What Is Insect Behavior?

A flashing firefly flits through the evening shadows. In a tree, a caterpillar pauses in its feeding, stiffens, and sways back and forth. Behind a stone, a cricket chirps, while nearby ants scurry along in precise single file.

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 total environment. As such, insect behavior encompasses the relationships an insect has with members of its own species, with members of other species, and with the physical environment. A species must behave in the ‘right’ ways in order to survive, and its members must survive (at least long enough to successfully reproduce) if it to be evolutionarily successful.

Admittedly, the term ‘behavior’ 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 hexapods) probably in the late Silurian Period. Bristletails and silverfish are living representatives of these earliest insect forms. Second was the development of wings, hypothesized to have occurred during the late Devonian or early Carboniferous. These early winged insects had a wing-hinging mechanism that did not permit the wings to fold, so they had to be held out from the body. The Ephemeroptera (mayflies) and the Odonata (dragonflies and damselflies) are surviving remnants of these ancient groups.

The third stage, the Neoptera, developed a different wing flexion mechanism, that had evolved by the late 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. Among contemporary insects, roughly 97% have flexing wings, and this mechanism is one reason for the dominance of insects today.

The fourth important stage was the development of complete metamorphosis (holometaboly), which also seems to have arisen by the late Carboniferous. The earliest insects remained essentially similar in their wingless body form through- out 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 familiar life cycle of a butterfly. 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.

1.3 Phylogeny’s Role

Phylogeny, the presumed history of ancestry of a group of taxa, provides a strong evidence line to help decipher the evolution of a trait. In a sense, phylogenetics can be thought of as ‘evolutionary geneology’. Its tools include the twin fields of taxonomy and systematics, the sciences involved in finding, describing, and naming organisms by an agreed-upon set of rules, and then classifying them into increasingly broader categories that are based on shared features that presumably reflect evolutionary relationships.

Incidentally, we have these fields to thank for introducing the useful general term *taxon* (plural taxa), meaning any taxonomic unit without specifying its rank. Thus, a species is a taxon, but so is a group of species or an entire order. A related term, *clade*, is a group of organisms that includes an ancestor and all its descendents (see Section 1.3.2).

As we have seen, much of behavior has a genetic basis, and traits with a genetic basis are capable of evolving over time. But what is the evidence for behavioral evolution? To answer this, using the comparative approach is a necessity, but in addition, one must consider phylogeny, which involves both microevolution and macroevolution.

1.3.1 Microevolution and Macroevolution

Long before it was ever given its name, people have recognized the reality of *microevolution* (genetic changes within populations or species) because of two A third language-related problem is that, because most behavior is described in terms of its end result, the very act of labeling a particular observed behavior tends to color subsequent interpretations of it. For example, labeling a chemical secreted by a female moth as a ‘sex attractant’ is done because the end result of her secretion is that males arrive and attempt to mate with her. This label suggests that such chemicals provide directional clues of use to an approaching insect orienting over some distance, but such cues may have not been demonstrated. Furthermore, use of the label ‘sex attractant’ potentially masks appreciation of a whole congregation of other behaviors by the respondent such as orientation to wind and light.

In a larger context, it is customary to label communication signals by apparent function such as sexual, aggressive, alarm, etc. However, it is often difficult to distinguish the responses that such categories of signals will actually elicit because the environment or ‘context’ of a signal may alter its message (see Chapter 6). For example, the same chemical in harvester ants may elicit alarm under one set of circumstances but elicit approach in another situation. A second problem is that the respondent’s first detectable behavioral response to many signals is just to change positions; as it moves, it enters new stimulus situations. In analyzing the insect’s ultimate behavior, it is difficult to separate the influence of these new situations from that of the initial signals.

Even labeling behavior in order to catalog it can color one’s observations. A widespread system for classifying communication sets its categories as visual, acoustic, chemical, tactile, or electrical, for example; for convenience, a similar sys- tem is used in this book. However, for insects this is admittedly simplistic. An insect may be receiving information simultaneously in a number of sensory modes, and in many cases the total message and its specificity may depend upon receipt of all these different channels together.

1.3.2 Phylogenetic Systematics and Cladistics

To deduce the evolutionary direction of apparent behavioral progressions, a useful procedure is to plot the behavioral evidence against a ‘family tree’ (see Figs. 1.2 and1.12). Recognizing that closely related species are more likely to share traits than are distantly related species, Darwin himself introduced the metaphor of a tree to describe the relationships among taxa.

Many of these trees have their roots in traditional taxonomy and systematics, and owe an intellectual debt to Carolus (Carl) Linneaus, the Swedish botanist, physician and zoologist who laid the foundations for the modern scheme of binomial nomenclature. Linnaeus also developed what became known as the Linnaean taxonomy. This system of scientific classification, still widely used in the biological sciences, assigned every organism its position within a nested hierarchy based on observable characteristics. Thus, above the basic level of genus and species, Linnaean classification placed groups of organisms into families, orders, classes, phyla, and kingdoms.

The underlying details concerning what are considered to be scientifically valid ‘observable characteristics’ have changed with expanding knowledge (for example, DNA sequencing was unavailable in Linnaeus’ time), but the fundamental principle remains sound. Some taxonomists point out, however, that Linnaean classification can be misleading because it implies that different groupings with the same rank data could change the outcome and support a different hypothesis about the way that the organisms are evolutionarily related.

Next, one must judge which species are most closely related to each other and thus are descended from a more recent common ancestor. This involves decisions concerning *homologies*—characteristics assumed to be shared by species through descent from a common ancestor rather than being a product of a similar environment. As theories go, homology is relatively simple, but since it involves judgments about past events that can never be known with absolute certainty, in actual practice it sometimes can be quite controversial. For whatever character set one has chosen, the most similar pairs are considered the most closely related; more differences are taken to mean a more ancient split in ancestry, based on the fact that it takes more time for multiple mutations to occur. Unfortunately, all this is assumptive. History is not something we can see. It happens only once, and only leaves clues behind for those who attempt to reconstruct evolutionary history.

1.3.3 Behavior and Speciation

Can behavioral patterns be used like morphological or genetic characters in constructing a phylogeny? At first the idea was hard to sell. Many scientists said no; behavior is too variable, and is under too much environmental influence. However, one of the cornerstone beliefs of ethological research has always been groups, by contrast, are ‘mixed bags’ that may seem to share similarities but actually arose from two or more different ancestors. This approach has two main differences from the Linnaean system. First, phylogenetic classification tells you something important about the organism: its evolutionary history. Second, phylogenetic classification does not even attempt to rank organisms. In contrast to the traditional Linnaean system of classification, phylogenetic classification names only clades, or groups that include both a single ancestor and all its descendents.

The most important assumption in cladistics is that characteristics of organisms change over time, because it is only when characteristics change that different lineages or groups can be recognized. The original state of the characteristic before it changed is called plesiomorphic; the new state after the change, apomorphic. Though some people use the term ‘primitive’ instead of plesiomorphic and ‘derived’ instead of apomorphic, biologists generally avoid using these words because they have inaccurate connotations. It is all too easy to think of primitive things as being simpler and inferior, but in many cases the original plesiomorphic state of a character is more complex than the changed, apomorphic state. For example, as they have evolved, many cave insects have lost effective vision, and many island-dwelling species have reduced wings.

Instead of a Linnean-based evolutionary tree, cladists construct (or in the words of some, ‘reconstruct’) a *phylogenetic tree.* This is a diagram intended to represent the evolutionary history of modern taxa. The trunk, or earliest ancestor, gives rise to limbs that give rise to branches that terminate in twigs. The tips of the twigs represent species that are alive today. Sometimes branches fall off, representing extinction. (Some scientists prefer to think of a phylogenetic bush with many branches, rather than a tree with a single trunk; both terms are used.)

How does one go about constructing such a phylogenetic tree? No diagram can take every trait into consideration, so the first thing one must do is identify the particular characters (inherited traits) one will consider, and then describe the ways they vary, i.e. their character states. Traits can be almost anything that has an assumed genetic base and that can consistently be measured. Historically, trait measurements were morphological or anatomical, and many were gathered from fossil evidence. Sometimes traits corresponded to a single structure (such as hind leg lengths in various grasshopper species). In other cases, traits were expressed as ratios that described the measurements of a set of related structures (such as the tibia: femur ratio for various grasshopper species). These ratios were helpful to account for environmental influences on factors such as absolute body size. Behavioral (see Section1.3.3 below) or physiological traits, such as reproductive modes (see Fig. 1.12), can be useful as well. With the advent of molecular genetics, many traits are measured as DNA sequences, and molecular genetic maps are used to help build phylogenies by comparing and contrasting sequences across different species. Hopefully, one’s wise choices will lead to trees that approximate reality.