unique does not prevent the physician from practising medicine, and the same facts should not deter the ecologist from analysing and prescribing treatments for natural ecosystems. Like the family doctor, the ecologist must use all the available scientific information and technology to make intelligent appraisals of probable cause (diagnosis) and possible remedial treatment (prescription). It is this basic philosophy that underlies the approach taken in this book.

### 1.3 SUMMARY

In this chapter we

1. Discussed some of the patterns and rhythms observed in natural populations, including unstable growth and decline, saw-toothed and cyclical oscillations, and shifts from one pattern to another.
2. Defined a theory as a systematic statement of the principles, processes and relationships underlying a natural phenomenon.
3. Showed why theory is necessary for understanding the causes of population changes and for intelligently managing populations of living organisms.

4. Demonstrated the effects of endogenous (feedback) processes, including stability (induced by "feedback"), cycles (induced by delayed "feedback"), and unstable dynamics (induced by "feedback").
5. Demonstrated the potential effects of exogenous (non-feedback) processes, including forcing factors that can change or destroy the feedback structure and random processes that disturb systems from their steady states.
6. Discussed the general philosophy and approach taken in this book.

#### 1.4 EXERCISE

Deer feed on certain woody shrubs and in so doing can severely reduce their abundance. Shrubs and trees compete with each other for space, sunlight, nutrients and water. Therefore, the more trees the less shrubs and vice versa. Shrubs, of course, are good for deer, but so are trees, for they provide protection. Draw the feedback structure of this system. How many feedback processes are there and are they negative or positive? Describe these feedback processes and explain how this system can be stabilized.

## Population: the central concept

*To search for the best concept is no idle conceit, because the experiments that a scientist may devise and therefore the facts he may discover, as well as the explanations that he offers for them, depend on how he conceives nature.* (H. G. Andrewartha and L. C. Birch, 1984)

Given that theory is necessary to understand and intelligently manage nature, then the next question to ask is "What should this theory be based upon?" Should ecological theory evolve around the idea of a population, or would it be better to base it on individual organisms, communities, or ecosystems? The fact of the matter is that ecological landscapes are really made up of individuals; individual trees, shrubs, deer, birds, insects and so on; multitudes of different individuals all going about their daily business and, in so doing, affecting each other in a multitude of different ways. Surely then a realistic theory of ecology should revolve around the individual organism and its innate genetic characteristics? The problem is that, although an individual-based theory may seem logical, it is not practical. First there is a computational problem, for if every organism in a large ecosystem were to be recognized as a separate entity, with its own particular character and behaviour, then keeping track of all the information, motion and interaction would be an impossible task, even for modern supercomputers. The second problem is one of measurement, for in order to forecast the future states of ecological variables we must first measure their present states. If an individual-based approach were to be employed, the state and location of every organism in the ecosystem would have to be measured before one could make a prediction! How can a pest manager measure the exact location, reproductive potential, and genetic make-up, of every insect in a field or forest? Thus, although an individual-based approach to ecology<sup>4</sup> may make sense, it is not practical.

One way to make a theory more practical is to work at a higher level of abstraction. The next level of ecological abstraction, above the individual, is the population. In this case we concern ourselves, not with the properties of individual organisms, but with the average properties of groups of individuals. Although variability from this average may be described statistically, say by the variance around the mean, the identity and uniqueness of the individual organism is lost in the abstraction. Thus, information about individual organisms is sacrificed in order to develop a manageable and practical theory. It should always be remembered, however, that a theory based on the characteristics of populations, although being more practical, is always less realistic or more abstract, than a theory based on individual organisms. On the other hand, a population-based theory is more realistic than a theory based on the idea of a community or ecosystem because it is a lower level of abstraction and, therefore, closer to reality.

## 2.1 THE POPULATION CONCEPT

Accepting the proposition that the population is the most practical unit for studying ecological dynamics, it is essential to clearly define what is meant by this term. Probably the most commonly used definition is a *group of individuals of the same species that live together in the same place*. This definition recognizes that populations are made up of individual organisms, but does not require us to know which individuals give birth or die, or where they are located in space. Instead the population is characterized by average birth and death rates, and variability in these averages is treated as a statistical property of the population.

The concept of population has certain similarities to that of *the species*. The two ideas are obviously interrelated and interdependent because a population is defined as a group of organisms of the same *species*, while a species is defined as a *population* of reproducing organisms that is reproductively isolated from other similar populations. The population is to ecology what the species is to systematics, the basic unit upon which the science is built. In addition, because the population is a central concept in systematics, evolution and ecology, it serves as a bridge to integrate and unify these areas of biology.

### 2.1.1 The spatial context

The definition of a population refers to individuals "living in the same place". Here place implies some kind of spatial resolution, as in "the population of New York" or "the population of aphids in a wheat field". But is "New York" or a "wheat field" an appropriate spatial scale in which to view human or aphid population dynamics?

Of course, spatial dimension can be defined rather arbitrarily, say by the preferences (or prejudices) of the individual observer. An informal approach such as this is inherent in statements like "the population of aphids in a wheat field". However, in order to build a general and robust theory of population dynamics, one that applies to all species, it would be well to start with a formal and precise definition of the object of study. A theory based on arbitrary or confused concepts is likely to be an arbitrary and confusing theory! Perhaps this is one of the reasons why there is so much controversy and confusion in ecology?

*Spatial dimension* is one of the most difficult problems to solve when trying to define a particular population. For example, is a "wheat field" an appropriate spatial scale in which to study an aphid population, for aphids can move long distances, and their numbers can be affected by conditions in perennial habitats, far from wheat fields? As aphids invariably migrate into the farmer's fields from these perennial habitats, the correct spatial scale to study their dynamics must include these habitats, and may, therefore, be of the order of "dozens of square kilometres" rather than "a field". Using a smaller area may give rise to misleading or even dangerous inferences. For example, the conclusion that an aphid population is extinct because no aphids are present in a field is obviously a dangerous assumption if you are a farmer, for they may arrive in numbers tomorrow!

The problem, of course, is to determine the correct spatial scale, and to locate the correct boundaries, for the population under study. This problem can be tackled by considering two very different kinds of organisms - bacteria and elk. Bacteria are minute creatures with limited capability for movement, while elk are large animals that range over huge areas. It may make sense to study a population of bacteria on a square metre of ground, because an area this size will contain many thousands of individuals, and bacteria cannot move very far in an active sense. But it makes no sense to study a population of elk on the same square metre! Thus, the correct spatial scale for viewing a population depends on the nature of the organism. In general, large organisms, or organisms that can move long distances, will need to be studied over larger areas than small or sedentary organisms.

Probably the best rule of thumb is to choose an area that minimizes or balances the rate of *emigration* (or movement out of the area) and *immigration* (or movement into the area). Imagine the elk population, for example: if the area is too small, elk will be absent from it most of the time but occasionally the area may be crowded with animals. Almost all of the changes in the "population" will be due to movement into and out of the area. As the size of the area is increased, however, the rate of movement in and out will decline, and changes in numbers will be associated more and more with births and deaths rather than movements. When the



elk population is correctly bounded, immigrations and emigrations should approach a minimum and be roughly balanced so that the variation in population numbers is almost entirely determined by births and deaths.

It is sometimes quite obvious where the actual boundaries of a population should be placed on the landscape. In the case of elk, for example, a specific region within which the population resides can often be identified; for example, an area surrounded by mountains, rivers, etc. With bacteria, on the other hand, it may be difficult or impossible to identify isolated populations and, in this case, the placement of boundaries may become rather arbitrary. However, the physical size of the area containing the population should still be large enough so that changes in numbers are associated more with births and deaths than with movements. The size of the area of study should, therefore, roughly correspond to the mobility of the organism, with more mobile organisms being studied over larger areas than sedentary ones.

It is now possible to provide a more precise definition, i.e. a *population is a group of individuals of the same species that live together in an area of sufficient size that they can carry out their normal functions, including migration, and where emigration and immigration rates are roughly balanced*. On occasion it may be necessary to talk about groups of organisms occupying smaller areas than the *true* population. When this occurs they will be identified as *sub-populations* or *local* populations. Local populations are characterized by unbalanced immigration and emigration rates and sometimes by local extinction. On the other hand, it may also be necessary to consider larger areas containing two or more distinct populations that occasionally share migrants. Groups of populations such as these will be identified as *meta-populations*.

## 2.2 POPULATION VARIABLES

Having defined a population, it is now necessary to determine which *variables* will be used to describe populations of living organisms, and how these variables can be estimated in the field. In the case of elk, for example, it may be possible to count every individual using aircraft or ground surveys at winter feeding sites. In this way one can obtain an accurate estimate of the total, or *absolute*, population present at a given time in a given area (the numbers of humans shown in Figure 1.1 are also absolute estimates). The absolute number can also be divided by the area of land within which the population resides to obtain an estimate of *population density* per unit area (e.g. gypsy egg masses are reported as numbers per hectare in Figure 1.1). Population density is a particularly useful variable because it relates population numbers to a standard area, say a hectare, and this enables us to compare populations of the same species

inhabiting different areas, or populations of different species occupying the same area. Density also relates numbers to a constant measure of resource availability, because food and space are often interrelated and interdependent. Sometimes organisms may live in specialized habitats and, in such cases, densities can be measured in terms of habitat units, such as insects per square metre of foliage or soil (e.g. larch budmoths in Figure 1.1 are related to kilograms of larch foliage).

In contrast to elk, it is virtually impossible to count all the bacteria in a square metre of soil, or all the aphids over several square kilometres. In these cases, it is usually necessary to develop a *representative* sampling procedure; i.e. a sampling scheme that attempts to represent all the variability in the population, in much the same way as an opinion poll attempts to represent the variability in people's feelings about a particular issue<sup>6</sup>. The simplest way to obtain an unbiased estimate of population density in a given area is to sample at random points in space – a *random sample*. However, a more efficient procedure is to take a *stratified* random sample: in this case the variation in population density over the area of interest is first studied, and then a sampling protocol is designed that takes this variability into account; for example, the total area can be divided into regions, or strata, representing different densities, say high, medium and low, and then samples can be taken randomly within each stratum. Stratified random sampling enables one to obtain unbiased estimates of the mean density of the population per unit area of ground or habitat with minimal cost and effort. This estimate can also be converted into an absolute population count if the total area within which the population resides is known; i.e. the total number of hectares or square metres of soil. However, density estimates obtained by sampling are often preferable to absolute estimates, particularly if difficulties are encountered in defining the boundaries of the population.

On occasion it may be possible to census populations at special places. Sandhill cranes, for example, gather on the Platte River in Nebraska each spring, and elk can be monitored at winter feeding stations. On other occasions population counts can be obtained by monitoring hunters and fishermen (e.g. captures of blue whales and whitefish in Figure 1.1) or by trapping the organism (e.g. flying aphids can be captured by suction traps and moths by light traps). However, population counts obtained in this way are not necessarily related to area or absolute numbers, in which case they are called *indexes* of abundance.

Finally, population numbers are sometimes measured by what is called the *mark-recapture* method. Here individuals are live-trapped, marked in some way, released, and then trapped again. The proportion of marked to unmarked individuals can then be used to obtain an index of abundance. If certain conditions are met, it may be possible to transform this index into an estimate of absolute numbers or density.



### 2.3 POPULATION CHANGE

This book is concerned with changes in populations of living organisms over time. For this reason it is important to consider the correct time scale for observing population change. In other words, how long and how frequently should the population be observed (sampled) before analysis can lead to sensible conclusions about the causes of the observed population fluctuations? On the first question, one rule of thumb is that the time scale should be at least twice as long as the period of fluctuation. Thus, if the population exhibits 10-year cycles, as many do (see the larch budmoth in Figure 1.1), then at least 20 years of observations would be required. On the other hand, if populations oscillate at higher frequencies, like the sycamore aphid (Figure 1.1), then they may not need to be studied for so long to obtain meaningful data. Unfortunately, observations of population change over long periods of time are not always available to natural resource managers, and when they are they are often of poor quality. The fact is, managers must often make do with what is available, even if the data are inaccurate or sparse. The stance taken in this book is that any data are better than none. It is also important to realize that data sets get longer (and usually better) with time, but for this to happen someone must start collecting the data and others must keep it going.

On the second problem, the frequency of observations, a good rule of thumb is to observe the system at its natural frequency. On the planet Earth, the underlying natural rhythm is set by the revolution of the Earth around the Sun – the annual cycle. If one observes the dynamics more frequently than this, then most of the changes in population numbers may be caused by seasonal effects (exogenous forcing) rather than feedback, and it may be difficult or impossible to determine the important stabilizing or destabilizing mechanisms. In some cases it may be necessary to observe population changes more frequently. This is particularly true in agricultural systems, where the seasonal build up of pests is a critical problem. Because this book is more about natural or semi-natural situations, it is usually assumed (unless otherwise noted) that the populations being studied are measured at roughly the same time each year, and that this string of annual observations forms the *time series* describing the fluctuations of the populations over time – its dynamics.

#### 2.3.1 The equations of change

Given a time series describing fluctuations in population density over time, then the change in density over a year can be represented by

$$\Delta N = N_t - N_{t-1}, \quad (2.1)$$

where  $N_t$  is the density of the population in year  $t$  and  $N_{t-1}$  is its density at the same time in the previous year. Of course, the change in a population of organisms over a year can also be measured if the numbers of births and deaths are known (assuming that immigrations and emigrations are balanced, as they should be if the spatial dimension of the population is properly defined). Hence, population change is also given by

$$\Delta N = \text{Births} - \text{Deaths}. \quad (2.2)$$

For reasons that will become clear later, it is preferable to express population birth and death rates as relative or *per capita* rates, so that population change over the year is written

$$\Delta N = BN_{t-1} - DN_{t-1} = N_{t-1}(B - D), \quad (2.3)$$

where  $B$  and  $D$  represent the per capita birth and death rates, respectively.

If the right-hand side of equation (2.1) is inserted for  $\Delta N$  in equation (2.3), then

$$N_t - N_{t-1} = N_{t-1}(B - D), \quad (2.4)$$

and, rearranging so that only  $N_t$  appears on the left-hand side,

$$N_t = N_{t-1} + N_{t-1}(B - D), \quad (2.5)$$

or

$$N_t = N_{t-1}(1 + B - D). \quad (2.6)$$

This is called a *step-ahead forecasting equation* because population numbers 1 year into the future can be forecast from their current numbers if the per capita birth and death rates are known.

The quantity  $1 + B - D$  in equation (2.6) measures the per capita rate of change over a finite period of time, say a year, and is sometimes called the *finite per capita rate of change* of the population. This quantity will be represented by the variable  $G$  (the Greek symbol  $\lambda$  is also used in the literature)

$$G = 1 + B - D, \quad (2.7)$$

so that equation (2.6) becomes

$$N_t = N_{t-1}G. \quad (2.8)$$

As will become clear later, it is often advantageous to express the growth rate of a population in natural logarithms; i.e.

$$\ln N_t = \ln N_{t-1} + \ln G, \quad (2.9)$$

where  $\ln$  represents the natural logarithm of the quantity that follows it.

Defining the *logarithmic per capita rate of change* as

$$r = \ln G = \ln(1 + B - D), \quad (2.10)$$

We will  
use  
"b" and  
"d"  
to denote  
per capita  
birth, death.

equation (2.9) becomes

$$\ln N_t = \ln N_{t-1} + R \quad (2.11)$$

Notice that if estimates of  $N_{t-1}$  and  $N_t$  are available, then the per capita rate of change,  $R$ , can be estimated from the relationship

$$R = \ln N_t - \ln N_{t-1} = \ln \left( \frac{N_t}{N_{t-1}} \right) \quad (2.12)$$

$R$  is often called the *instantaneous* or *intrinsic* rate of increase of the population, and is often given the lower case symbol  $r$ . In this book, however, the symbol  $r$  is reserved for the correlation coefficient and so the upper case is used for the logarithmic rate of change.

## 2.4 SUMMARY

1. The concept of population is an abstraction that is necessary for practical reasons.
2. The correct spatial scale for viewing a population depends on the size and mobility of the species. The best rule of thumb is that the spatial scale be such that emigration and immigration rates are roughly balanced.
3. A population is defined as a group of individuals of the same species living together in an area of sufficient size that they can carry out their normal functions, including migration, and where emigration and immigration rates are roughly balanced.
4. The state of a population at a given instant in time is described by the population variables absolute numbers, density, or indexes of abundance.
5. Variables can be measured by total counts, random or stratified random samples, harvest records, traps or mark-recapture techniques.
6. The longer the series of observations on population changes (time series) the better, but we must often make do with what we have.
7. In order to avoid the complications associated with exogenous seasonal effects, population dynamics is usually studied on estimates of population size taken at the same time each year.
8. Rates of change are described in terms of per capita birth and death rates and the finite and instantaneous per capita rates of change ( $G$  and  $R$ ).

## 2.5 EXERCISES

1. 758 elk spend 3 months each winter in a 5 hectare feed lot. These elk are known to range over a watershed of 1230 hectares. What is the absolute size of the population and what is its density?
2. A scientist sampled the white grubs in a 3.4 hectare pasture by taking 200 randomly located 1 decimetre (= 100 square centimetres) soil cores. He counted 7564 white grubs in these samples. Calculate the density of white grubs per square metre of soil, per hectare, and the absolute population in the pasture.
3. The elk population discussed above produced 58 calves in 1990 but only 22 were alive by 31 December 1990. In addition, 37 yearling and older elk died during 1990. What was the per capita birth and death rate and the logarithmic net per capita rate of change ( $R$ ) over the year? Is this elk population increasing?