

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 ecology⁴ 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 dynamics⁵?

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 issue⁶. 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, respectively⁷.

If the right-hand side of equation (2.1) is inserted for ΔN 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 λ 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

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

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?