CHAPTER ONE

An Ecological Scenario and the Tools of the Ecological Detective

AN ECOLOGICAL SCENARIO

The Mediterranean fruit fly (medfly), *Ceratitis capitata* (Wiedemann), is one of the most destructive agricultural pests in the world, causing millions of dollars of damage each year. In California, climatic and host conditions are right for establishment of the medfly; this causes considerable concern. In Southern California, populations of medfly have shown sporadic outbreaks (evidenced by trap catch) over the last two decades (Figure 1.1). Until 1991, the accepted view was that each outbreak of the medfly corresponded to a "new" invasion, started by somebody accidentally bringing flies into the state (presumably with rotten fruit). In 1991, our colleague James Carey challenged this view (Carey 1991) and proposed two possible models concerning medfly outbreaks (Figure 1.2). The first model, M_1, corresponds to the accepted view: each outbreak of medfly is caused by a new colonization event. After successful colonization, the population grows until it exceeds the detection level and an "invasion" is recorded and eradicated. The second model, M_2, is based on the assumption that the medfly has established itself in California at one or more suitable sites, but that, in general, conditions cause the population to remain below the level for detection. On occasion, however, conditions change and the population begins to grow in time and spread over space until detection occurs. Carey argued that the temporal and spatial distributions of trap catch indicate that the medfly may be permanently estab-

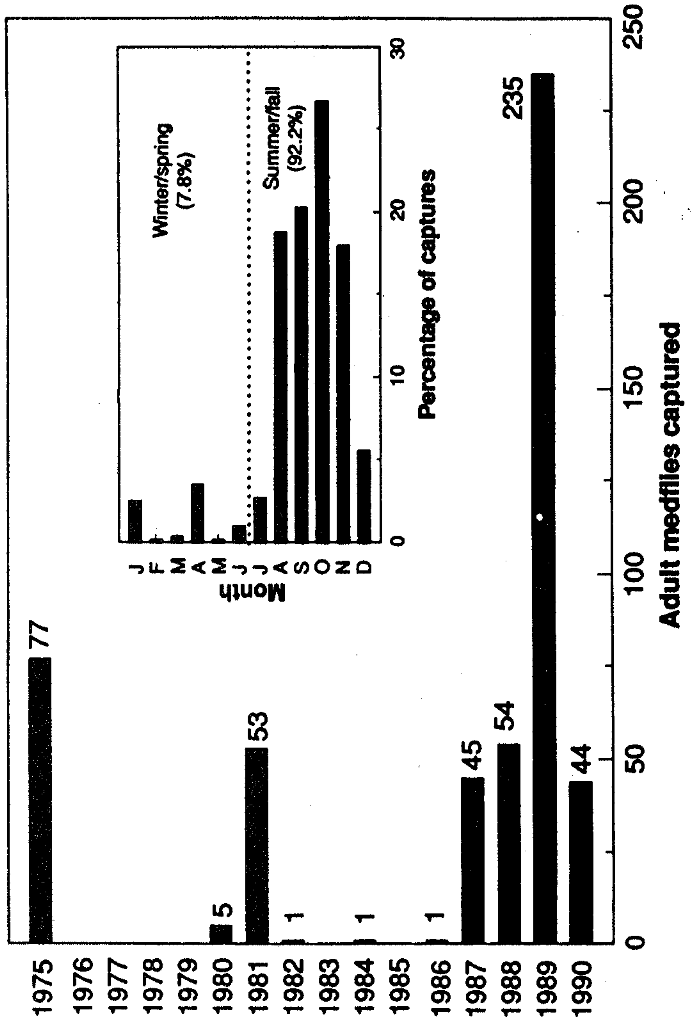

FIGURE 1.1. The capture of adult medfly in Southern California, from 1975 to 1990. (Reprinted with permission from Carey 1991. Copyright American Association for the Advancement of Science.)

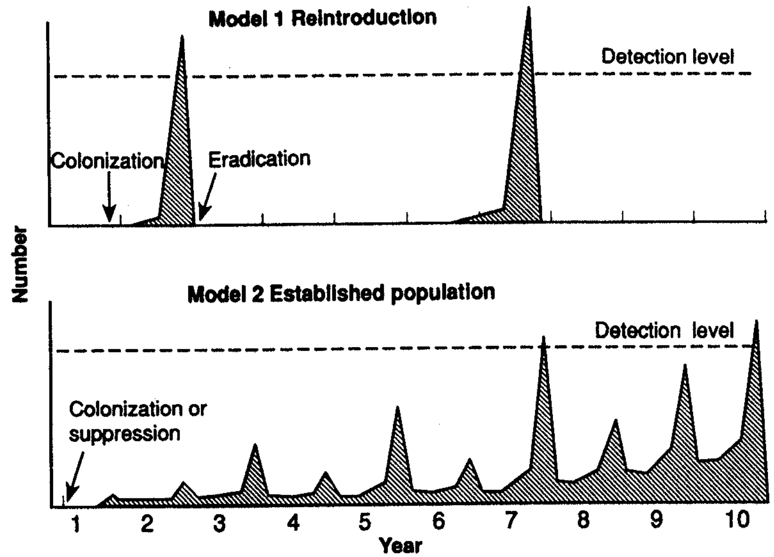

FIGURE 1.2. The outbreak of medfly can be described by two different methods. In model 1, we assume that there is continual reintroduction of the pest. After a reintroduction, the population grows until it exceeds the detection level. In model 2, we assume that the medfly is established, but that ecological conditions are only occasionally suitable for it to grow and exceed the detection threshold. (Reprinted with permission from Carey 1991. Copyright American Association for the Advancement of Science.)

lished in the Los Angeles area. Knowing which of these views is more correct is important from a number of perspectives, including the basic biology of invasions and the implications of an established pest on agricultural practices.

Determining which model is more consistent with the data is a problem in ecological detection. That is, if we allow that either model M_1 or model M_2 is true, we would like to associate probabilities, given the data, with the two models. We shall refer to this as "the probability of the model" or the "degree of belief in the model." How might such a problem be solved? First, we must characterize the available data, which are the spatial distribution of trap catches of medfly over time (Figure 1.3). We could refine these by placing

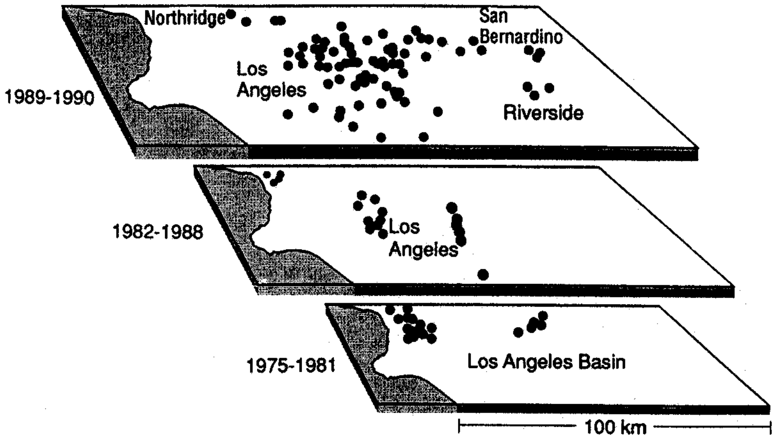

FIGURE 1.3. The data available for ecological detection in this case would be the spatial distribution of the catch of adult medfly over time. (Reprinted with permission from Carey 1991. Copyright American Association for the Advancement of Science.)

small grids over the maps and characterizing a variable that measures the number of flies that appear in cell i in year y. Second, we must convert the pictorial or verbal models shown in Figure 1.2 into mathematical descriptions. That is, some kind of mathematical model is needed so that the data can be compared with predictions of a model. Such models would be used to predict the temporal and spatial patterns in detected outbreaks; the mathematical descriptions would generate maps similar to the figures. The models would involve at least two submodels, one for the population dynamics and one for the detection process. Courses in ecological modeling show how this is done. Third, we confront the models with the data by comparing the predicted and observed results. At least three approaches can be broadly identified for such a confrontation.

Classical Hypothesis Testing. Here we confront each model separately with the data. Thus, we begin with hypotheses:

H_0: Model M_1 is true

H_a: Some other model is true

Here the alternate model might be that outbreaks are random over time and space. Using the mathematical descriptions of the models, we construct a "p value" for the hypothesis that M_1 is true. It might happen that we can definitely reject H_0 because the p value is so small (usually less than 0.05 or 0.01). Alternatively, we might not be able to reject H_0 (i.e., $p > 0.05$), but then might discover that the power of the statistical test is quite low (we assume that most readers are probably familiar with the terms "p values" and "power" from courses in elementary statistics, but we shall explain them in more detail in the following chapters). In any case, we use such hypothesis testing because it gives the "illusion of objectivity" (Berger and Berry 1988; Shaver 1993; Cohen 1994).

After we had tested the hypothesis that model 1 is true against the alternate hypothesis, we would test the hypothesis that model 2 is true against the alternate. Some of the outcomes of this procedure could be: (i) both models M_1 and M_2 are rejected; (ii) model M_1 is rejected but M_2 is not; (iii) model M_1 is not rejected but M_2 is; and (iv) neither model is rejected. If outcome (ii) or (iii) occurs, then we will presumably act as if model M_1 or M_2 were true and make scientific and policy decisions on that basis, but if outcome (i) or (iv) occurs, what are we to do? Other than collecting more data, we are provided with little guidance concerning how we should now view the models and what they tell us about the world. There is also a chance that if outcome (ii) or (iii) occurs, the result is wrong, and then on what basis do we choose the p level?

Likelihood Approach (Edwards 1992). In this case, we use the data to arbitrate between the two models. That is, given the data and a mathematical description of the two models, we can ask, "How likely are the data, given the model?" Details of how to do this are given in the rest of this book, but read on pretending that you indeed know how to do it. Thus, we first construct a measure of the probability of the observed data, given that the model is true—we shall denote this by Pr{data|M_i}. We then turn this on its head and interpret it as a measure of the chance that the model is the appropriate description of the world, given the data. This is called the likelihood and we denote it by $\mathcal{L}_i\{M_i|\text{data}\}$. We now compare the likelihoods of the two models, given the data. If $\mathcal{L}_1\{M_1|\text{data}\} \gg \mathcal{L}_2\{M_2|\text{data}\}$, then we would argue that model M_1 is a better description of the world; if $\mathcal{L}_1\{M_1|\text{data}\} \ll \mathcal{L}_2\{M_2|\text{data}\}$, then we would argue that model M_2 is a better description of the world; and if $\mathcal{L}_1\{M_1|\text{data}\} \sim \mathcal{L}_2\{M_2|\text{data}\}$, then we would argue that the data do not differentiate between the models. A smart decision maker would not act as if the most likely model were true, but would weigh the costs and consequences of each action against the relative probabilities of the alternative hypotheses. But what exactly is meant by "$\gg$," "$\ll$," or "$\sim$" in this approach?

In this book, we shall work out methods for determining when one likelihood is much larger than another, and what that means in terms of confronting models with data.

Bayesian Approach. Finally, we might have other information that allows us to judge a priori which model is more likely to be true. For example, we might know the ecology of invasion and establishment of medfly in other places. Or we might know that before certain outbreaks people had been caught bringing fruit into the country from places where medfly is established. This kind of information can be summarized in a "prior probability that model M_i is true," which we denote by p_i. If we allow only two models of the world (medfly are established or they reinvade), then $p_1 + p_2 = 1$. Now, given information consisting of trap catches and the mathematical model, we want to "update" these prior probabilities. That is, we want to evaluate a "posterior probability that model M_i is true, given the data." Procedures for doing

this require an understanding of conditional probability and are generally called "Bayesian methods," named after the Reverend Thomas Bayes, who introduced such ideas. In biology and mathematics, one of the earliest modern proponents was Sir Harold Jeffreys (1948), who called the method "inverse probability." His goal was to find methods that allow us to combine prior information with the chance of observing the data to evaluate a posterior probability of different hypotheses, given a scenario associated with the prior information. Interestingly, although Jeffreys is most famous for his work in applied mathematics, astronomy, and geophysics, he was one of the earliest contributors to the *Journal of Ecology* (Sheail 1989). In this book, we shall illustrate how Bayesian methods can be developed and applied. They are particularly appropriate for cases in which studies cannot be replicated (e.g., Reckhow 1990) and for assessment of the risk and safety in various environmental settings in which "expert opinion" is sought (Emlen 1989; Apostolakis 1990; Bolt 1991). There are arguments that Bayesian reasoning is the only way to provide a unified and consistent approach to deterministic and statistical theories (Howson and Urbach 1989, 1991).

This ecological scenario illustrates three approaches that can be taken when confronting models with data. It is our opinion that the process of science consists of confronting more than one description of how the world works with data. Thus, in the rest of the book we spend little time on classical methods of hypothesis testing but focus on likelihood and Bayesian methods. Two recent special features in the journal *Ecology* contain a number of papers that deal with nonclassical approaches to the use of statistics in ecological problems (Carpenter 1990; Jassby and Powell 1990; Reckhow 1990; Walters and Holling 1990; Potvin and Roff 1993; Potvin and Travis 1993; Shaw and Mitchell-Olds 1993; Trexler and Travis 1993) or with particularities of ecological situations (Dutilleul 1993; Legendre 1993). They provide a good complementary background for this book.

THE TOOLS FOR ECOLOGICAL DETECTION

The modern ecologist usually works in both the field and laboratory, uses statistics and computers, and often works with ecological concepts that are model based, if not model driven. How do we make the field and laboratory coherent? How do we link models and data? How do we use statistics to help experimentation? How do we integrate modeling and statistics? How do we confront multiple hypotheses with data and assign degrees of belief to different hypotheses? How do we deal with time series (in which data are linked from one measurement to the next) or put multiple sources of data into one inferential framework? These are the kinds of questions asked and answered by the ecological detective.

Like all other forms of creative activity, ecological detection is a craft that requires the right tools as well as the skills and materials to use the tools. We envision four components.

Hypotheses are the first component. Notice the plural, which is essential to our viewpoint. Science consists of confronting different descriptions of how the world works with data, using the data to arbitrate between the different descriptions, and using the "best" description to make additional predictions or decisions. These descriptions of how the world might work are hypotheses, and often they can be translated into quantitative predictions via models. In Chapter 2, we review different kinds of models, the purposes of models, and how models are related to hypotheses.

Data are the second component. You cannot do good analysis if the data are not good. But what does "good" mean? Sometimes the role of analysis is to show that a set of data—at least within the context of a particular view of the world—is not as informative or as useful as one thought it would be. In Chapter 3, we stress that it is important to "Know Your Data" and we provide a sufficient review of

probability and the stochastic processes that you will need to conduct the work of the ecological detective.

Goodness of fit is the third component. When the data are used to arbitrate between different hypotheses or models, we must have a measure to determine how well each description of the world fits the observations. In Chapters 5, 7, and 9, we describe a variety of measures of goodness of fit that can be used in the confrontation of models and data. We provide recommendations about when it is good to use a particular method.

Numerical procedures are the fourth component. Having a measure of goodness of fit between the model and the data is not enough—you must to be able to evaluate it quickly and efficiently and explore the goodness of fit of other models. Thus, in Chapter 11, we provide an introduction to numerical methods needed to assess goodness of fit and to find the best fit. There is a history of the use of numerical procedures in ecology (examples from a generation ago are given by Conway et al. 1970, Melzer 1970, and Marten et al. 1975), but it is the development of microcomputers that really allows the full richness of numerical procedures to be exploited by practicing ecologists.

Overarching these components are alternative views of the scientific method and the role of models in science, which we discuss in Chapter 2. There we present four of the major philosophies of science and show how two of them are closely connected to our work of ecological detection.

A final warning. We are practicing ecologists. We are not statisticians, numerical analysts, or philosophers, and the appropriate chapters will no doubt offend the appropriate experts. For this we make no apologies other than stressing that for the ecological detective the problem is paramount. Because of that, we bring to the problem whatever techniques—from wherever they come—needed to solve it. And if the techniques do not exist, then we must invent them.

The Ecological Detective

Confronting Models with Data

RAY HILBORN
AND
MARC MANGEL

PRINCETON UNIVERSITY PRESS
PRINCETON, NEW JERSEY
1997

Published by Princeton University Press, 41 William Street,
Princeton, New Jersey 08540
In the United Kingdom: Princeton University Press,
Chichester, West Sussex

Library of Congress Cataloging-in-Publication Data

Hilborn, Ray, 1947–
The ecological detective : confronting models with data / Ray Hilborn and Marc Mangel.
p. cm. — (Monographs in population biology ; 28)
Includes bibliographical references and index.
ISBN 0-691-03496-6 (cloth : alk. paper). — ISBN 0-691-03497-4 (pbk. : alk. paper).
1. Ecology—Mathematical models. I. Mangel, Marc. II. Title. III. Series.
QH541.15.M3H54 1997 96-9638
574.5′0151—dc20 CIP

This book has been composed in Baskerville

Princeton University Press books are printed on acid-free paper and meet the guidelines for permanence and durability of the Committee on Production Guidelines for Book Longevity of the Council on Library Resources

Printed in the United States of America by Princeton Academic Press

10 9 8 7 6 5 4 3 2 1
10 9 8 7 6 5 4 3 2 1
(Pbk.)