EVOLUTIONARY BIOLOGY OF

Parasites

PETER W. PRICE

MONOGRAPHS IN POPULATION BIOLOGY · 15

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MONOGRAPHS IN POPULATION BIOLOGY

EDITED BY ROBERT M. MAY

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Preface

"The challenge of diversity" as Mayr (1974) put it, is still with us. Mayr (1976) has noted that the diversity of life is spectacular and its study requires mental exercises not generated in other sciences. Requiring a blend of systematics, ecology, behavior, genetics, and geography, the study of diversity poses one of those "middle-sized questions" that appealed to Bonner (1965) because the whole of biology becomes involved in the answers.

Some of the aspects of diversity such as the better representation of taxa in tropical latitudes have received considerable attention (e.g. Pianka, 1966), and the theory of island biogeography (MacArthur and Wilson, 1967) has contributed enormously to solutions of questions on diversity. Other questions such as the reasons for the varying sizes of taxa have hardly surfaced as debates in biology. Where attempts have been made to answer such questions, they have been qualitative rather than quantitative (Mayr, 1974).

Having been involved with research on a family of parasitic Hymenoptera, thought to be represented by some 60,000 species (Townes, 1969), I have considered questions on the evolution of diversity. No entomologist can escape these questions when such a large proportion of the world's fauna so far described consists of insects. Two events stimulated my interest further. In 1971 Richard Askew published his excellent book on parasitic insects that treated parasitoids and insect parasites on vertebrates for the first time in one volume. Apart from the fund of knowledge and the ecological approach in this book, one thing struck me as important. He mentions that many Hymenoptera in the superfamily Chalcidoidea and some in the superfamily

Cynipoidea were parasitic. Actually, almost all the species in these taxa are parasitic, but some feed on plant tissues (e.g. gall wasps and seed wasps) and others on animal tissues (parasitoids). If parasitic taxa span the plant and animal kingdoms, so must the parasitologist. The second idea came in conversation with Guy Bush, for it became apparent that the tephritid flies he knew so well behaved in ways similar to the cocoon parasitoids I had studied, although the fruit flies utilize plants as hosts and the parasitoids attack animals. The common feature here was utilization of a discrete, small resource such as a fruit, a seed, or a cocoon. When the female is free-living, she can protect her progeny within the food package by leaving a deterrent chemical, thus reducing competition. With such evidence of evolutionary convergence between parasites on plants and animals we agreed that a symposium on parasitic insects would be profitable. This was organized for a national meeting of the Entomological Society of America in 1974 and subsequently published as "Evolutionary Strategies of Parasitic Insects and Mites" (Price, 1975a). The participants, Richard Askew, Guy Bush, Don Force, Daniel Janzen, Robert Matthews, Rodger Mitchell, and Bradleigh Vinson contributed significantly to a synthesis of the evolutionary biology of insects parasitic on plants and animals. It became evident that a large number of insects were parasitic, some on plants, and others on animals and that the diversity of insects and life in general may be at least partly understood by gaining knowledge of the parasitic way of life. The stage was set for a comparative approach to the phenomenon of parasitism.

Parasites are more of a phenomenon than I had thought! They are exceedingly numerous in species and numbers of individuals per species, some taxa having undergone the most spectacular adaptive radiations. New adaptive zones have been frequently created throughout evolutionary time and repeatedly colonized by new parasites with only slight modification from the free-living mode of life. Parasites affect the life and death of practically every other living organism.

How, then, can one small book cover such a diverse array of organisms and interactions between organisms? This book represents an attempt to find the features common to parasites. The task necessitates a synthesis of evolutionary biology and the many disciplines involved with the study of parasites. This synthesis, I believe, leads into several unconventional areas of ecology that deserve more attention. The emerging generalizations represent my attitude toward parasites that, while I find helpful, I do not regard as the only valid point of view. Those who generalize are always faced with those who exceptionalize. Bonner (1965:15) made a plea to the latter: "Yet when we make generalizations about trends among animals and plants . . . it is almost automatic to point out the exceptions and throw out the baby with the bath. This is not a question of fuzzy logic or sloppy thought; it is merely a question whether the rule or the deviations from the rule are of significance in the particular discussion." I do not claim that any principle will apply to all parasites, but rather that it is relevant to more parasites than those to which it does not apply. In addition, discovery of exceptions should be followed by a search for explanations, and these may then help to support the generality or cause its modification to a more useful form. Science proceeds as a progression of approximations toward the truth. Early endeavors, of which I think this is one, may turn out to be far from the truth in many ways, but they are justifiable, even when wrong, if further study is stimulated.

Parasites are so abundant and diverse that examples could be found to defend practically any thesis. They are also small and relatively specialized and thus share with other organisms of such size and specificity a multitude of problems because of these features, independent of the parasitic mode of life. Such correlated attributes make discovery of the essence of parasitism more difficult than one might think. While I feel that parasites possess a unique set of features, as I explain in Chapter 1, many of the attributes I discuss will be commonly found in other small and specialized organisms, although mention may not be made of this at the time.

Much of this book was prepared during 1977 and 1978 while I was on sabbatical leave from the Department of Entomology at the University of Illinois. I am grateful to the university for supporting my leave. Financial support was also provided by a fellowship generously awarded by the John Simon Guggenheim Foundation. This facilitated a seven-month visit to the British Isles and continental Europe and a shorter time in Central America, where I gained enormously by meeting many scientists who shared their knowledge with me. I am most grateful for the opportunities and support the fellowship provided. The monograph was completed with support from a National Science Foundation grant DEB 78-16152.

Many colleagues have contributed significantly to this book. I am grateful to those who read earlier drafts in whole or in part and provided critical comments and positive response: Roy C. Anderson, Roy M. Anderson, Paulette Bierzchudek, Carl Bouton, Paul Gross, John Holmes, Peter Kareiva, John Lawton, Robert May, Bruce McPheron, Beverly Rathcke, Richard Root, John Thompson, Jeffrey Waage, and Arthur Weis. These and others were generous enough to provide information, important leads, reprints, and preprints of papers: Richard Askew, Jeremy Burdin, Guy Bush, Howard Cornell, Doug Futuyma, John Harper, John Jaenike, Clive Kennedy, Robert Morris, Patrice Morrow, Klaus Rohde, John Schneider, Don Strong, A. C. Triantaphyllou, John Whitaker, Tom Whitham, and Peter Yeo. For the artwork I am grateful to Alice Prickett, Mike Paulson, and Carol Kubitz. Donna Mohr, Peggy Vaughan, and Donna Stowe all helped with typing and other essentials for which I am most thankful. For supervising a department in which the climate is so conducive to enterprises such as this, I thank Stanley Friedman. To Maureen, Gavin, and Robin goes my deep appreciation for creating a home environment in which this monograph could be written.

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CHAPTER ONE

Introduction: The Parasite's Lot in Evolutionary Biology

Parasites form a large proportion of the diversity of life on the earth. Therefore in attempts to reach generalizations or to identify patterns in biology they should have received a preponderance of attention. This has not been the case largely because small organisms in general are poorly known, but also because many biologists do not appreciate the commonness of the parasitic way of life. Also, we tend to see organisms as if they lived within the limits of our own limited experience. But of course parasites live in a very different world from ours, more like the worlds of the water-beetle and the bacillus described by Thompson (1942). As he says "we have come to the edge of a world of which we have no experience, and where all our preconceptions must be recast" (1942:77).

Indeed, I think there is much room for recasting the image of parasites held among biologists, and in so doing certain views in ecology, evolutionary theory, and parasitology must also be recast. It has not been generally realized that the most extraordinary adaptive radiations on the earth have been among parasitic organisms. Ecological and evolutionary principles should address such spectacular speciation and provide the basis for an understanding of the mechanisms involved. I do not think that a coherent body of theory exists for the evolutionary biology of parasitic organisms.

This recasting cannot be evaluated fairly without a review and a reappraisal of the conventional wisdom on parasites as a basis for understanding the evolutionary biology of parasites. This chapter is largely devoted to such tasks, concentrating on three areas: the definition of a parasite, parasite ecology, and parasite evolution.

There are probably as many definitions of a parasite as there are books on parasitism. Rather than construct my own definition and incorporate my own biases or preconceptions I resort to *Webster's Third International Dictionary* for what must be a generally acceptable definition: *a parasite is an organism living in or on another living organism, obtaining from it part or all of its organic nutriment, commonly exhibiting some degree of adaptive structural modification, and causing some degree of real damage to its host.* The *Oxford English Dictionary* definition is similar. It must be emphasized that an individual of any parasitic species will usually gain the majority of its food from a single living organism. Although a species of parasite may utilize several or many host species, each individual obtains most of its nutrition from an individual host. Species with complex life cycles may exploit two or three hosts in a predictable sequence. This contrasts with the more generalized grazers, browsers, and predators that feed on many organisms during their life time and with saprophages that feed on dead organic matter.

Anderson and May (1978) argue that an organism should be classified as a parasite only if it has a detrimental effect on the intrinsic growth rate of its host population. This is a realistic operational definition for those concerned with modelling ecological impact of parasites on host populations. But my focus is on the parasite itself and its evolutionary biology in which intimate association with and unfavorable impact on its host, however small, are the crucial qualities of its life style.

When the above definition of a parasite is applied objectively without taxonomic or disciplinary constraints, many organisms must be recognized as parasites. Many insects that feed in or on plants fit the definition well. The large order Homoptera including leafhoppers, froghoppers, aphids, scale insects, and whiteflies is composed almost completely of parasitic species. The larvae of the even larger order Lepidoptera usually feed and mature on a single individual of the host plant species and gain a large percentage of the total nutritional requirements for the organism's life span. Other orders such as the Thysanoptera, Hemiptera, Coleoptera, and Diptera swell the ranks of parasitic insects on plants, to which should be added the large numbers of mites, nematodes, fungi, bacteria, and viruses of interest to the plant breeder (e.g. Day, 1974). Parasitic angiosperms are frequently ignored when parasitism is discussed (Kuijt, 1969).

Parasites on animals include those of interest to the conventional parasitologist: viruses, bacteria, protozoa, flatworms (flukes and tapeworms), thorny-headed worms (Acanthocephala), nematodes, and arthropods (crustaceans, insects, mites). Other parasites such as the parasitic Hymenoptera and Diptera are of more interest to the entomologist and specialist in biological control.

A few organisms that have been regarded as parasites should also be excluded. Blood-sucking organisms are often considered as parasites, but mosquitoes and black flies have very brief contact with the animal they feed on so that the relationship should not be regarded as parasitic. Other blood feeders remain on an animal for a considerable time such as many fleas (e.g. see Rothschild and Ford, 1973), ticks (e.g. Arthur, 1965; Hoogstraal, 1967), and sucking lice and may be considered as parasites. However, as pointed out by Askew (1971) and Kennedy (1975a), there are no discrete limits to the parasitic habit that are biologically meaningful. Ticks utilize several hosts in the course of a lifetime. The pollinating fig wasps are parasitic in their habits except that benefits to the host plant outweigh the damage, making them, in the balance, mutualists. Some fungi, such as *Rhizoctonia solani* and *Armillaria mellea* are important plant parasites, each attacking at least 100 plant species (see Moore, 1959), but they also become mycorrhizal on orchids (Harley, 1969). Indeed Garrett (1970) stresses that initially the seedling orchid must be parasitic upon the mycorrhizal fungus. Thus the majority of this book will deal with organisms that fit the definition quite well, but on occasion those more loosely associated with hosts will be considered. Social parasites and brood parasites represent phenomena of a different kind and will remain largely unconsidered.

Thus parasite species are incredibly numerous, and they probably affect every living organism at some stage in its lifetime. Yet it is very difficult to obtain a clear picture of how many parasite species there are compared to those that are free-living. Parasites are small and usually cryptic and unobstrustive members of any biota. Probably the most concerted regional effort on a taxon represented by both parasitic and free-living species has been on insects in the British Isles. A check list of British insects by Kloet and Hincks (1945) permits an evaluation of the commonness of the parasitic habit (Table 1.1). Of the 20,244 insect species listed in the check list, 16,929 can be readily classified into the categories in the table. For the remainder there is a diversity of feeding habits within a family or poor information on food eaten by immature and adult stages, so they have not been classified.

The categories in Table 1.1 are designed to cover all possible feeding types including the self-explanatory head-