CHAPTER ONE

Introduction

A central challenge, perhaps the central challenge, for population ecology is to explain the persistence of species. In the variable, uncertain, and sometimes catastrophic natural world, species extinction is rare—why? The broad answer is that most natural populations are regulated most of the time at some spatial scale. The study of population dynamics is therefore a search for regulatory mechanisms and their effects.

Regulated populations can exhibit a range of dynamics. These include stability; instability, for example in the form of population cycles; local extinction but regional regulation; and local instability but regional stability (all discussed in more detail in chapter 2). Population ecology therefore also needs to explain when and how dynamics take one rather than another of these forms.

WHY CONSUMER-RESOURCE INTERACTIONS?

The consumer-resource interaction is arguably the fundamental unit of ecological communities. Virtually every species is part of a consumer-resource interaction, as a consumer of living resources, as a resource for another species, or as both. Consumer-resource interactions are, in addition, fundamentally prone to being unstable (chapters 3 and 4). If we are to understand population regulation and its various manifestations, we therefore need to focus on consumer-resource interactions.

Our major focus is either on generic (that is, simple) consumer-resource models, typically developed with predators and prey in mind, or on more detailed models developed initially to portray parasitoid-host interactions. We treat disease-host models only briefly and hardly mention herbivore-plant interactions. In chapter 11, however, we show

that models for all of these types of consumer-resource systems have a common origin, and we suggest that many of the insights that emerge from the models examined are likely to apply broadly to different classes of consumers and living resources.

Except in chapter 8, we focus mainly on one consumer and one resource population. The book is thus frankly reductionist. In real communities, of course, consumers frequently attack several species, and resource populations are often attacked by several consumer species. We believe that understanding simpler systems is a useful prelude to understanding more complex ones for reasons explored next; in addition, chapter 11 gives some, perhaps surprising, reasons for believing that few-species models are often appropriate for populations living in many-species food webs.

ON THEORY AND MODELS

This book focuses on mathematical models as a means of understanding population dynamics. Here we give reasons why we think this approach is essential to understanding such real-world dynamics.

The ecological world bristles with particulars. Each species is unique. Most species are represented by many populations, each living in an environment that differs from those of other populations. There are surely at least 100 million such populations. We can study and understand the population dynamics of pitifully few—a miniscule fraction of the total—and if all we can get is an account of these few populations, it is not worth beginning the task. The goal and promise of theory are to reach into this thicket of particularity, grasp what is general, and express it in ways that let us test the predictions in real systems.

Theory expresses our current understanding of the real world. In ecology, theory may never be all-encompassing. Furthermore, theory will never predict, even for one particular population, most details of future dynamics—the exact age distribution on 4 July next year, for example. Theory might nevertheless explain how various types of dynamical behavior (stability, long-period cycles, etc.) can arise and how a range of different natural histories and life histories can give rise to the same kind of dynamics. It might predict new types of dynamics or define field observations and experiments that can tell us which among

several potential mechanisms is actually operating in a real system. Theory in this book does just these things, and thus extracts generality from particularity and also achieves testability.

A model is a set of assumptions about how nature works, together with an algorithm for calculating the consequences. The assumptions abstract from the real situation those features one considers "more important" and ignore those that are less important. The model then deduces the consequences of these assumptions. Since none of us can think simultaneously about all the details of any ecological system, we all use models all the time. The model may be verbal, or a vague picture in our head, but it is a model.

We all have models in our heads all the time. The major value of mathematical models, in a subject that is quintessentially quantitative, is explicitness. A mathematical model forces us to say exactly what our ideas/assumptions are. If the calculations are correct, the model establishes the consequences of the assumptions, consequences we often could not derive purely by intuition. A mathematical model may be wrong, but it makes the assumptions explicit, so they can be examined and disputed, and the conclusions follow logically from the assumptions, so with luck they can be tested.

We do not suggest that the models in this book are correct. We know that, like all models, they are at some level wrong. We hope they are not wrong in fundamentally important ways. But if they are, exploring the errors will point the way to better insights.

The key question is not whether a model is true, but whether it is useful. Models are tools to understand the real world and can serve this purpose in various ways. They can sharpen our intuition about ecological mechanisms. Even the simplest model, which may match no living system, can be useful. For example, it can still tell us that delays in density dependence can lead to instability, population cycles, fewer recruits next year if we have more adults this year, and so on.

Simple Models and (or versus) Complex Models

Every model is a judgment about what is more, and what is less, important; i.e., about what to include and what to omit. Theorists typically love simple models. This is partly because they are more mathematically

tractable, and because their lack of ecological detail suggests they may be broadly applicable. (A counter argument, of course, is that lacking so much ecology they cannot be relevant.) But simpler models have another key property that is often overlooked: they are easier to understand, so their assumptions and mechanisms are more transparent.

Simple models do of course lack ecological features that may be important to answering the question posed. And there is a school of modeling that argues that as much as possible of the real system should be represented in the model. But whereas more realism might always seem better, increasing complexity poses increasing difficulties. Two seem to us especially important.

First, complex models are harder to understand. It is often not at all clear how each component of a complex model affects the outcome. Since most models in this book are developed as theory, they are the simplest consistent with the need to include the crucial natural history. We also argue that complex models need to be placed in the context of simpler and more easily understood models, which gives rise to the notion of theory as a hierarchy of models (chapter 12).

Second, and perhaps paradoxically, beyond a certain point models become more difficult to test as they become "more realistic" and hence more complex. One reason is simply that the field biologist cannot supply the data needed to estimate the functions and parameters. But in addition, as more complexity is added, the greater is the chance that the model will "explain" the observations for entirely spurious reasons. When fitting a model to real data, the best predictive models have a small to intermediate number of parameters (Burnham and Anderson 1998). We do little model fitting in this book.

THEMES

Here we adumbrate themes that run through the book. It will be useful to keep them in mind, for they can explain why sometimes we may spend time on matters that do not immediately seem of prime importance.

- *Effects of ecological realism.* We are concerned in much of the book about exploring the dynamical effects of adding realism to models. In particular, we show how differences between individuals, associated with growth and development, offer new

explanations for existing phenomena, including new routes to stability, and predict new phenomena, including novel kinds of population cycles.

- *Realism, scope, and generality.* Adding realism to models usually implies tying them more explicitly to particular systems or kinds of systems, with a potential loss in the range of systems to which they are relevant—a loss of generality. However, whereas we focus for stretches on particulars, we are consistently concerned with the range of real systems to which models may apply, and with exploring the extent to which they can be generalized.
- *Coherent theory.* An aspect of generality is the extent to which different models are connected in a larger, coherent body of theory. We explore this issue explicitly at several points through the book and especially in chapter 11. We also continually check for properties of the simple models we start with that survive to our ultimate, more complex models. Such persistent properties are the threads that connect the range of models we explore. These connections build to the final notion of coherent theory that takes the form of a hierarchy of models (chapter 12).
- *The role of cycles.* We focus on three main dynamical aspects of the models in this book: equilibrium densities, stability properties, and the form of population cycles the models produce under certain circumstances. We focus on cycles because they provide a strong signal determined by the structure of the interacting populations and the mechanisms through which they interact. If the details of particular types of cycles seem at first sight arcane, we counsel patience. It turns out there are rather few classes of cycles, and we can put them to good use as probes of real systems.