

EG Matthews

INSECT ECOLOGY

Insect Ecology

E.G. Matthews



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Preface

Ecology is the science involved with the interactions of organisms and their physical and biotic environments. This field has always been a source of fascination to professional biologists, naturalists and conservationists. In recent years, as human population has progressively increased, environmental problems have also become of vital interest and importance to the public as well. It has now become imperative that ecological principles, and the ecology of specific regions be understood by a wide variety of people. The present series was designed to aid in filling this need.

It is felt that these volumes will serve as a source of information for those university students, teachers and the interested public who require a basic factual knowledge for broadening their understanding of ecology, or those conservationists, agriculturalists, foresters, wild life officers, politicians, engineers, etc., who may need to apply ecological principles in solving environmental problems. In addition, these books are expected to be a valuable reference work and source of stimulation for professional ecologists, botanists and zoologists. The writing is at a level that will neither encumber the layman with unnecessary jargon (although he may need to consult reference works and dictionaries in order to understand some of the terminology) nor be too elementary to be of interest to the professional ecologist.

The study of ecology can be approached on various levels. For example, one can emphasize the biotic community and analyze the kinds and numbers of organisms living together in a particular habitat, the way they are organized

in space and time and the interactions they have with each other. This type of ecology is known as synecology.

Another way of studying ecology is to use Systems Analysis. In this method, the biotic community and the physical environment which together make up what is known as an ecosystem, are looked upon as a functioning unit. In this approach the main emphasis is on the cycling of energy, minerals, or organic materials within the ecosystem and the factors influencing these processes rather than specifically upon the organisms themselves. Often mathematical or theoretical models are constructed and tested.

Both of the above approaches are synthetic and take an overview of entire communities or systems and do not emphasize individual species. By contrast the following two approaches are concerned mainly with individual species, or at most groups of only a few species.

The population approach is concerned with (1) fluctuation in abundance and distribution of individuals of a given species in an area, (2) the contributing phenomena such as birth rates, death rates, immigration, emigration, longevity and survival, and (3) the influence of the physical environment and of other species on these characteristics. Of major interest are mechanisms regulating population density and factors influencing population stability.

The final approach is one primarily concerned with the effect of the environment on the individuals of a species, e.g. how they are affected by temperature, moisture, light or other environmental factors. This approach is known variously as Autecology, Environmental Physiology or Physiological Ecology. The keynote is adaptation to specific environments.

In looking at *Ecology in Australia* in the volumes of this series, all of the above approaches will be employed. Certain topics like Ecology of Grasslands, Ecology of Forests and Woodlands, or Ecology of Deserts lend themselves to a community approach; grasslands, forests, and deserts are types of communities and if studied as an entity must be approached on the community or ecosystem level. On the

other hand, where specific taxa such as reptiles, birds, or mammals are treated the population and/or autecological approach is used. Which one is emphasized varies from group to group, depending on the information available.

The volume on insects combines the synecological and autecological approaches with emphasis on the former. The major biotic communities in Australia are examined in terms of (1) the role insects play in their functioning and (2) their effect upon insect adaptation and evolution.

Some new interpretations of previous concepts have arisen from the writing of that volume and appear for the first time in it. It is hoped these will stimulate discussion about, and investigation into, the ecology of this important group of organisms.

In each book in this series, regardless of the emphasis, the available information on a particular field is critically reviewed and summarized in order that the reader might be brought abreast of current knowledge and developments. Recent trends are indicated and the way for future development prepared by emphasizing conspicuous gaps in knowledge and pointing out what appear to be fruitful avenues for research.

Harold Heatwole
Armidale, N.S.W.
February 1974

Introduction

Ecology is a diverse science which permits a variety of approaches. My approach to the subject of this book has been to focus on the diversity of insects — not to list or describe this diversity, but to look for general principles and common patterns which underlie the varied roles insects play in different ecosystems. In doing this I have chosen to place emphasis on the ways insects utilize available energy, on how natural selection forces the adoption of certain adaptive strategies, and on how insects interact and coevolve with other organisms with which they are associated.

This approach is intended to complement the other existing books on the ecology of Australian insects, which have adopted the population and autecological approaches.

On reading a descriptive account of what an insect does, I am constantly nagged by the question: why? Why does an insect behave the way it does? Why does it have certain structures and colours? In my opinion, the answers to these questions are to be sought in the context of the ecosystem — the forces, both biotic and physical, which operate on the individual in its community environment. It is in an attempt to formulate more precise questions (and a few tentative answers) that this book has been written.

Theodosius Dobzhansky (1966 and other papers) has drawn attention to the two contrasting philosophies biologists follow, often subconsciously, in attempting to answer "why?": reductionism and compositionism (or holism). The reductionist tends to explain natural phenomena, including evolution and species distributions, in terms of organismal

traits and molecular events such as mutations, chromosomal changes, biochemical and physiological properties, and morphology. The element of chance plays an important part in the reductionist's explanations. The compositionist (naturalist, or Darwinian), on the other hand, believes that all of the above phenomena are regulated in turn by natural selection. His explanations will always be in terms of natural selection, and he will assume that there always is an explanation in these terms, even if it is not immediately obvious. The events and structures which preoccupy the reductionist will be considered by the compositionist to be mechanisms on which, or through which, natural selection exerts its influence and it is the selective influences, not so much the mechanisms, which interest him in his constant search for answers to the question "why?". He will not be satisfied merely with descriptions of events or structures and will not accept the possibility that there could be no reason (in terms of selection) for any phenomenon.

Reductionism in the form of non-evolutionary and descriptive "explanations" is the major obstacle to our understanding of ecological principles (Janzen 1973a). At the same time, too vigorous an effort to escape reductionism may lead us to succumb to the opposite fallacy, which is teleology or determinism. The latter philosophy assumes that the course of natural events is somehow goal-oriented. In this book I have tried to steer a middle course between the Scylla of reductionism and the Charybdis of teleology.

Throughout this book I will be looking for common patterns and for unifying concepts in terms of adaptive values. I am not attempting to assemble all current knowledge of Australian insect ecology, and particular facts may be omitted if they are redundant in illustrating a principle. On the other hand, work done outside Australia may be included to help explain concepts. In general, recent summaries or reviews are cited, but not always the articles on which they are based. Consequently, the present book is not a complete coverage of the literature but an introduction to it.

Insect control (by man) and economic and medical

entomology are not directly treated, although many data from the literature in these fields are included. I have also found it necessary to omit the subjects of parasites of vertebrates and of inquilines in the nests of ants and termites as being too specialized. These types of associations are examples of animal-to-animal coevolution, the general principles of which are discussed using examples from the interactions with insectivorous vertebrates and with parasitoids. The subject of coevolution with plants is given a prominence which reflects its overwhelming importance in the life of insects.

The willing cooperation of all Australian biologists approached in the course of preparing this book has been most gratifying. Most of these are mentioned by name in the text as providing personal communications, but I am also indebted particularly to the following individuals for offering extensive help and in some cases unpublished manuscripts: Dr. E. B. Britton (Division of Entomology, CSIRO), Dr. S. W. Cowling (Division of Land Use Research, CSIRO), Dr. P. J. M. Greenslade (Division of Soils, CSIRO), Mr. G. F. Gross (South Australian Museum), Dr. K. H. L. Key (Division of Entomology, CSIRO), Dr. K. E. Lee (Division of Soils, CSIRO), Mrs. J. Lowry (University of New South Wales), Mr. G. B. Monteith (University of Queensland), Dr. R. A. Perry (Division of Land Use Research, CSIRO), Dr. J. J. H. Szent-Ivany (South Australian Museum), Dr. D. F. Waterhouse (Division of Entomology, CSIRO).

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CHAPTER 1

Some General Principles

Before proceeding with a survey of patterns of adaptation of insects to specific ecosystems, it would be desirable to review some general principles. I shall concentrate in this chapter on the general ways insects play the ecological game of survival in a heterogeneous and dynamic environment, on prey-predator and plant-herbivore interactions, and on speciation as an adaptive strategy.

1.1 THE GAME OF LIFE

It is convenient to view species as players in a game and some of the concepts of Games Theory have found their way into ecological writing. This should be seen as a way of organizing thoughts about how animals and plants adapt to their environments — as a sort of analytical tool to help reconstruct, in the imagination, a model which is a simplified representation of what exists in reality. On the other hand, the proponents of the games analogy insist that it is not an analogy at all, but a precise description of what actually happens in evolution, providing the rules are carefully defined.

It should be emphasized at the outset that every move is opportunistic, in no way goal-oriented, and governed by a combination of natural selection and chance; with only the former providing direction. The payoff of the existential game can be a quantity of energy, but the real “aim” of the players (species) is not to maximize their energy winnings, but to maximize the duration of their part in the game. The only way to leave the game is to become extinct. One way

for the player to survive in the short run is to increase his fortune (population size), but in the long run his duration of play depends only on his ability to minimize his stakes — the proportion of his energy supply committed to each play (an event or perturbation). This minimization of commitments is achieved through an overlapping sequence of responses to the event. Each response in the sequence entails increasing stakes, and the higher-stake responses continue in operation only to the extent that lower-stake responses have failed to counter (or take advantage of) the influence of the event. The lowest-stake response is a behavioral one at the individual level, whilst the highest-stake one consists of permanent genetic changes at the species level. If the low-stake, short-duration response is adequate, the remaining responses do not run their full course (see Slobodkin and Rapoport, 1974). I will be pointing out later (section 1.6) that insects have recourse to the genetic responses much more frequently than most vertebrates, but nevertheless this strategy has paid off with some very long periods of continuous play. This phenomenon requires some further explanation in terms of the games analogy.

I will also be using the concept of r and K selection (MacArthur and Wilson 1967; King and Anderson 1971; Pianka 1972) as a common thread running through the book. Here again, this provides only a unifying framework on which to hang facts and ideas, and whilst I believe the concept has validity, it is by no means necessary to formulate questions and answers in its terms, and the reader should feel free to restate the same facts and ideas on some other basis if he so wishes.

R selection is said to predominate during colonizing episodes which arise after some environmental change has altered or destroyed the former habitat, and favours a high population growth rate (r is the symbol used to represent a population's unrestrained rate of natural increase), whilst K selection predominates during periods of prolonged stability and favours a more efficient utilization of resources (K represents the carrying capacity of the environment).

Whereas the ultimate strategy adopted by the players is always the same (that of staying in the game), the successful tactics for pursuing it are different under the two types of selection, as we shall see presently. I shall follow the usual terminology and refer to " r and K strategists" rather than "tacticians".

1.2 TWO KINDS OF STRATEGISTS

A species, when first moving into a suitable environment which contains an abundance of food, is subjected to " r selection", which can simply be defined as a situation of high food density and low population density. Such a situation may occur when there are changes in weather or other physical factors, when a species has managed to reach an environment previously inaccessible, or sometimes through human activity, such as the planting of a food crop. R selection will favour species with a rapid intrinsic rate of natural increase (r), since the most successful species in an r environment will be the one most quickly able to build up its numbers to exploit favourable conditions. Initially there are no constraints on this build-up as the influence of competitors and predators will not yet be felt, and little energy need be invested in individual defence. There is no advantage in food specialization.

As the species subjected to r selection builds up its numbers, and competitors and predators also build up theirs, the environment becomes crowded, the carrying capacity (K) is approached, and the conditions of r selection no longer prevail. As individual resources become scarcer, it is no longer so important to multiply rapidly. In fact, it may benefit the species to keep its numbers down so the fitness of existing individuals can be maintained. It is now more important to compete successfully with other species, to avoid predators, perhaps to defend territories, to expend more energy on individual and progeny defence, and to spend more time on courtship (the latter is a device to ensure conspecific matings — necessary when there are closely-related species about). It becomes mutually advantageous to co-operate with other

species (form symbioses) and to specialize in one kind of food (to minimize wasteful conflict and maximize efficiency).

In short, r selection typically favours fecundity, mobility, and polyphagy. K selection favours intrinsic population density control, lack of mobility (for reasons which will be explained later), food specialization, individual defence, competitive ability, and symbiosis.

A few species can adjust to both r and K selection, notably flour beetles (*Tribolium* spp.) which adopt some K strategies, such as population density control (see below), when their environment becomes crowded. The granary or flour bin is rather a special situation, however, and most species which succeed under r selection are not able to compete with other species under K selection, and they tend to emigrate. R strategists, as such species are called, are thus particularly good at moving, or getting moved about — not only to retreat when their environment gets crowded, but also to be on hand when new, favourable situations arise. In order to succeed as an r strategist, a species must exist in an area subject to frequent and unpredictable changes (for example, the temperate zone, arid areas, or the culture steppe). However, a few r strategists can survive in even the most stable general environment if they are adapted to those aspects of that environment which do change unpredictably. For instance, if we take one of the most stable known environments, the tropical rain forest, there is still change there in the form of tree fall, animal deaths, landslides, and the falling of fruits and objects acting as small water containers (to select but a few r situations). Some of the terms long used in the literature to describe r strategists are: fugitive, tramp, weedy, colonizing, opportunistic, mobile, or vagile species.

In general, the relative influence of r or K selective forces depends on the degree of stability of the environment. Stability does not necessarily mean a lack of fluctuation. Temperate climates are unstable not so much because of seasonal changes, but because given seasons can differ unpredictably from year to year.

Stable environments will contain a high proportion of K strategists. However, for the largest number of such species to occur it is also necessary for the conditions of stability or predictability to have been in continuous existence for a long time. K strategists are adapted to one particular environment (including the complex of species with which they are associated) and have usually been evolved *in situ*. Their evolution is the culmination of a long process of interaction with a particular set of factors. Even an apparently unstable environment can produce its quota of K strategists if its fluctuations have been within circumscribed limits long enough — for instance, the Australian arid zone.

Greenslade (1972) has introduced the concept of “beyond- K ” selection. This type of selection operates in environments which may have something in common with r environments in that they are dominated by harsh physical limiting factors. However, unlike r environments, these factors are highly stable and predictable. Their stability permits species to become closely adapted to them, whilst their severity has the effect of keeping out most competitors. Furthermore, the specialized adaptations required to meet this severity, once evolved, enable beyond- K strategists to out-compete most potential invaders. If a given beyond- K environment has persisted long enough unchanged, it can contain some extraordinarily ancient relict species. The sorts of environments which are beyond K are mountain streams, high mountain tops, the marine littoral and intertidal zones, and caves (Chapter 5). The more severe and ancient deserts are probably also included, as are the arctic and antarctic zones.

Thus r , K , and beyond- K environments select for different adaptive strategies and, in general, species are able to adapt to only one such set of selective forces, although some special, small habitats may contain the same species throughout their succession. Also, species occurring at an intermediate stage in the process of ecosystem maturation may show both types of adaptation in combination.

The two main types of selection, then, can be thought