

Prologue

When a university professor retired or died, it often happens that his/her former students get together to compile a festschrift to commemorate their teacher. But, I was not a professor, just a plain research scientist of the Canadian Forestry Service. I had no students who would compile my past works. But that is a good thing after all because, in retrospect, I find that many of my early ideas were neither adequately conceived nor well presented in writing. However, over the later years of my research career, the ideas became consolidated to higher levels of clarity, coherence, and integrity, such that these would now be readily put to a practical use in the study of animal populations. Thus, when I retired from my active research career, I decided to assemble those ideas to share them with younger-generation population ecologists.

The present book comprises ten selected topics as Chapters 1 to 10. Each of these focuses on the subject that is, despite its fundamental importance, still inadequately understood or even misunderstood in the current ecology. I selected only these subjects with which I am familiar through my own personal experiences in the field and theoretical studies. So, these topics cover only specific and restricted areas within the whole realm of ecology. Nonetheless, my perspective presented in this book will hopefully, and in principle, serve as methodological bases for much wider areas of population ecology to be explored by ecologists in general.

Chapter 1 investigates the strategies of predators for hunting their prey, based on my study of the great tit, *Parus major* (Royama, 1966, 1970) with which I started my research career. I found that the birds were able to assess how much food (insects) they could collect (per unit effort of hunting) at a certain site, or how 'profitable' the site would be. Then, I found that the birds allotted time for hunting at a given site according to the profit they could gain there in comparison with the profitability of other sites. This chapter describes how I made observations, interpreted the results, and deduced the idea of hunting by profitability. The idea serves as a basis in Chapters 8 and 9 where I investigate multi-species

2 · Prologue

interaction processes, in particular with respect to the evolutionary process of niche selection by animal species.

Chapter 2 is an extension of Chapter 1 to discuss the evolution of crypsis (or mimesis) among insects as a defensive device against visual predation. Contrary to the common belief that crypsis is effective and therefore has evolved, I found cryptic and well-camouflaged insects comprise a majority of food that the great tits fed to their chicks in the nest: there was little sign that the crypsis, as assumed by these prey species, was effective against bird predation. Here, I attempt to resolve this apparent paradox.

Chapter 3 examines the nature of the logistic law of populations in terms of a theoretical model I develop from first principles, comparing it with the classical model first proposed by P.-F. Verhulst (1838) and later (independently) by R. Pearl and L. J. Reed (1920). The comparison reveals commonly held misconceptions about the logistic law, such as the notion of the ‘carrying capacity of the environment’, popularly designated by the parameter K . I contend that K is not the environmental capacity. As has already been recognized among mathematicians, it is the stable equilibrium level of the logistic process through competition among the members of the population. The model developed here provides a theory for understanding the real nature of the law and serves as a basis for exploring the principles underlying single-species population processes discussed in a few of the subsequent chapters.

Chapter 4 explores the utility of the ‘reproduction curve’, a graphical method used by W. E. Ricker (1954) in his analysis of fish populations. I extend the method for general use in animal population ecology. As an example, with this method, I re-analyse the US census data since 1790, which Peal and Reed used for demonstrating the descriptive capability of their model of population growth. My re-analysis provides insight into major factors that governed the US population changes during the past two centuries, demonstrating the potential capability of the reproduction curve to reveal the ecological mechanisms underlying observed population changes. Also, the graphical method exposes some logical problems in the conventional interpretation of the iconic sigmoidal logistic growth curve. In particular, I demonstrate that the sigmoidality has no ecological significance, and suggest an alternative interpretation.

Chapters 5 and 6 examine the nature of intraspecific competition. In Chapter 5, I develop a theoretical model of competition as a generalization of the model developed in Chapter 3. The generalized model enables us to investigate the nature of competition among individuals of a

population, the theme of Chapter 6. In this chapter, I look into the nature of scramble and contest competition to show that these are elements of a continuum in that we cannot draw a sharp line between them to distinguish one from the other. Then, I further include sociality as another element of the continuum to show that no sharp line can be drawn between competition and sociality. Thus, we recognize an animal population process as a continuum, made up of competition and sociality as major elements. This recognition serves as a basis for understanding the nature of interspecific competition discussed in Chapter 9.

Chapter 7 critically examines the conventional notion of population regulation as a density-dependent process. I show that the notion has been inadequately defined and caused unproductive controversies in the history of ecology. A fundamental problem is the misconception that density-dependent regulation ensures the persistence of a population. To eliminate the problem I define the notion of ‘regulation’ and ‘persistence’ from the stochastic process point of view, and examine the roles played by density-dependent and density-independent processes in regulating a population. In particular, I show that density-independent regulation is theoretically possible but fragile and, hence, would not be realizable in a fluctuating natural environment. On the other hand, I show that density-dependent regulation, too, is defenceless against the adverse effect of environmental changes: that is, the regulation is necessary but *not sufficient* for ensuring that the population persists. A major point of my contention here is to expose, and to rectify, some logical inadequacies and myths in the conventional notion of population regulation.

Chapter 8 develops a theoretical model of predator–prey interactions as a generalization of the single-species process model developed in Chapter 3. The theoretical model generates a variety of dynamical (time-dependent) processes, and I interpret their ecological and evolutionary significance in terms of the variation in the parameter values that characterize the interaction processes. Mainly, I investigate the interaction between one predator species and one prey species to find the principles of the processes. Then, I generalize this one-to-one system to a multi-species system, so as to apply the principles to the study of natural populations in which a complex of predator species interacts with a complex of prey species.

Chapter 9 delves into the interaction between two competing species with particular reference to the controversial notion of the ‘competitive exclusion principle’ or ‘Gause’s law’. I first develop a model, similar to the predator–prey process model, but adapted to two-species

4 · Prologue

competition processes. My theoretical investigation here suggests that there are four categories of interactions in accordance with the variations in values of the model parameters, each of which is given an ecological meaning. I show that, in one category, the two species coexist in a stable manner, whereas the elimination of one species is inevitable in the remaining categories. Based on these theoretical studies, I look into multiple-species interaction processes in general and into the ecology (evolution) of niche selection by species in natural environments.

The final Chapter 10 promotes thoughts on the methodology of carrying out an ecological investigation through observations, analyses of data, and interpretation of the results. These are the thoughts that I have conceived while studying outbreak processes of the spruce budworm, *Choristoneura fumiferana*, in eastern Canada. In particular, I critically examine the early ideas (hypotheses) of the processes in which an outbreak is initiated and is spread over wide areas: namely, the formation of epicentres and the dichotomy of epidemic–endemic states of budworm populations. My re-analyses of the original data reveal that these ideas are neither conceivable theoretically nor substantiated observationally. This finding leads me to delve into methodological fundamentals in ecological studies of populations in general: the amalgamation of empirical and theoretical ecology and how to achieve it.

These chapters are arranged in the order that the concepts and methods developed in a given chapter are used (or generalized) in the subsequent chapters. So, I recommend that readers do not skip a chapter, or at least have a quick glance through it to get an outline, at first reading. This is important because, after all, these chapters are concerned with critical examinations of the issues that the readers have most likely been taught at the undergraduate level of ecology. Reading a given chapter in isolation without being aware of the problems that have been dealt with in the preceding chapters, the reader might still be trapped in a pitfall of misconceptions.

I write this book in an informal manner, assuming that I am leading a small workshop with students of ecology at graduate levels, often intervened by questions, answers, and discussions. For example, when I feel additional information might help some readers to readily follow the argument, I insert a [Note: ...] in an appropriate place, even amid the paragraph concerned. That is to say, a [Note: ...] is an answer to a question that is assumed likely to be asked during my talk. Likewise, when I feel a little break might help amid a very involved argument,

I may even insert a [Digression: ...] to relax the readers and encourage them on through the argument.

All chapters but the first two are mathematically inclined. I often build models to be used for the analyses of ecological processes which may require an elementary knowledge of calculus (e.g. how to calculate derivatives or to solve simple differential equations) or certain basic concepts of statistics (e.g. expectation of a random variate or moments of a probability distribution). I do not assume that every reader would readily follow the mathematical arguments involved. So, as these concepts and methods appear in the passages concerned, I explain them in an easy-to-follow manner, either on the spot or in appendices, so that readers do not lose track of the arguments. The only prerequisites for the readers are to have knowledge of a simple algebraic operation like $(a + b)^2 = a^2 + 2ab + b^2$ and a rule like $\log(ab) = \log(a) + \log(b)$ or $a^m a^n = a^{m+n}$.

Any mathematical formula (equation, inequality, etc.) that is going to be subsequently referred to is designated by the chapter number and the order of appearance, e.g. (3.10) is the 10th formula in Chapter 3: if not referred to subsequently, the formula is undesignated. If it is referred to again (e.g. in a different chapter) but I feel that going back to it might interrupt the reader in following the flow of logical argument at that moment of reading, I might *repeat* it with the supplemental acronym 'rpt', e.g. (3.10 rpt) or in another appropriate way.

Similarly, each figure is coded numerically by the chapter number, followed by the ordinal number of the chapter, e.g. Figure 4.3 means the third figure of Chapter 4. The caption for each figure is made as simple as possible such that it serves as a title, so to speak. The full explanations are amalgamated into the argument concerned in the text: in fact, the 'explanations' are part of the argument.

Many chapters have Appendices to help those readers with a minimum background in mathematics to follow the arguments concerned in the main text without losing track. These appendices are coded by the chapter number followed by an uppercase letter, e.g. Appendix 3A means the first appendix in Chapter 3. If mathematical formulae are included, each is coded, e.g. (3A.1) means formula 1 in Appendix 3A.

The bottom line is to bring those readers with limited mathematical skills up to the level at which they can comprehend the ecological meaning of each mathematical model without compromising the level of rigour. After all, I maintain that one cannot do population (or quantitative) ecology without elementary-level mathematics on which the majority of my arguments are based. I realized the necessity of mathematics very

6 · Prologue

early in my research career. But, as I was not a mathematician by trade, I taught myself on the basis of my high school mathematics; I am still learning. The way I write this book has stemmed from my own experience of reading advanced, hard-to-follow textbooks.

My ultimate objective here is to provide the readers, graduate students in particular, with the necessary bases for reasoning and inferences so that they can develop their own methodological skills to tackle the problems that they face in their own research. I suggest that the readers never uncritically believe and accept what I write. Rather, I want them to think with me and digest the ideas. I would feel my mission accomplished if this book successfully motivates young ecologists to venture into the vast and still unexplored realms of population ecology.

Acknowledgements

My words of gratitude are due to the following people. Two old friends of mine, Peter W. Price, Professor Emeritus, University of Northern Arizona, and Stuart L. Pimm, Doris Duke Professor of Conservation, Duke University, acted as my consultants and advisers in preparing the manuscript. Michael B. Usher, Honorary Professor, University of Stirling, and the general editor of the *Ecology, Biodiversity and Conservation* Series, advised me to improve the manuscript in various aspects.

Sara Brunton, a UK-based freelance copyeditor, looked after my English, and my sons, Kenn and Sami Royama, helped me in computer-based technicalities of writing. In particular, Kenn managed, updated and maintained my computer system to suit my needs, while Sami digitally formatted all figures to conform to the typesetter's specification.

Dominic Lewis (Senior Commissioning Editor for Life Sciences) of Cambridge University Press evaluated and accepted my proposed book, while Aleksandra Serocka (Senior Editorial Assistant for Life Sciences) looked after miscellaneous issues, such as handling the copyrighted materials and composing the book covers. Samuel Fearnley (Content Manager at the Press) and Divya Arjunan (Senior Project Manager of SPi Global) coordinated the final stage of the publication process.

I would like to express my sincere thanks to them all for their cordial support and encouragement to make the publication of this (most certainly) final work of mine realized.

T. R.

November 2020, on my ninetieth birthday