ECOLOGICAL METHODOLOGY

Second Edition

Charles J. Krebs

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Ecological Methodology

Dedicated to the many biometricians working in ecology, fisheries, and wildlife who over the last 60 years have established a rigorous foundation for our ecological methods.

Preface

This book attempts to present to ecologists in a coherent form the statistical methodology that is general to ecological field measurements. Scientific progress depends on good methods, and there are two components to progress in ecological methodology. The first component is biological and technical—you must have a good sampling device that catches the animals you wish to study or marks them with tags or bands that will not fall off. There has been great progress in designing better and better sampling devices in all areas of ecology, from mouse trapping to sampling the deep benthos of the oceans. The techniques and equipment used for sampling vary greatly for different groups of animals and plants and are the subject of many handbooks specific to a given area of ecology or specific group of plants or animals.

The second component of scientific progress is good statistical design. This component is general to all disciplines, and ecology is no exception. Over the past 60 years there has been superb development of statistical methods for increasing precision and avoiding bias in the estimation of ecological parameters like population size. Much of this has now penetrated ecological journals, but there have been few attempts to put these methods together in a textbook. Southwood (1978) has been the standard, followed by Ludwig and Reynolds (1988) and Sutherland (1996). Smaller books like Elliott (1977) cover some methods extremely well but are not comprehensive, and ecological methods books are still relatively scarce.

This book will not tell you what plankton sampler is best for oligotrophic lakes, but it will tell you how to design your plankton sampling in the most efficient way so that you need to do minimal work for maximal precision. All the methods presented here are well known to statisticians; that they are not always known to ecologists is one of the weaknesses of modern ecology. I hope that this book will assist field ecologists in the statistical design and analysis of ecological measurements.

Students using this book should have the basic knowledge of statistics presented in a one- or two-semester course in statistics. If your statistics are rusty, keep an introductory statistics text at hand to remind you of the basic ideas of standard errors, variances, and confidence limits. Since I am not a statistician and this is not a book for statisticians, I do not prove any theorems or present rigorous arguments about statistical expectations. I do attempt to translate the recommendations of statisticians into ecological English so that they can be used in the real world. I use approximations when they are needed, because in an ecological study an approximation is better than nothing.

To assist students, I work out numerous examples in boxes in each chapter, as well as in the text. For most of the statistical calculations I discuss, I have written FORTRAN programs to do the tedious arithmetic. Computer-literate students can do many of these calculations in EXCEL or other spreadsheets or in Visual Basic.

If you encounter mistakes in the book, I will be grateful to hear about them. I will maintain a website on the World Wide Web at *www.zoology.ubc.ca* to keep a list of the mistakes that come to my attention. Feedback can be delivered via e-mail to *krebs@zoology.ubc.ca*. One of the things I learned as I wrote this book was the frequency of errors of computation in the ecological literature. The computer should help us avoid mistakes of arithmetic, but of course we must be careful not to institutionalize mistakes in computer programs. Computers do not yet design experiments. If they did, you would not need this book.

I am grateful to my students at the University of British Columbia for helping me develop these thoughts on methodology, and to all those who have suggested improvements in this edition. In particular I thank James Bogart, Leslie Bowker, Robert Frederick, James Gilbert, C. Edward Miller, Jon Mendelson, John Yunger, Brad Anholt, and Lorne Rothman for their suggestions. I thank Nils Stenseth and Grant Singleton for arranging quiet time for me to work on this book, and Alice Kenney for assistance in getting all the material together efficiently.

A tremendous explosion of interest in the statistical problems of ecological methods has occurred during the last decade, and hope that this book brings these to the attention of field ecologists trying to make the measurements that will help us understand the natural world.

Charles J. Krebs
8 October 1997

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CHAPTER 1

Ecological Data

Ecologists, like other biologists, collect data to be used for testing hypotheses or describing nature. Modern science proceeds by conjecture and refutation, by hypothesis and test, by ideas and data, and it also proceeds by obtaining good descriptions of ecological events. Ecology is an empirical science that cannot be done solely on the blackboard or on the computer; it requires data from the real world. This book is about ecological data and how to wrestle it from the real world.

But data or ecological measurements are not all there is to ecology. At best, data may be said to be half of the science. Ecological hypotheses or ideas are the other half, and some ecologists feel that hypotheses are more important than data, while others argue the contrary. The central tenet of modern empirical science is that both are necessary. Hypotheses without data are not very useful, and data without hypotheses are wasted.

One problem that all the sciences face is what to measure, and the history of science is littered with examples of measurements that turned out not to be useful. Philosophers of science argue that we should measure only those things that theory dictates to be important. In abstract principle this is fine, but every field ecologist sees things he or she could measure about which current theory says nothing. Theory develops in a complex feedback loop with data, and an ecologist measuring the acidity of precipitation in 1950 would have been declared unfit for serious science. More typically, the mad ecologist is seen as a person who tries to measure everything. Do not try this, or you will waste much time and money collecting useless data. Data may be useless for several reasons. It may be unreliable or unrepeatable. It may be perfectly reliable and accurate but irrelevant to the problem at hand. It may be reliable, accurate, and very relevant but not collected at the right season of the year. Or the experimental design may be so hopeless that a statistical analysis is not possible. So start by recognizing the following rules.

Rule # 1 Not everything that can be measured should be.

Collect useful data and you have jumped the first hurdle of ecological research. But how do you know what data are useful? It is a mistake to think that statistical analysis by itself will give you any crisp insight into what data you should be collecting. Do not get the proverbial statistical cart in front of your ecological horse. Ecological theory and your ecological insight will give you the distinction between useful things to measure and useless ones, and you will not find this absolutely fundamental information in this book. So, before you do anything else, follow Rule # 2.

Rule # 2 Find a problem and state your objectives clearly.

Often your objective will be to answer a question, to test an ecological hypothesis. Do not labor under the false impression that a statistician can help you to find a problem that is ecologically important or to define appropriate objectives for your research. Many excellent ecology books can help you at this step. Start with Begon et al. (1996) or Krebs (1994) and move to Caughley and Sinclair (1994) or Diamond and Case (1986) for more advanced discussions of ecological theory. The key here is to find an important problem that, once solved, will have many ramifications in ecological theory or in the management and conservation of our resources.

When all the intellectually hard work is over, the statistician can be of great assistance. This book will try to lay out the ways in which some statistical knowledge can help answer ecological questions. We now proceed to describe in detail the statistical cart and forget about the ecological horse, but remember that the two must operate together.

Rule # 3 Collect data that will achieve your objectives and make a statistician happy.

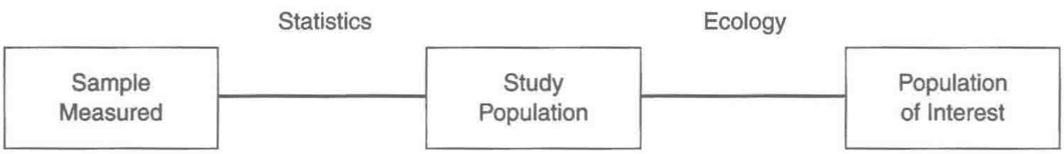
Usually these two goals are the same, but if you ever find a dichotomy of purpose, achieve your objectives, answer your question, and ignore the statistician. In nearly all the cases ecologists have to deal with, a statistician's information can be vital to answering a question in a definitive way. This is a serious practical problem because all too often insufficient data are collected for reaching a firm conclusion. In some cases it is impossible to collect a sufficient amount of data, given normal budgetary constraints.

Some ecologists pick exceedingly interesting but completely impossible problems to study. So please beware of the following possible pitfall of the enthusiastic ecologist.

Rule # 4 Some ecological questions are impossible to answer at the present time.

You do not need to get depressed if you agree with this statement; realizing that adequate data cannot be obtained on some questions would save tax money, ulcers, and some marriages. Constraints may be technical, or it may be simply impossible to collect a large enough sample size. It might be interesting, for example, to map the movements of all the killer whales on the Pacific Coast in real time in order to analyze their social groupings, but it is not possible financially or technically to achieve this goal at this time.

We must always keep in mind that there are three populations out in the real world that keep getting confused.



We actually measure a sample of animals or plants, and these are the primary data that an ecologist gathers. If we do our sampling correctly, this will be a representative sample of a *study population.* Often this is a random sample of the study population, and statisticians tell us that with a random sample, we can make valid inferences about the study population. In some cases the population studied is the population of interest, but the ecologist is often interested in yet another, broader population and would like to draw some conclusions about this population. Keep in mind the population of interest when designing your sampling methods.

Given these general warnings about the interface between statistics and ecology, we will review a few basic ideas about designing field studies and taking measurements. We will then consider a few problems in applying statistical inference to ecological data.

1.1 DESIGNING FIELD STUDIES

Is the event you wish to study controlled by you, or must you study uncontrolled events? This is the first and most important distinction you must make in designing your field studies. If you are studying the effects of natural forest fires on herb production, you are at the mercy of the recent fire season. If you are studying the effects of logging on herb production, you may be able to control where logging occurs and when. In this second case you can apply all the principles you learned in introductory statistics about replicated experimental plots and replicated control plots, and the analyses you must make are similar to those used in agricultural field research, the mother lode of modern statistics. If, on the other hand, you are studying uncontrolled events, you must use a different strategy based on sampling theory (Eberhardt and Thomas 1991). Figure 1.1 illustrates these two approaches to ecological field studies. Sampling studies are part of descriptive statistics, and they are appropriate for all ecological studies that attempt to answer the question *What happened?* Hypothesis testing may or may not be an important part of sampling studies, and the key question you should ask is what is your objective in doing these studies.

Figure 1.1 lists several types of statistical analysis that are often not familiar to ecologists; they are discussed in subsequent chapters of this book. *Intervention analysis* is a method for analyzing a time series in which, at some point in the series, an event like

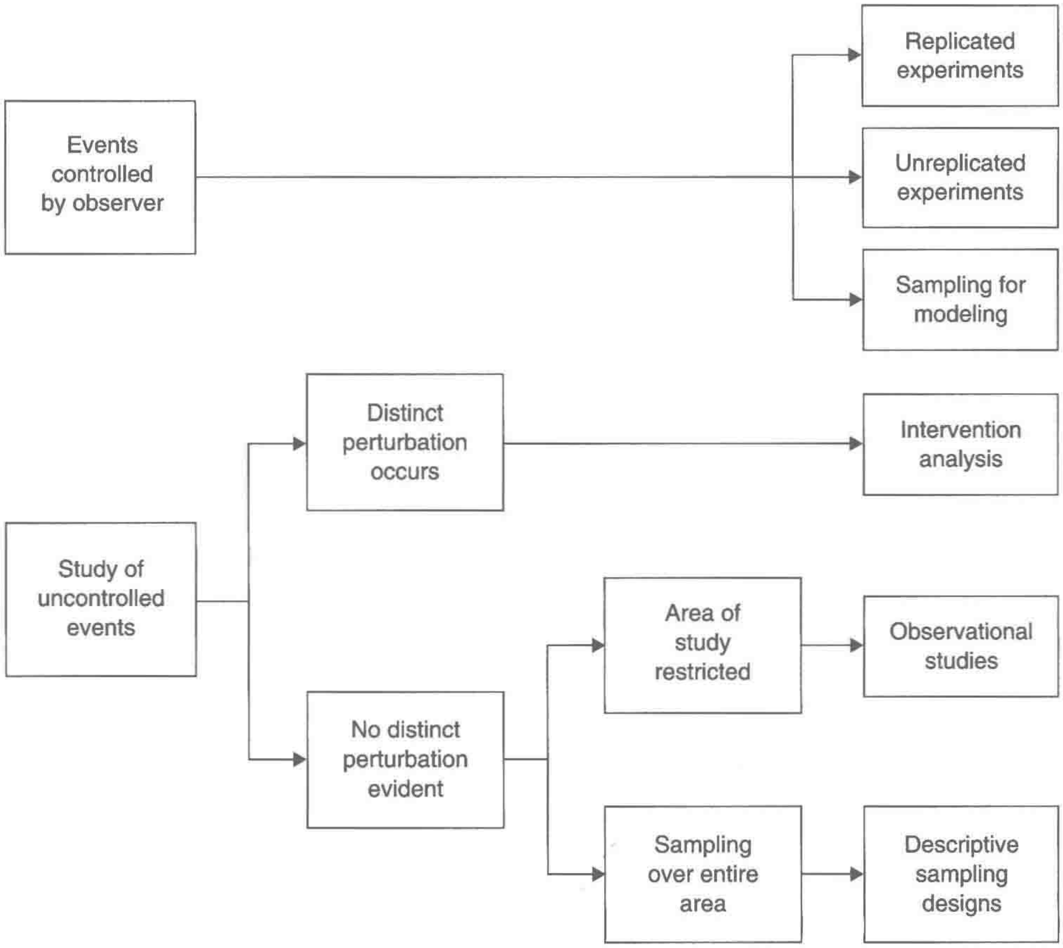


Figure 1.1 A classification of the methods used in ecological field studies. The key dichotomy is whether or not you are studying events you can control. (Modified after Eberhardt and Thomas 1991.)

a forest fire occurs, or a power plant is constructed. By comparing some environmental variable before and after the event, you may be able to detect an impact (Chapter 8). The remaining methods in Figure 1.1 are based on sampling, and they differ in one's objective in doing the work. Consider a study of the productivity of a complex forest ecosystem that contains many different communities. For an observational study, we may pick two forest communities and compare their production. Descriptive sampling could be applied to all the forest communities in the region to estimate productivity of the entire region, and analytical sampling could use these sampling data to test hypotheses about why one forest community differed in productivity from another. Chapters 8 and 9 discuss these sampling problems. Sampling may also be done to look for a pattern, which implies that one is interested, for example, in the pattern of geographical distribution of a species or a pollutant. We will discuss this type of sampling in Chapters 4 and 6.

Ecologists often attempt to determine the impact of a treatment applied to a population or community. One illustration of why it is important to think about experimental design before you begin is shown in Figure 1.2. Suppose that you are the manager of a nature reserve, and you wish to determine if fox and coyote control on the reserve will increase the nest success of ducks. If you do a single measurement before and after the fox