PHYSIOLOGICAL ECOLOGY SERIES

POPULATION DYNAMICS

Alternative Models

Bertram G. Murray, Jr.

ACADEMIC PRESS, INC.

A Subsidiary of Harcourt Brace Jovanovich, Publishers

POPULATION DYNAMICS

Alternative Models

PHYSIOLOGICAL ECOLOGY

A Series of Monographs, Texts, and Treatises

EDITED BY

T. T. KOZLOWSKI

University of Wisconsin
Madison, Wisconsin

T. T. KOZLOWSKI. Growth and Development of Trees, Volumes I and II – 1971

DANIEL HILLEL. Soil and Water: Physical Principles and Processes, 1971

J. LEVITT. Responses of Plants to Environmental Stresses, 1972

V. B. YOUNGNER AND C. M. MCKELL (Eds.). The Biology and Utilization of Grasses, 1972

T. T. KOZLOWSKI (Ed.). Seed Biology, Volumes I, II, and III – 1972

YOAV WAISEL. Biology of Halophytes, 1972

G. C. MARKS AND T. T. KOZLOWSKI (Eds.). Ectomycorrhizae: Their Ecology and Physiology, 1973

T. T. KOZLOWSKI (Ed.). Shedding of Plant Parts, 1973

ELROY L. RICE. Allelopathy, 1974

T. T. KOZLOWSKI AND C. E. AHLGREN (Eds.). Fire and Ecosystems, 1974

J. BRIAN MUDD AND T. T. KOZLOWSKI (Eds.). Responses of Plants to Air Pollution, 1975

REXFORD DAUBENMIRE. Plant Geography, 1978

JOHN G. SCANDALIOS (Ed.), Physiological Genetics, 1979

BERTRAM G. MURRAY, JR. Population Dynamics: Alternative Models, 1979

In Preparation

J. LEVITT. Responses of Plants to Environmental Stress, 2nd Edition. Volume I: Chilling, Freezing, and High Temperature Stresses, 1979, Volume II: Water, Radiation, Salt, and Miscellaneous Stresses, 1980

JAMES A. LARSEN. The Boreal Ecosystem, 1980

POPULATION DYNAMICS

ALTERNATIVE MODELS

Bertram G. Murray, Jr.

University College
Rutgers University
New Brunswick, New Jersey

ACADEMIC PRESS
A Subsidiary of Harcourt Brace Jovanovich, Publishers
New York London Toronto Sydney San Francisco 1979

ACADEMIC PRESS, INC.
111 Fifth Avenue, New York, New York 10003

United Kingdom Edition published by
ACADEMIC PRESS, INC. (LONDON) LTD.
24/28 Oval Road, London NW1 7DX

Library of Congress Cataloging in Publication Data

Murray, Bertram G
Population dynamics.

(Physiological ecology series)
Bibliography: p.
Includes index.
1. Population biology. 2. Population biology--Mathematical models. I. Title.
QH352.M97 574.5'24 79-52790
ISBN 0-12-511750-4

PRINTED IN THE UNITED STATES OF AMERICA

79 80 81 82 9 8 7 6 5 4 3 2 1

CONTENTS

PREFACE

The examination, and, where need be, revision of our fundamental premises is a task of a wholly different order from that of rearing upon these premises a structure of logical argumentation. . . . Most of us are held back by our preconceived, intuitive judgments, which, blindly entertained, blind us also against the recognition of possible alternatives.

Lotka, 1925

The central topic of ecological interest in the 1950s was population dynamics. The peak occurred in 1954 with the publication of books by H. G. Andrewartha and L. C. Birch, by David Lack, and by Umberto D'Ancona; lengthy papers by A. J. Nicholson, by L. C. Cole, and by W. E. Ricker; a symposium on population cycles; and many additional papers, representing a diversity of views. In 1957 the Cold Spring Harbor Symposium of Quantitative Biology was devoted to population ecology and demography. At this meeting the proponents of opposing theories faced each other but failed to resolve their differences. The majority view held that population growth rates and population sizes were in one way or another regulated by density-dependent factors. The minority view contended that populations could not grow beyond limits set by the availability of resources or of time in which to grow, both of which were often influenced by the weather. Without resolving the differences that gave rise to these opposing ideas, ecologists shifted their attention to community ecology—structure, stability, diversity, competition, and coexistence. The

debate resurfaced briefly in 1970 when an international symposium convened in the Netherlands to discuss the "Dynamics of Numbers in Populations," but the majority view held firm.

Unfortunately, ecology textbooks only skim the issues of the 1950s' discussion of population dynamics. The usual treatment is to present the exponential and logistic equations, to mention density-dependent and density-independent factors, and to present examples that are said to support the notion that the growth in numbers of a population is regulated by density-dependent factors. But the significance of particular data cannot correctly be evaluated unless the predictions of alternative theories are explicitly clear. The minority view of population dynamics, however, is not clearly stated by its critics or by textbook authors, and, thus, the alternative models proposed to explain the dynamics of populations have not been justly evaluated. Perhaps the minority view has been rejected prematurely.

In this book I return to the central ecological problem of the 1950s. My purpose is to establish a theoretical framework for thinking about population dynamics different from the "density-dependent regulation" paradigm, which prevails at this time. It is not my purpose to review the many interpretations of population dynamics that have already been reviewed so many times. I do not attempt to sort out the arguments for and against previous views, and I do not include many papers written within the "density-dependent regulation" paradigm whose purpose was to fill in the details of that paradigm. I do attempt to present an explicit view of population dynamics, always keeping in mind the controversies surrounding past discussions.

I believe that past controversies were more the result of ambiguous presentation than of legitimate differences of interpretation. Different terms may be used interchangeably by one author and as contrasting alternatives by another. Often, assumptions are unstated, or perhaps unrealized, leaving the reader to puzzle out for himself the logical argument leading to an author's conclusions. Therefore, I have attempted to avoid these problems in communication by defining terms as I intend to use them, by identifying sources of ambiguity, by stating my assumptions, and by framing the questions I propose to answer. This is done throughout the book, but Chapters 1 and 2 provide a general introduction to the terminology, the mathematical background, and the philosophical approach that lie behind the theoretical development. There follows in Chapter 3 a series of models accounting for variations in population growth rates, sizes, and fluctuations, and in Chapter 4, a model accounting for the evolution of life history patterns. A more detailed examination of the effects of predation on prey populations, especially with respect to determining a prey population's maximum sustainable yield, is taken up in Chapter 5. In Chapter 6,

interspecific competition theory is put in terms of the population dynamics models presented in Chapter 3. Chapter 7 presents a summary discussion of population dynamics as it has been developed in this book.

I am most grateful to H. G. Andrewartha and L. C. Birch for writing their book, "The Distribution and Abundance of Animals," which has provided a continuing stimulus to think about the dynamics of populations during the past two decades when it was my misfortune to fail to find a colleague who could discuss population dynamics outside the "density-dependent regulation" paradigm. As an ornithologist, I am grateful to the late David Lack for his series of books, which synthesized the literature on avian population biology and always focused on the important problems of population dynamics. Several friends read and commented on one or more versions of the manuscript, reducing, if not eliminating, the number of errors: Lawrence J. Corwin (Chapter 2), Kenneth A. Crossner (an early version of the manuscript), Erica Dunn (Chapter 4), Michael Gochfeld (an early version), David J. T. Hussell (Chapter 4), Charles Leck (an early version), Steward T. A. Pickett (the final version), and William Shields (earlier versions). Comments by Robert M. Mengel and Marion Anne Jenkinson, made in response to an oral presentation of mine on the evolution of clutch size, led to substantive additions to the text. Finally, my wife, Patti, provided moral support and patiently put up with me in my struggle to put ideas on paper.

Bertram G. Murray, Jr.

This page intentionally left blank

1 INTRODUCTION

An understanding of the dynamics of populations has been attempted by naturalists (e.g., Lack, 1954, 1966), by experimentalists (e.g., Nicholson, 1933, 1954a), and by mathematicians (e.g., Lotka, 1925). This three-pronged approach has produced the prevailing view that the size of populations is usually regulated by density-dependent factors. The size of many populations fluctuates between limits around some mean value, frequently characterized as the carrying capacity of the habitat. As the population grows, density-dependent factors, such as intraspecific competition for resources, predation, or disease, increase in intensity and lower the population's growth rate, bringing the population into balance with its environment. In some populations, density-dependent factors are inadequate, nonfunctional, or nonexistent; thus, periods of exponential growth are followed by population crashes.

To generalize the prevailing view in this way is hazardous, as a careful reading of primary sources shows. The contributions of Nicholson (1933, 1954a,b, 1958a,b), Nicholson and Bailey (1935), Solomon (1949, 1957, 1964, 1969), Lack (1954, 1966), Ricker (1954), Huffaker (1958a), Chitty (1960, 1967), Wynne-Edwards (1962), and Huffaker and Messenger (1964a), among others, provide a diversity of interpretations of population dynamics, particularly with respect to the nature and action of the regulating factors. Nevertheless, these authors agree that density-dependent factors play an important role in regulating a population's size.