Dynamics: theoretical ecology and the rules of change

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.

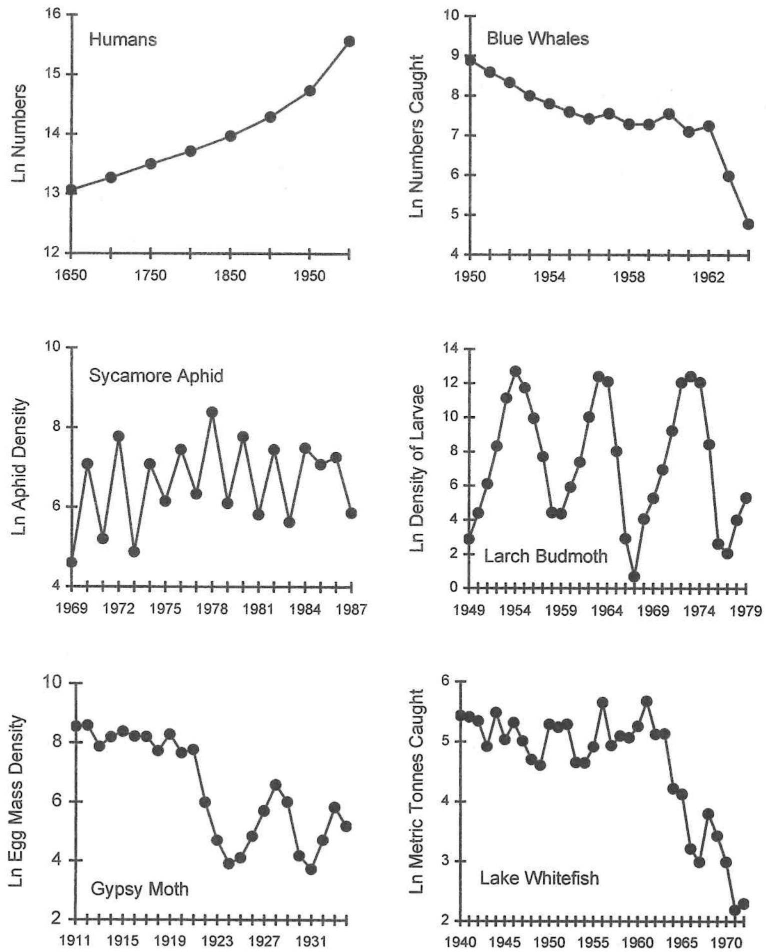

Figure 1.1 Dynamics of various animal populations with numbers, expressed as natural logarithms, plotted against time (see reference 3 for data sources).

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[2].

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

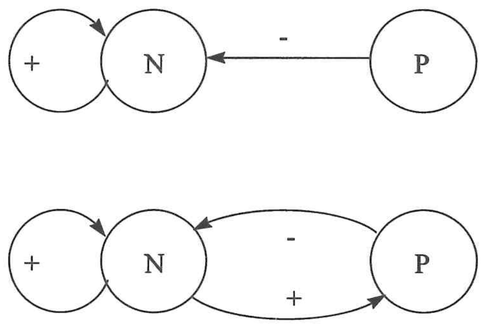

Figure 1.2 Flow diagram for the effects of a population of predators P on the numbers of its prey N: top, predators act as a negative exogenous factor on the prey population (i.e. negative arrow from P to N), and the prey have a positive effect on their own numbers (i.e. the arrow from the prey to itself 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[4] may make sense, it is not practical.