INSECT BEHAVIOR

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Preface

This book has been written for all students of the biological sciences. Besides being of interest to those who have had some basic introduction to entomology and/or animal behavior, we hope it will appeal to newcomers interested in insect behavior from the perspective of the science educator or comparative psychologist, for whom most books on insects are either oversimplified or too technical.

An outcome of a senior level course offered in the Department of Entomology at the University of Georgia since 1970, the book has been guided by the same objectives that have shaped the course. The first of these has been to help the student understand how a number of major behavioral systems function. Thus, this is not an encyclopedia; it does not document numerous strings of examples merely for "completeness of coverage," but offers a comparative evolutionary approach to processes and fundamental concepts. The second objective has been to help the student gain insight into the ways in which behavioral research can be conducted. Whenever possible, we have included discussions of important experiments and investigations rather than presenting a simple rhetoric of conclusions. In addition, selected principles are interwoven with case studies which explore them in relation to specific situations, presenting actual examples in a manner compatible with the dynamic, open-ended field and laboratory experiences in which they have arisen.

Each chapter concludes with a list of selected references (predominantly published in the past decade) for those wishing more detail on a particular subject. These materials are accessible in most college libraries; many of the suggested readings are reviews or articles from *Scientific American*, the majority of which are available as offprints.

Like any writer of a general textbook, we recognize a deep obligation to many others—to those of whose work we write, to other authors whose ideas we use, to our own teachers who have shaped our perspective and interests, and to our students and colleagues with their many stimulating and invaluable suggestions and criticisms. We would like to express special gratitude to M. C. and M. L. Birch, Murray S. Blum, Paul Decelles, Thomas Eisner, Howard E. Evans, Darryl T.

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We also thank the many scientists and editors of scientific journals who have freely granted permission for the use of published material. Numerous colleagues have generously provided us with photographs; special thanks are due to Robert L. Jeanne, Carl W. Rettenmeyer, and Robert E. Silberglied. We are especially grateful to Joan W. Krispyn for the numerous original drawings. Figure captions carry the appropriate figure credits.

Finally, we sincerely thank the editorial and design staffs of John Wiley & Sons, Inc., for their efforts on behalf of the book.

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Insect Behavior

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1
Insect Behavior: an Introduction

An overview of the insect world reveals two paradoxical characteristics: great diversity and equally great constancy. On the one hand, there are over one million named insect species, with estimates ranging up to three million. How can such a great diversity be explained? Study of this basic question has become the domain of evolutionary biology. On the other hand, each kind of organism tends to reoccur in virtually the same form with the same basic features for generation after generation. Why do they tend to show such constancy, such resistance to change? The study of this question, in turn, is largely the domain of genetics. Together, these two great branches of biology—evolution and genetics—form a powerful tool for the investigation of nearly every aspect of life. This introductory chapter deals briefly with their application to the study of behavior and then turns to an historical overview of behavior as a field of study to provide a perspective for the chapters that follow.

THE BIOLOGICAL BASIS OF INSECT BEHAVIOR

Insects belong to the phylum Arthropoda, a very large assemblage of animals with jointed legs and a hard outer skeleton. One major group in this phylum, the Chelicerata, have sickle-shaped chelicerate jaws and lack antennae; they include the Arachnida (spiders, mites, scorpions, etc.) and two smaller marine groups. The other major group, the Mandibulata, possess antennae and have mandibles that work against each other. They include six classes: the insects, the crustaceans (a predominantly aquatic group), the centipedes, the millipedes, and two smaller classes, Symphyla and Paurapoda. Of all the land arthropods, insects are by far the most abundant (Fig. 1-1), followed by spiders and mites.

Ordinal divisions within the class Insecta remain a matter of dispute but in general reflect present understanding of the evolutionary history

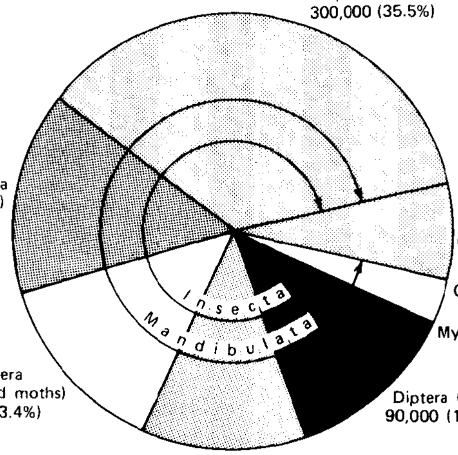

Figure 1-1 The relative abundance of major groups of arthropods. (Adapted from Levi, Levi, and Zim, 1968.)

of the class. Broadly speaking, four important stages are distinguished. First was the appearance of primitively wingless insects (Apterygota), probably during the Devonian Period. Silverfish (Thysanura) and springtails (Collembola) are living representatives of these earliest insect forms. Second was the development of wings, thought to have occurred during the Lower Carboniferous. These early winged insects had a wing-hinging mechanism that did not permit them to fold, so wings had to be held out from the body. The Odonata (dragonflies and damselflies) and the Ephemeroptera (mayflies) are surviving remnants of these ancient groups.

The third evolutionary stage, the development of the wing flexion mechanism, occurred during the Upper Carboniferous. Now able to fold their wings down tightly over their abdomens, insects could more easily run and hide from predators and move into a wide variety of previously inaccessible niches. Of contemporary insects, roughly 97% have flexing wings, and this mechanism is in large part responsible for the dominance of insects today.

Fourth was the development of complete metamorphosis (holometaboly), which seems to also have arisen in the Upper Carboniferous. The earliest insects remained essentially similar in their wingless body form throughout their entire lives. More advanced groups developed the simple metamorphosis exhibited by insects such as grasshoppers today, where immature stages resemble miniature adults but wings are lacking (although external wing buds are plainly visible) until the last molt, when the insect becomes sexually mature. The most highly advanced groups, however, evolved the complete metamorphosis illustrated by the life cycle of a butterfly or honey bee. The immature stages, the larvae, bear no resemblance to adults, and wing buds are developed internally, becoming visible only when the larva transforms into the pupal stage, from which the winged adult emerges.

A summary of the evolutionary relationships of the insect orders is depicted in Fig. 1-2. A discussion of the geological history and evolution of insects is provided by Carpenter (1973).

What Is Behavior?

Behavior can be simply defined as what animals do. More precisely, it is the ways in which an organism adjusts to and interacts with its environment. Admittedly, the term covers a very wide range of activities, and it can be helpful to recognize some subcategories. General locomotion, grooming, and feeding, for example, are essentially individual matters. These **maintenance activities** keep an insect in good shape but usually have little influence on others of his kind. On the other hand, a broad range of **communicatory activities** are "other oriented." They are concerned with conveying information to, and influencing the moods and activities of, others of the same species. Often such actions are conspicuous and stereotyped, and not surprisingly they have been a favorite study material for behaviorists.

Although movement is essential for most behavior, stillness is also behavior. For example, while many insects react to danger by fleeing, the survival of many others depends upon camouflage attained by freezing in some posture so completely as to seem to vanish (Fig. 1-3). As this example shows, behavior operates in circumstances that vary from one species to another and in ways that have **survival value.** In any situation insects that respond more appropriately have a better chance of living—and of leaving more progeny—than individuals responding less appropriately. Thus, a weeding-out process is continually in progress, a natural selection of behaviors that enhance the chances of survival and success for individuals of a species. The behavior patterns one observes today have had a long history of evolutionary development.

Natural selection dictates that everything an animal does should ultimately contribute to the optimization of its reproductive success. The rather limited amount of energy available to an individual must be

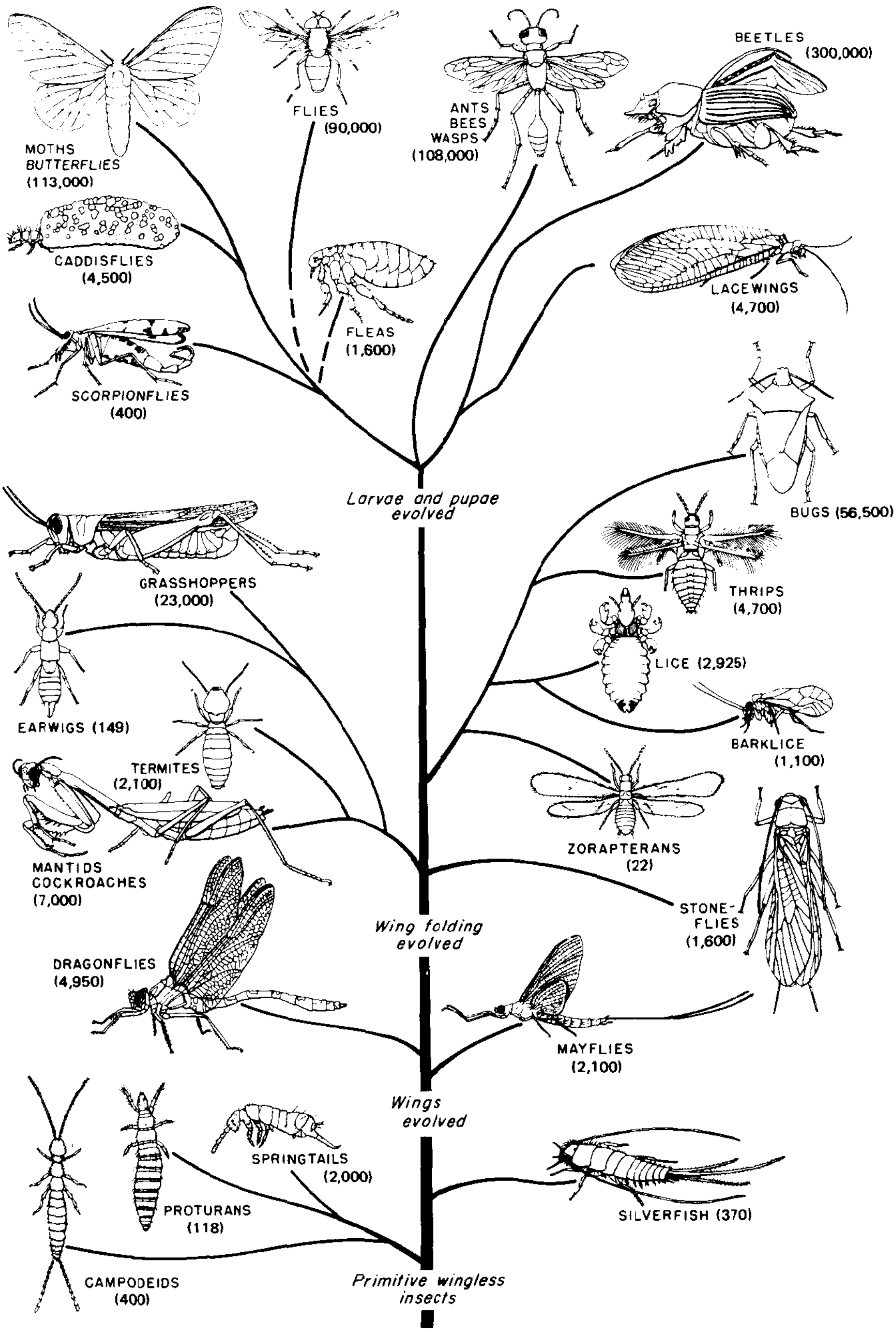

Figure 1-2 Presumed evolutionary relationships among the living insect orders. Numbers of described species based on data taken from Borror, DeLong, and Triplehorn, 1976. (Modified from Ross, 1962; courtesy of Illinois Natural History Survey.)

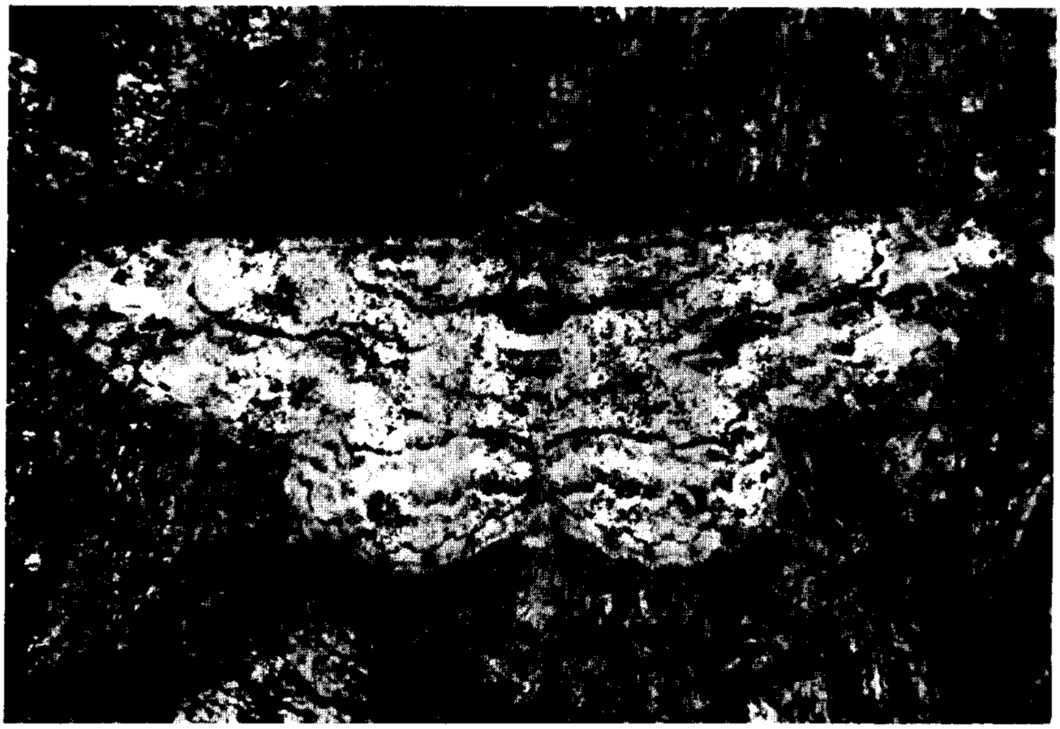

Figure 1-3 A geometrid moth as it rests motionless by day on a tree limb. The scalloped wing margins and mottled coloration blend into its background, making visual discovery difficult unless the moth moves. (Courtesy of R. E. Silberglied.)

divided between maintenance and reproductive activities, the latter being basically matters of communication. This division is broadly reflected in the book's organization. The first several chapters concern behavior of the individual insect—how it moves, orients, disperses, and feeds, including the role of the nervous and endocrine systems in integrating behavioral responses. The next three chapters on communication in a sense form the core of the book and lead logically to consideration of defensive, reproductive, and social behaviors, all of which are mediated by communicative codes.

The Phylogeny of Behavior

Again and again, research has demonstrated a strong concurrence between behavior and phylogeny based on morphology and taxonomy. That is, behavioral differences and similarities within a group of species reflect phylogenetic relationships as determined morphologically. As Tinbergen (1968) has said, ". . . comparison of present-day species can give us a deep insight, with a probability closely approaching certainty, into the evolutionary history of animal species."