

Population Ecology of Individuals

ADAM ŁOMNICKI

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Population Ecology of Individuals

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Preface

This book has been written with the conviction that further progress in ecology requires taking into account the fact that ecological systems are made up of individuals that differ among themselves, and not only in their taxonomic affiliation, sex, and age. The idea that individuals differ is not a new one, but for a long time attempts to develop ecological theory have been made without taking this fact into account. Individual variation seemed to be nothing more than an unimportant hindrance in the study of the structure and stability of ecological systems. In this book I shall attempt to convince the reader that ecology, like other parts of biology, should apply a reductionist approach more consistently, by deriving the properties of ecological systems from the properties of their elements, i.e. individuals, and that for this an understanding of variation among individuals is essential. Biologists are well aware of the importance of hereditary variation, especially where the theory of evolution is concerned, but the importance of any individual variation, both hereditary and environmental, is only now becoming recognized in ecological theory.

By applying some simple mathematical models, I will try to show that within population variation in resource intake may explain certain phenomena that until now have been poorly understood and that not so long ago were still explained by the action of group selection. More detailed theoretical analyses of individual variation can lead to a better understanding of such problems as, for example, the mechanism of intraspecific competition; but on the other hand these analyses give rise to new questions. For example, I think that we have not yet fully understood the relation between contest competition and the dispersal behavior of animals in nature.

PREFACE

I began to write this book during my stay at Carleton College, Northfield, Minnesota, and I have finished it due to encouragement from Robert M. May, who suggested the possibility of publishing it in the Princeton Monographs series. Early drafts of the first three chapters were read by Paul Jensen, Bruce R. Levin, Richard E. Lenski, Edward B. Swain, Jonathan Brown, Janusz Uchmanski, and January Weiner; the complete manuscript was read by Michał Jasienski, Jan Kozłowski, Danuta Padley, and two reviewers: Michael P. Hassell and H. Ronald Pulliam. The suggestions and criticisms I have received were a great help in my attempts to improve the manuscript.

Population Ecology of Individuals

Contents

Preface	ix
1. Introduction: Basic Models of Population Ecology and Intrapopulation Variability	1
1.1. Individuals and Superorganisms	1
1.2. Unlimited Population Growth	5
1.3. Limited Population Growth	11
1.4. Limited Growth in Discrete Places	15
2. Individual Variation in Resource Partitioning and Population Dynamics	20
2.1. Resource Partitioning among Individuals	20
2.2. Four Versions of the Model of Resource Partitioning	25
2.3. Population Stability and Persistence	30
2.4. Laboratory and Field Data	34
2.5. Scramble and Contest Competition	42
3. Individual Variation of Body Weight in Plant and Animal Populations	46
3.1. Empirical Data	46
3.2. Some Simple Explanations and Their Shortcomings	48
3.3. Weight Differentiation under Stochastic Growth	53
3.4. Deterministic Growth and the Importance of Early Differentiation	57
3.5. Weight Differentiation in Competition for Space	59
3.6. Weight Distribution and General Properties of the Function $y(x)$	61

CONTENTS

4. Individual Differences and Hereditary Variation	65
4.1. Variation as an Adaptation	66
4.2. Differential Mortality and the Soft Selection Concept	72
4.3. Genetic Determination of Individual Success in the Ecological World	81
5. Age and Overlapping Generations	86
5.1. Age-Dependent Individual Success	86
5.2. Distinct Life Stages within a Population	91
5.3. Simple Extension of the Models of Population Dynamics to Overlapping Generations	95
5.4. Discrete Versus Continuous Models of Population Dynamics	100
6. The Mechanism of Contest Competition	106
6.1. Definition of Contest Competition	107
6.2. Population Effects of Contest Competition	111
6.3. The Case Study: Competition among Gall Aphids <i>Pemphigus betae</i>	116
6.4. Social Hierarchy, Territoriality, and Contest Competition	118
6.5. Evolutionarily Stable Arms Investments, or How Contest Competition Can Be Regarded as a Result of Arms Races	120
7. Self-regulation of Population Size	124
7.1. Self-regulation in Terms of Game Theory	126
7.2. Self-regulation in Confined Laboratory Populations	132
7.3. Optimal Reproduction in Populations with Unequal Resource Partitioning	136
8. Emigration and Unequal Resource Partitioning	143
8.1. Emigration from Groups of Related and Unrelated Individuals	143

CONTENTS

8.2. Impermanent Local Habitats in Heterogeneous Space	150
8.3. Evolution of Emigration from Local Populations without Unequal Resource Partitioning	155
8.4. Emigration from Local Populations with Unequal Resource Partitioning	161
8.5. Emigration, and Scramble and Contest Competition	166
8.6. Free and Despotic Distribution of Animals	170
9. Field and Laboratory Populations of Animals	174
9.1. Limitations of Field Studies	174
9.2. Animal Populations in the Laboratory	176
9.3. Free and Confined Laboratory Populations of <i>Hydra</i>	178
9.4. Free and Confined Laboratory Populations of Flour Beetles	183
9.5. Confined Populations of Animals in the Field	186
10. Spatial and Temporal Heterogeneity and Stability of Ecological Systems	189
10.1. Reproduction in Spatially and Temporally Heterogeneous Environments	190
10.2. Spatial Microheterogeneity	194
10.3. Direct Relations between Spatial Heterogeneity, Individual Variability, and Stability	197
10.4. Spatial Heterogeneity and Species Diversity	199
10.5. Spatial Heterogeneity and Ecosystem Stability	201
References	205
Author Index	217
Subject Index	220

CHAPTER ONE

Introduction: Basic Models of Population Ecology and Intrapopulation Variability

1.1. INDIVIDUALS AND SUPERORGANISMS

Although ecology and the theory of natural selection are parts of biology, their concepts and methods are far removed from those of other areas of biology. Traditional biology has been concerned with identifying many different kinds of plants and animals, describing their morphology and anatomy; more recently, it has been concerned with physiological and biochemical processes within a single organism. To understand the relations among individuals, which are of fundamental importance in ecology and the theory of natural selection, requires different approaches and methods.

Gould's (1980) account of how Charles Darwin formulated the theory of natural selection is convincing evidence that traditional biology had not provided its students with the methods to study population processes. It seems that Darwin's enormous biological knowledge alone was not sufficient for him to grasp clearly the mechanisms of evolution. Only after reading Thomas Malthus' "An Essay on the Principle of Population" and Dugald Stewart's "On the Life and Writing of Adam Smith," as well as some statistical articles by Adolph Quetelet, was he able to understand these mechanisms and to formulate his theory. He obviously required a knowledge of population processes that in

CHAPTER ONE

those days was available only in books on economics, demography, and statistics.

Biologists who started to practice ecology at the beginning of our century did not look for inspiration in economics and statistics; they were relatively uninterested in the theory of natural selection. Rather, they attempted to develop ecological theory by applying methods specific to the study of separate organisms. But they did not try to predict the properties of populations or communities from the properties of organisms that belong to these large units. Such an approach was represented by a rather narrow group of theoreticians: V. Volterra, A. J. Lotka, and V. A. Kostitzin. Most ecologists of those days were fascinated by the idea of ecological systems as kinds of superorganisms, with properties analogous to those of individual organisms.

The enormous diversity of relations among the many different species of plants and animals living in a forest or in a lake can discourage anyone who might be tempted to give a detailed description of such systems. On the other hand, biologists have been relatively successful in understanding a single organism, or at least in predicting its behavior. If forests and lakes are kinds of large organisms, it should be possible to describe them, to find out how they work, and to predict their behavior by applying the concepts developed for studying separate organisms. When reading old ecological textbook such as that by Allee et al. (1950), or studying the phytosociological ideas of Braun-Blanquet (1932), one can see just how common was the concept of ecological units as kinds of superorganisms. Nor was such an image limited to ecology; a similar approach was applied to the theory of natural selection, in which not only individuals but also populations, species, or even ecosystems have been regarded as the units of selection. Unfortunately, such views were rarely expressed explicitly, which made them difficult to criticize. The most explicit and important presentation of the concept of group selection, i.e. selection acting above the level of individuals, was published by Wynne-Edwards (1962). That such an idea was stated explicitly must be seen as a great con-

tribution to evolutionary and ecological theory. The critique that followed has made it possible to abandon the concept of group selection and, consequently, the concept of superorganism in biology. Criticism of this concept can also be seen in more recent ecological textbooks (e.g., Colinvaux [1973]).

Progress in evolutionary biology during the last decades has enabled ecologists to see that within the hierarchy from cell to tissue, to individual organism, to population, to community, and finally to biosphere, the individual organism is something distinct. Within this hierarchy, the systems ranging from sexually reproducing individuals down to cells, are sets of genetically identical elements, whereas those ranging from groups up to ecosystems are sets of genetically different individuals. Even if one assumes after Dawkins (1982) that gene-replicators, not individuals, are the units of selection, we can still regard an individual as an entity that is adapted to survive and to reproduce. Neither populations of sexually reproducing individuals nor individual cells are adapted by natural selection, as individuals are. Where such adaptation can be found, it is an exception that occurs under special circumstances, as in the case of clones (sections 7.1 and 9.3).

The genetic uniqueness of individuals has important ecological consequences. One can say that cells and tissues within a single individual have common goals; their behavior can be controlled by a single decision center; and therefore one may expect them to be much more strongly integrated than members of populations or communities. Thus, from the point of view of contemporary evolutionary theory, ecological analogies between cells, individuals, and populations are not justified.

In the study of ecological systems, the concept of the superorganism has to be rejected, and not only for theoretical reasons. The history of ecology seems to confirm the theoretical supposition that this concept does not generate testable scientific hypotheses. In my opinion, some old theoretical models of the predator-prey system that are aimed at predicting the behavior of ecological systems from the simple properties of individuals

CHAPTER ONE

are still useful and important, whereas descriptions of communities based on analogies with individual organisms appear to be of little value.

Does this mean that the mathematical portion of ecological theory is free of ideas derived from the concept of the superorganism? When contemplating the basic ecological model of limited growth, the logistic equation (section 1.3), one sees that in fact individuals and their properties are not included in this model. It seems that mathematical ecologists, as well as other ecologists, were tempted by the holistic approach in their belief that a disregard for the properties of individuals is not a real obstacle to understanding ecological systems.

In order to understand how a given organism works, a biologist attempts to identify its elements, the elements' properties, and the relations among the elements. This reductionist approach seems to be the most efficient scientific method. If some biologists do not apply it, it is because they find identifying the system's elements and their properties either very difficult or simply impossible. Ecologists are in a completely different position: they usually know more about the elements of a system than about the system itself. With a few exceptions, it is easy to distinguish the individuals that are the elements of an ecological system and to identify their properties, but the entire system is much less integrated, and more difficult to define and to study. Ecological holism unfortunately ignores the knowledge already acquired about individuals and allows ecology to lose touch with the real world.

The reductionist method in ecology must derive the properties of ecological systems from the properties of their elements, i.e. individual organisms. To do this, the appropriate hypotheses and their more formal counterparts, mathematical models, are applied. There is a limit to the number of properties and factors that can be taken into account in a model; therefore, some factors and properties are assumed to be fundamental, while others are assumed to be random interferences of minor importance. We are also inclined to assume that all factors that

are difficult to describe mathematically are random interferences that do not alter the basic prediction of the model.

Intrapopulation variability is the basis of the most general biological theory—the theory of natural selection—but this variability complicates enormously any mathematical description of ecological processes. Thus it is not surprising that current ecological theories usually ignore individual variation other than that due to sex, age, and some qualitative genetic differences. This book is an attempt to show how individual variability can be incorporated into the model of population dynamics and what the consequences of such an inclusion are. In this introductory chapter, the basic models of unlimited and limited growth are briefly discussed (section 1.2 and section 1.3, respectively), and then an alternative derivation of the logistic equation is given (section 1.4).

1.2. UNLIMITED POPULATION GROWTH

The model of unlimited population growth in discrete time, for nonoverlapping generations and generation time equal to the time unit, is given by the equation

$$N(t) = N(0)R^t, \quad (1.1)$$

where $N(t)$ is the population size at time t , and R is a constant parameter called the net reproductive rate. This model in its continuous form, for both overlapping and nonoverlapping generations, is given by

$$dN/dt = rN, \quad (1.2)$$

where r denotes the intrinsic rate of natural increase.

The model of unlimited growth has a much wider application than simply to populations of separate organisms: it can be used

CHAPTER ONE

to represent strictly physical or chemical processes or the growth of biological tissues, as well as the growth of an entire single organism. A population of separate organisms can also be viewed as a homogeneous substance, and the fact that it is made of individuals can be ignored. When growth is unlimited, it often does not matter whether a population is treated as a homogeneous substance or as a set of individuals. But this does matter when resources are limited, as I will try to show in Chapter 2; for this reason I will discuss later only models that explicitly consider individuals and that take into account differences in their individual properties.

The model of unlimited growth is the oldest and most general model in theoretical ecology, and it can be regarded as well established in ecological theory. Its generality stems from the phenomenon that all organisms originate by reproduction from other organisms, and therefore the number of organisms in the next generation is assumed to be related to the number in the previous generation. This model is based on individual properties of plants and animals, namely, the average number of progeny and the probability of survival.

It is an open question whether the probability of survival may be regarded as an individual's property. Since it can only be estimated as the proportion of survivors within a population, it is not strictly an individual feature. The point I would like to make is that although we cannot determine this probability from the fate of a single individual, we may conduct a separate experiment outside the studied population in order to estimate it. Therefore, the probability of survival may be regarded as an individual feature, like other features that are subject to independent estimation.

In a population with nonoverlapping generations, the net reproductive rate R can be defined as a product of the probability of survival from birth to reproduction, S , and the number of offspring per individual, B , namely,

$$R = SB. \tag{1.3}$$

INTRODUCTION

This equation predicts the expected value of the net reproductive rate R of a single individual or of a group of identical individuals, but if the parameters S and B are mean values of random variables, and there is a correlation between them, the mean value of R cannot be calculated as their product. Consider, for example, three individuals whose probabilities of survival are

$$S_1 = 0.25, S_2 = 0.50, S_3 = 0.75,$$

and whose offspring number

$$B_1 = 1, B_2 = 2, B_3 = 3.$$

The arithmetic mean of the probabilities of survival equals 0.5; these individuals produce two offspring on average; and the product of these two values equals 1.0. The net reproductive rate calculated in this way is not equal to the arithmetic mean of the three reproductive rates characteristic of the three considered individuals. The reproductive rates are:

$$R_1 = 0.25, R_2 = 1, \text{ and } R_3 = 2.25,$$

and their arithmetic mean equals 1.17. Weak individuals usually have both a low rate of reproduction and a low rate of survival, while strong individuals have high reproduction and survival rates; therefore, it is necessary to consider this correlation when calculating the net reproductive rate from the proportion of surviving individuals and the mean clutch size.

The variation in the net reproductive rate R among individuals does not change the model's prediction of population growth in future generations, unless this variation is hereditary. Thus, R can be applied both as a single value and as an arithmetic mean. This is obvious, because the arithmetic mean of R for N individuals, multiplied by N , equals the sum of the reproductive rates, which in turn equals the number of progeny