CHAPTER 11

Natural Selection and Adaptation

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Adapting an adaptation. Nudibranchs such as *Flabellina iodinea* are marine gastropod molluscs that lack shells. Many nudibranchs are unpalatable or dangerous because of stinging nematocysts they acquire by feeding on coral tissue and storing the noxious structures in their own bodies as a defense against predators. Bright "warning coloration" like this individual's is adaptive in toxic animal species, a signal to would-be predators that consuming this particular prey is not a good idea. (Photo © Ralph A. Clevenger/ Photolibrary.com.)

The theory of natural selection is the centerpiece of *The Origin of Species* and of evolutionary theory. It is this theory that accounts for the adaptations of organisms, those innumerable features that so wonderfully equip them for survival and reproduction; it is this theory that accounts for the divergence of species from common ancestors and thus for the endless diversity of life. Natural selection is a simple concept, but it is perhaps the most important idea in biology. It is also one of the most important ideas in the history of human thought—"Darwin's dangerous idea," as the philosopher Daniel Dennett (1995) has called it—for it explains the apparent design of the living world without recourse to a supernatural, omnipotent designer.

An **adaptation** is a characteristic that enhances the survival or reproduction of organisms that bear it, relative to alternative character states (especially the ancestral condition in the population in which the adaptation evolved). Natural selection is the only mechanism known to cause the evolution of adaptations, so many biologists would simply define an adaptation as a characteristic that has evolved by natural selection. The word "adaptation" also refers to the process whereby the members of a population become better suited to some feature of their environment through change in a characteristic that affects their survival or reproduction. These definitions, however, do not fully incorporate the complex issue of just how adaptations (or the process of adaptation) should be defined or measured. We will touch on some of these complexities later in this chapter.

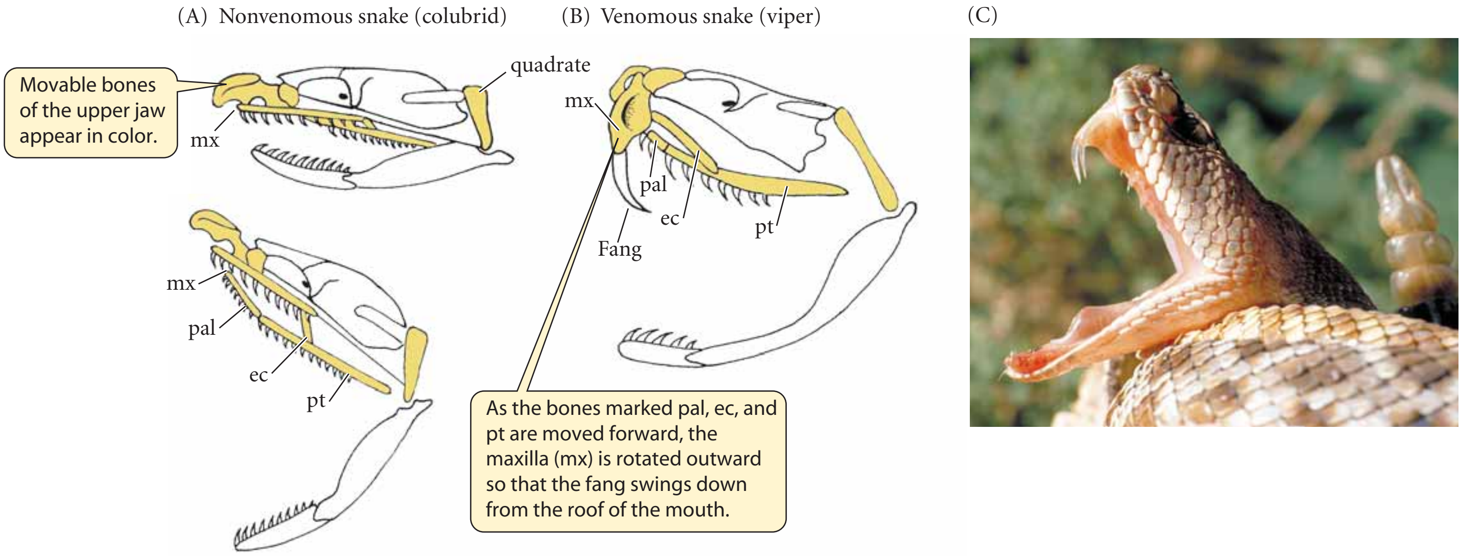


Figure 11.1 The kinetic skull of snakes. The movable bones of the upper jaw are shown in gold. (A) The skull of a nonvenomous snake with jaws closed (top) and open (bottom). (B) A viper's skull. (C) The head of a red diamondback rattlesnake (*Crotalus ruber*) in strike mode. (A, B after Porter 1972; C © Tom McHugh/Photo Researchers, Inc.)

Adaptations in Action: Some Examples

We can establish a few important points about adaptations by looking at some striking examples.

- In most terrestrial vertebrates, the skull bones are rather rigidly attached to one another, but in snakes they are loosely joined. Most snakes can swallow prey much larger than their heads, manipulating them with astonishing versatility. The lower jawbones (mandibles) articulate to a long, movable quadrate bone that can be rotated downward so that the mandibles drop away from the skull; the front ends of the two mandibles are not fused (as they are in almost all other vertebrates), but are joined by a stretchable ligament. Thus the mouth opening is greatly increased (Figure 11.1A). Both the mandibles and the tooth-bearing maxillary bones, which are suspended from the skull, independently move forward and backward to pull the prey into the throat. In rattlesnakes and other vipers, the maxilla is short and bears only a long, hollow fang, to which a duct leads from the massive poison gland (a modified salivary gland). The fang lies against the roof of the mouth when the mouth is closed. When the snake opens its mouth, the same lever system that moves the maxilla in nonvenomous snakes rotates the maxilla 90 degrees (Figure 11.1B), so that the fang is fully erected. Snakes' skulls, then, are complex mechanisms, "designed" in ways that an engineer can readily analyze. Their features have been achieved by modifications of the same bones that are found in other reptiles.
- Among the 18,000 to 25,000 species of orchids, many have extraordinary modifications of flower structure and astonishing mechanisms of pollination. In pseudocopulatory pollination, for example (Figure 11.2), part of the flower is modified to look somewhat like a female insect, and the flower emits a scent that mimics the attractive sex pheromone (scent) of a female bee, fly, or thynnine wasp, depending on the orchid species. As a male insect "mates" with the flower, pollen is deposited precisely on that part of the insect's body that will contact the stigma of the next flower visited. Several points are of interest. First, adaptations are found among plants as well as animals. For Darwin, this was an important point, because Lamarck's theory, according to which animals inherit characteristics altered by their parents' behavior, could not explain the adaptations of plants. Second, the floral form and scent are adaptations to promote reproduction rather than survival. Third, the plant achieves reproduction by deceiving, or exploiting, another organism; the insect gains nothing from its interaction with the flower. In fact, it would surely be advantageous to resist the flower's deceptive allure, since copulating with a flower probably reduces the insect's opportunity to find proper mates. So organisms are not necesssarily as well adapted as they could be.

(A)

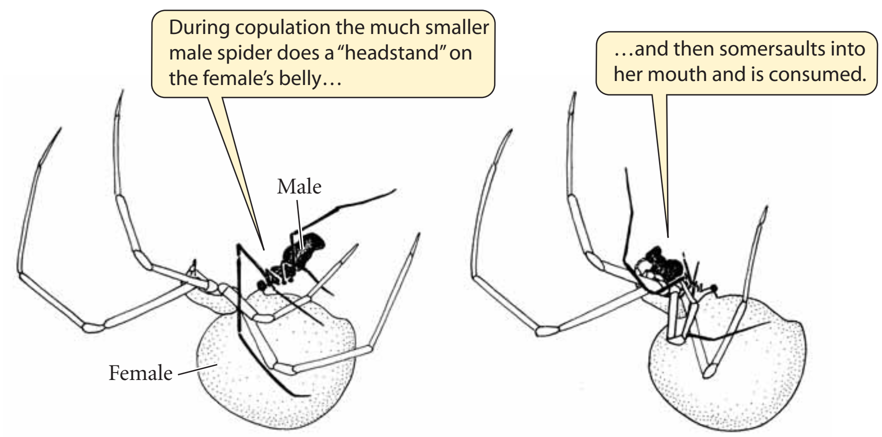
(B)

Figure 11.2 Pseudocopulatory pollination. (A) *Ophrys apifera*, one of the "bee orchids," uses pheromones to attract male bees and is shaped such that, in attempting to copulate with the flower, pollen adheres to the insect's body. (B) A long-horned bee (*Eucera longicornis*) attempts to mate with an *Ophrys scolopax* flower. A yellow pollen mass adheres to the bee's head. (A © E. A. Janes/Photolibrary.com; B © Perennou Nuridsany/Photo Researchers, Inc.)

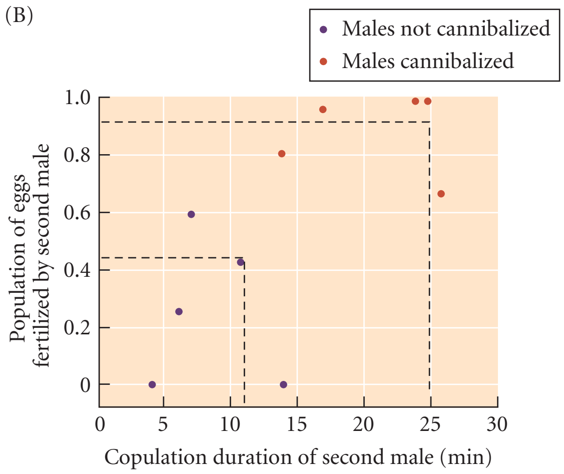
- After copulation, male redback spiders (*Latrodectus hasselti*; relatives of the "black widow" spider), often somersault into the female's mouthparts and are eaten (Figure 11.3A). This suicidal behavior might be adaptive, because males seldom have the opportunity to mate more than once, and it is possible that a cannibalized male fathers more offspring. Maydianne Andrade (1996) tested this hypothesis by presenting females with two males in succession, recording the duration of copulation, and using genetic markers to determine the paternity of the females' offspring. She found that females that ate the first male with whom they copulated were less likely to mate a second time, so these cannibalized males fertilized all the eggs. Furthermore, among females that did mate with both males, the percentage of offspring that were fathered by the second male was greater if he was eaten than if he survived. (Figure 11.3B). Both outcomes support the

Figure 11.3 (A) The small male redback spider somersaults into the large female's mouthparts after copulation. (B) The proportion of eggs fertilized by the second male that copulated with a female was correlated with the duration of his copulation. On average, copulation by cannibalized males lasted longer than that by noncannibalized males. (A after Forster 1992; B after Andrade 1996.)

(A)



(B)



hypothesis that sexual suicide enhances reproductive success. This example suggests that prolonged survival is not necessarily advantageous, and illustrates how hypotheses of adaptation may be formulated and tested.

- Many species of animals engage in cooperative behavior, but it reaches extremes in some social insects. An ant colony, for example, includes one or more inseminated queens and a number of sterile females, the workers. Australian arboreal weaver ants (genus *Oecophylla*) construct nests of living leaves by the intricately coordinated action of numerous workers, groups of which draw together the edges of leaves by grasping one leaf in their mandibles while clinging to another (Figure 11.4). Sometimes several ants form a chain to collectively draw together distant leaf edges. The leaves are attached to one another by the action of other workers carrying larvae that emit silk from their labial glands. (The adult ants cannot produce silk.) The workers move the larvae back and forth between the leaf edges, forming silk strands that hold the leaves together. In contrast to the larvae of other ants, which spin a silk cocoon in which to pupate, *Oecophylla* larvae produce silk only when used by the workers in this fashion. These genetically determined behaviors are adaptations that enhance the reproductive success not of the worker ants that perform them, since the workers do not reproduce, but rather of their mother, the queen, whose offspring include both workers and reproductive daughters and sons. In some species, then, individuals have features that benefit other members of the same species. How such features evolve is a topic of special interest.

Figure 11.4 Weaver ants (*Oecophylla*) constructing a nest. Chains of workers, each seizing another's waist with her mandibles, pull leaves together. (Photo from Hölldobler and Wilson 1983, courtesy of Bert Hölldobler.)

The Nature of Natural Selection

Design and mechanism

Most adaptations, such as a snake's skull, are *complex*, and most have the appearance of *design*—that is, they are constructed or arranged so as to accomplish some *function*, such as growth, feeding, or pollination, that appears likely to promote survival or reproduction. In inanimate nature, we see nothing comparable—we would not be inclined to think of erosion, for example, as a process designed to shape mountains.

The complexity and evident function of organisms' adaptations cannot conceivably arise from the random action of physical forces. For hundreds of years, it seemed that adaptive design could be explained only by an intelligent designer; in fact, this "argument from design" was considered one of the strongest proofs of the existence of God. For example, the Reverend William Paley wrote in *Natural Theology* (1802) that, just as the intricacy of a watch implies an intelligent, purposeful watchmaker, so every aspect of living nature, such as the human eye, displays "every indication of contrivance, every manifestation of design, which exists in the watch," and must, likewise, have had a Designer.

Supernatural processes cannot be the subject of science, so when Darwin offered a purely natural, materialistic alternative to the argument from design, he not only shook the foundations of theology and philosophy, but brought every aspect of the study of life into the realm of science. His alternative to intelligent design was design by the completely mindless process of natural selection, according to which organisms possessing variations that enhance survival or reproduction replace those less suitably endowed, which therefore survive or reproduce in lesser degree. This process cannot have a goal, any more than erosion has the goal of forming canyons, for *the future cannot cause material events in the present*. Thus the concepts of goals or purposes have no place in biology (or in any other of the natural sciences), except in studies of human behavior. According to Darwin