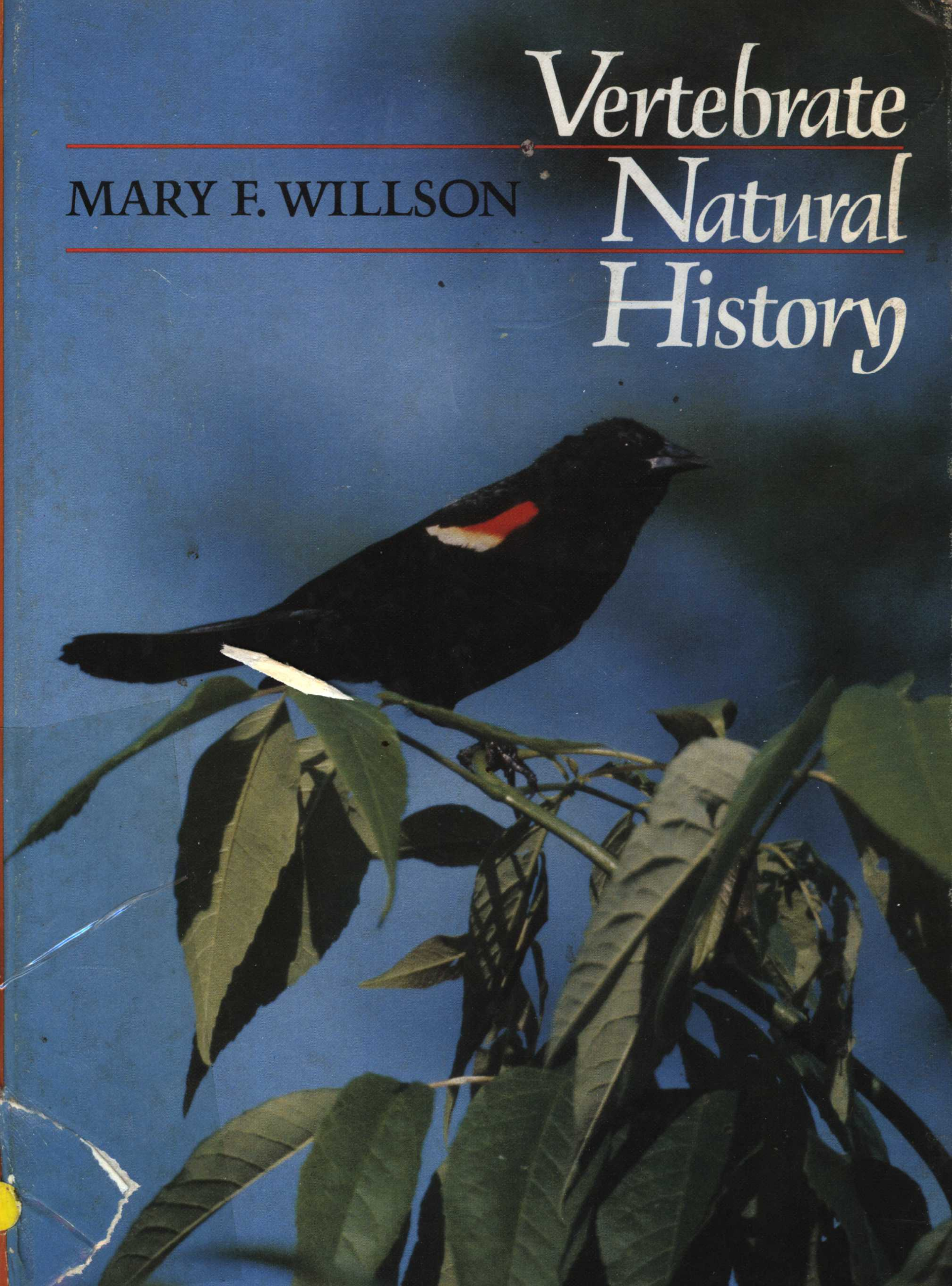
Vertebrate Natural History

MARY F. WILLSON



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Preface

Many of my students are perplexed to learn that science is not just an ordered collection of facts but a process of discovery. The gaps in our knowledge distress some of them but excite others, who like to think about unanswered questions and ways of finding good answers. The latter are usually the students who learn the most and have the most fun doing it. This book presents what we regard as facts as well as reasoned speculation in an effort to encourage students to think more about this subject and initiate the process of discovery.

I have not provided references in the text itself for every assertion made in this book. This is particularly true in the first 10 chapters; much of this material is readily available in standard textbooks of physiology or anatomy and in surveys indicated in the reference sections for each chapter.

This book has been a long time coming. It has matured and improved as it sat on the shelf or passed through periodic revisions. I am sure that more improvement will be appropriate and I will welcome constructive criticism. Over the years I have accumulated a debt of gratitude to a number of colleagues and friends, who have explained, commented, corrected, found references, encouraged, and provided help of various other sorts: E. M. Banks, J. L. Brown, J. S. Findley, T. H. Frazzetta, C. Gans, N. H. Goldberg, H. W. Greene, J. R. Karr, J. H. Kaufmann, J. R. King, L. J. Miller, L. M. Page, P. W. Price, C. L. Prosser, B. J. Rathcke, R. R. Roth, D. W. Schemske, C. C. Smith, R. M. Storm, R. L. Trivers, J. Verner, G. P. Waldbauer. I have not wittingly left out the names of any who have helped over the years; I hope that any omissions will be ascribed to the passage of years and forgiven. I am also grateful to those who provided photographs and permissions, as credited *in situ*, and to the three artists, whose talents, hard work, and patience are vastly appreciated. R. C. Snyder and E. E. Provost provided constructive overviews of the manuscript. K. P. and H. W. Ambrose III gave staunch assistance in the early days. The librarians of the Biology Library (University of Illinois) and the Illinois Natural History Survey were, as usual, uncommonly helpful. P. L. Katusic was indispensible in the preparation of the final manuscript. Completion of this task would not have been possible without such assistance.

I dedicate this endeavor to my family—all of them, but especially to my mother and the memory of my father.

Mary F. Willson

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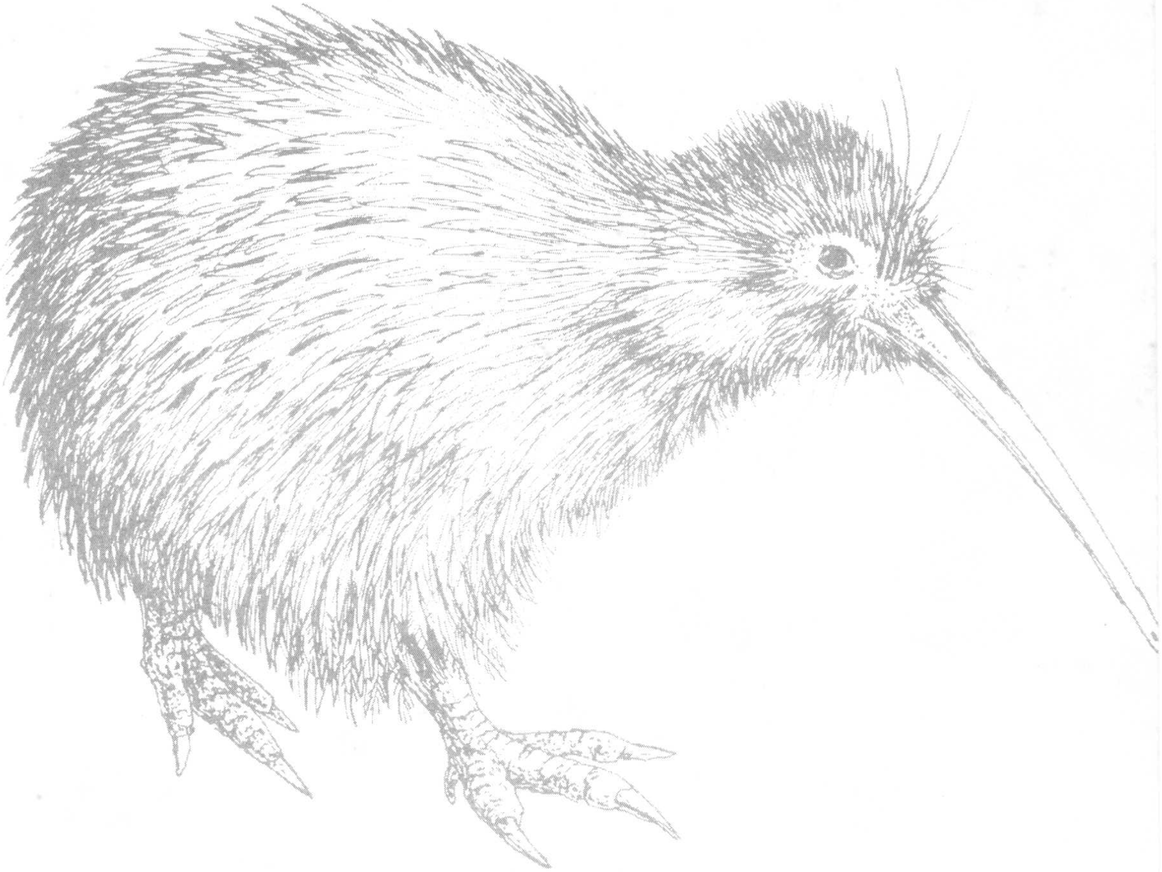


PART 1

PERSPECTIVE

1

Introduction and Principles

- **Evolution**
  - Variation and Natural Selection
  - Fitness
  - Adaptation
  - Speciation and Adaptive Radiation
- **Body Size**
  - Size and Metabolism
  - Size and Proportion
  - Allometry and Evolution

What is "natural history"? My dictionary defines "history" as a systematic written account of events that is usually connected with a philosophical explanation of their causes. The word "history" is derived from a Greek word meaning a process of learning by inquiry. "Natural history," therefore, refers to the recording and explaining of events in nature; in its present usage, the term usually applies to biological (more than chemical, physical, astronomical, or geological) events. Although chemistry, physics, and sometimes geology are often involved in the explanation of biological features, biology is the focus of attention. The subjects of natural history are whole organisms, not the genes, cells, or tissues that compose the organisms, even though the functioning of genes and tissues is closely related to the behavior and functioning of the whole organism in its natural setting. Natural history involves the study of not only anatomy, physiology, systematics, distribution, but also behavior and ecology. This book is about the natural history of vertebrates (animals with backbones); in this text, I try to place vertebrate form and function in an evolutionary and ecological context.

Humans have long been interested in the natural history of other vertebrates. At first, this interest centered on how to capture them, how to escape from them, and how to maintain or diminish their populations. Recently, the usefulness of animals has again claimed our attention. Animals are useful as agents of population control for species that humans think are desirable or undesirable, as regulators of the balance of nature, as alternatives to domesticated protein sources, as sources of genetic variability for the development of new domestic strains, and as aesthetic phenomena. From such utilitarian motives, our observations of other animals lead to the development of general principles about the relationships of animals with each other and with their environment.

Much human activity is centered on imposing order upon our observations; we do this by trying to *explain* what we observe. Primitive attempts to create order result in myth; more sophisticated orderings represent significant steps toward rationally comprehensible patterns. The first generalizations of natural historians stem from observations and experience. For example, a series of observations could tell us that the long toes of jacanas (*Jacana spinosa*) provide adequate support for these aquatic birds as they walk across lily pads and floating debris (Fig. 1–1). Because the engineering principles involved are already well known, however, an engineer could design a "lily-trotter" of some sort (although it might not be very birdlike)

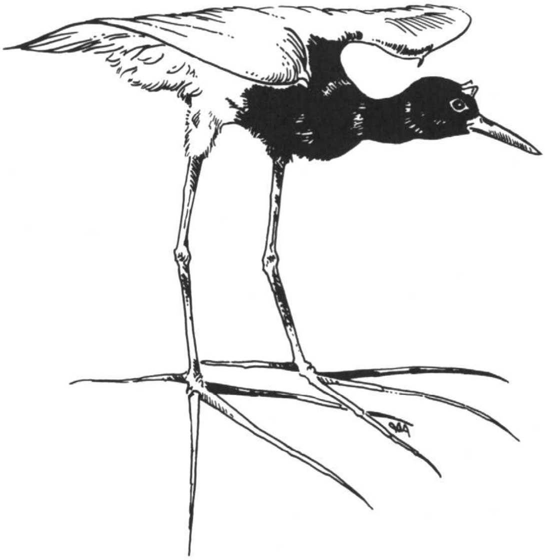


Figure 1–1 The American jaçana, *Jacana spinosa,* total length about 25 cm. This species lives in Central and South America. There are seven members of the family Jacanidae distributed around the world in tropical marshes where lily pads and other floating vegetation provide a walking surface for the lily trotters. Their name comes from a Spanish version of a Tupi Indian name for the bird in the Amazon basin.

from data concerning the weight of the bird, the buoyancy and flexibility of lily pads, and the customary speeds of the bird. In this example, some elements of jacana anatomy could be predicted from basic principles of physics.

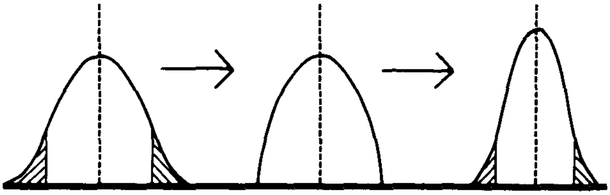
In a similar way, by making many observations of the habitats in which field sparrows (*Spizella pusilla*) are commonly seen, we can learn to expect where, within their geographic range, they will be found. But, unlike the physical principles involved in lilytrotting, the mechanisms that determine patterns of habitat selection are less well understood, and we cannot yet make predictions from basic principles alone. Clearly, any species that survives must be able to exploit food resources, utilize nest or den sites, and escape from predators in some piece of habitat; and they must do these things better than any other organism in those particular circumstances. Some of the physiological and morphological principles involved (temperature tolerance, tooth structure, vision, for example) are understood, but how they combine to produce an animal capable of exploiting a given habitat is still a matter of observation and correlation rather than of prediction. Much of modern natural history is concerned with the progress from observational pattern to predictable pattern.

EVOLUTION

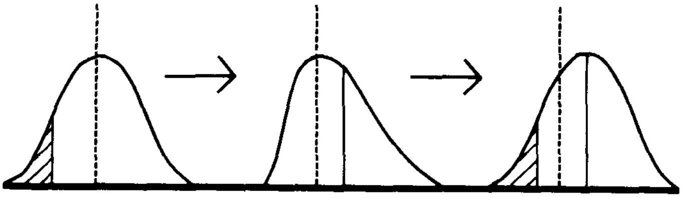
Evolution is the fundamental principle of biology. Comprehension of evolutionary processes is essential for full understanding of any aspect of biology, from medicine (the evolution of fever) to sociology (the evolution of altruism) to the technology of "pest" control (the evolution of resistance). Similarly, for the modern study of natural history, it is inadequate to construct a catalog of cute little tricks employed by organisms and call that "natural history." In some cases, our specific knowledge extends only as far as observing that a certain trick exists, and we lack sufficient knowledge to explain the evolution of that feature. Closer study will undoubtedly reveal something of that evolution, however, as it has so many times before. Conversely, our lack of knowledge regarding certain specific features cannot prevent us from understanding the general process of evolution and its relevance to many characteristics of living organisms.

Evolution is defined as a change in the frequencies of genes in the gene pool of a population. Evolution depends on genetic variation (the existence of more than one allele at a locus); obviously, there could be no change in the gene pool without it. The original source of genetic variation is mutation, supplemented by chromosomal rearrangements that place different genes in different orders that may influence their activity. Evolution is a result of a variety of processes (to be discussed below) that affect the individuals composing a population.

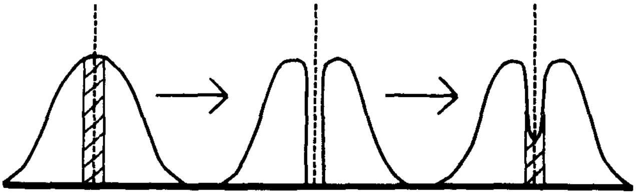
Each organism possesses a complement of genes that is its genotype. During meiósis and gamete production in sexually reproducing organisms, chromosome sets are broken up and chromosomes are randomly assorted into haploid gametes. When gametes unite to form a zygote, then, that zygote contains a different collection of chromosomes than either of its parents. This process, taken alone, does not change gene frequencies. It does, however, create different genotypes. Because different genotypes usually are outwardly expressed in different phenotypes, existing genetic variation is exposed to the environment. Some phenotypes are better suited to certain environments than others. As a result, they survive better and reproduce more successfully; that is, they leave more descendants than others. Because of this differential effect of the environment on the array of phenotypes, genotypes differentially and nonrandomly contribute genes to future generations. This is called "natural selection." Natural



(a) Stabilizing



(b) Directional



(c) Disruptive

Figure 1–2 The three modes of selection. On the horizontal axis is the degree of development of a phenotypic character; the vertical axis shows the frequency of each phenotype in the population. The shaded areas indicate the phenotypes that are selected against. For each mode, the first curve shows the frequency distribution of phenotypes in the original population; the second suggests the distribution after the indicated mode of selection has eliminated some phenotypes; and the third illustrates the condition after reproduction and recombination have produced additional variability. The dotted vertical lines indicate the initial mean for each distribution.

selection generally produces adaptations that suit the animal's environment in some way. Selection changes the array of genetic variation present in a population and, therefore, is one of the major processes of evolution.

Not all changes in the gene pool may involve adaptation. First of all, genes are linked together on chromosomes, and although bits of chromosomes may break off and attach to other chromosomes, chromosomes (or parts of them) form linkage groups that are usually transmitted as intact entities. Therefore, certain groups of genes tend to be found together consistently, and selection that favors one gene will automatically and indirectly favor others in the linkage group. If the linked genes all confer selective advantage to the owners, the linkage group may persist. If some of them are disadvantageous, selection will favor unlinking those genes or the evolution of modifier genes (which alter the effects of other genes). In the meantime, however, disadvantageous genes may be temporarily and indirectly favored because of their physical association with other, advantageous genes.

Furthermore, in populations in which breeding is sometimes accomplished by just a few random members, changes in the gene pool may take place as a result of "sampling error" or genetic drift. Not all genes in the pool are represented in zygotes and the ensuing generation, because not all individuals bred. Since breeding was at random and not related to suitability, such changes in the gene pool are not related to adaptation. Drift may be far more common and important than is generally believed. Migration into or out of a population (gene flow) may also result in changes in gene frequency. The effect of migration depends on the size of the population, the frequency of migration, and whether or not it is random with respect to the genotype of the migrants.

Another source of change in gene frequency derives from a number of "anomalies" that may take place during cell division and result in the loss of certain chromosomes. Although these anomalies have the appearance of mistakes, they actually may have some as yet unknown adaptive value.

Variation and Natural Selection

Much variation in a population is continuous variation; that is, all individuals exhibit a characteristic, but to varying degrees. If we were to choose some characteristic—length of the jawbone, for example—we would probably find that most individuals have jawbones of medium length, but members of the population can be found with extremely long or short ones. Given such a distribution of phenotypic frequencies, which we will suppose has a genetic basis, selection can act on that distribution in three basic ways (Fig. 1–2).

Individuals at the tails of the distribution (those with very long or very short jawbones, in this case) may be less successful than those in the middle. As a result, such phenotypes are continually eliminated from the population more rapidly than those in the middle. In this condition, the

Figure 1–3 Directional selection by differential predation on color patterns in the water snake *Nerodia sipedon* living on islands in Lake Erie. Dark-colored snakes tend to be eliminated from the population because they are more conspicuous against the light-colored backgrounds found on the islands. Dark adults, migrating to the islands from the mainland, apparently reintroduce genes for dark color into the island gene pool. (From *The Process of Evolution* by P. Ehrlich and R. Holm. Copyright © 1965 McGraw-Hill Book Company. Used with the permission of McGraw-Hill Book Company.)

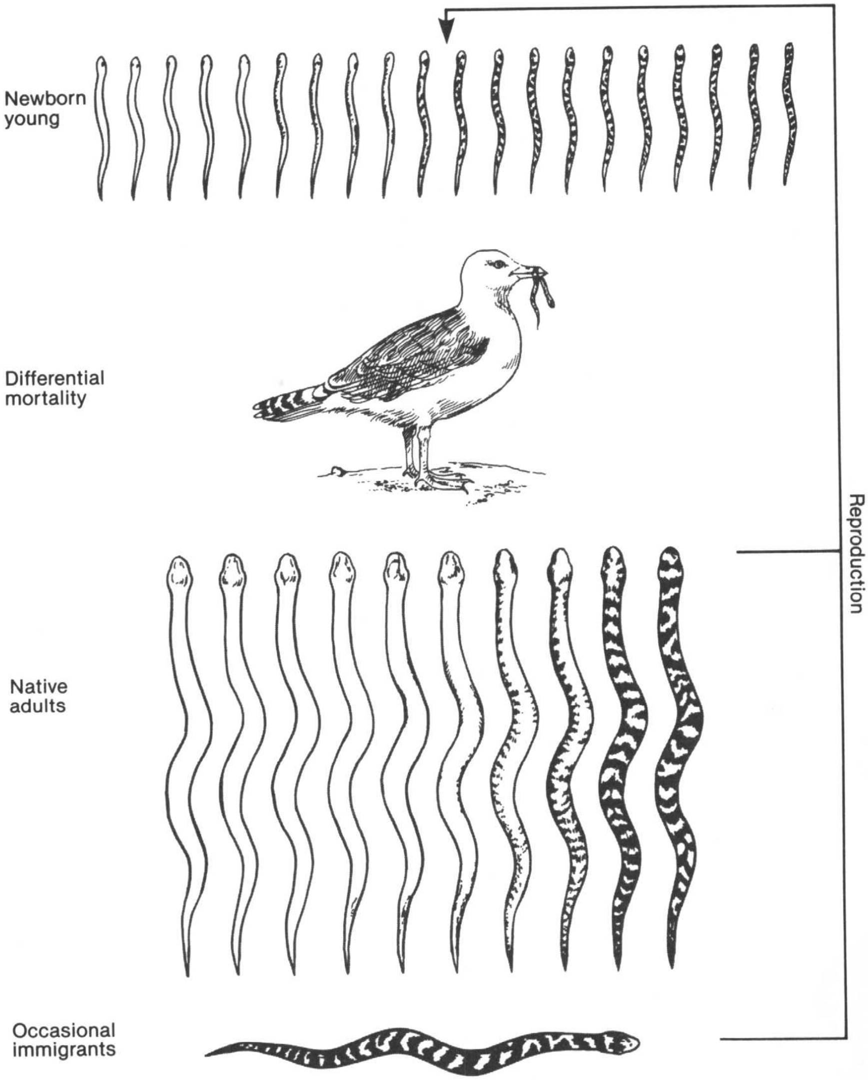
peak of the distribution (the mean of the characteristic) stays at the same value from generation to generation. This is called stabilizing selection.

Selection may also discriminate against only one tail of the distribution (for example, individuals with short jaws). Individuals genetically constituted to produce longer jaws then provide more genes to future generations, and, gradually, the distribution of jawbone lengths in our example shifts toward longer and longer jaws. This process is called directional selection.

In a third case, selection may discriminate against individuals close to the mean and favor those at either extreme. This results in a bimodal frequency distribution of phenotypes and is called disruptive selection.

These three modes of selection can be exemplified by cases from the real world. The now classic case of stabilizing selection is that of house sparrows (*Passer domesticus*) brought down by a severe storm in New England. Of 136 stunned birds, 72 recovered and 64 died. Bumpus (1898) made many skeletal measurements on both groups and found that individuals whose measurements were near the average had a higher probability of recovery than those either larger or smaller than the average. Grant (1972), and others, reanalyzed these data and showed that the results applied to female sparrows but not to males. He suggested that female sparrows are subordinate to males in most social interactions; they may be kept from food resources by the dominant males and, therefore, have a higher risk of death in severe conditions. Small females probably have small energy reserves and are unable to replace them when they are depleted; large females perhaps can mobilize stored energy less rapidly in response to metabolic stress. These circumstances may result in selection against both size extremes.

One of the best examples of directional selection comes from Camin and Ehrlich's (1958) study of water snakes (*Nerodia sipedon*) on islands in Lake Erie. All *N. sipedon* on the surrounding mainland and some of those on the islands are patterned with dark bands, but the island populations also include numerous lightly banded or completely unbanded individuals (Fig. 1–3). Litters of young snakes comprise both banded and unbanded forms, but unbanded individuals occur significantly more frequently among adult snakes than among young snakes. This change in pattern frequency is not due to age-related changes in color of individuals but



rather to the differential elimination of the darker patterns. Differential survival of light-colored individuals occurs consistently on several islands and is undoubtedly related to differential removal by predators such as gulls. Most island snakes inhabit limestone rocks and beaches, where light color is a better camouflage than dark bands (which are valuable as camouflage in the typical swamp habitat of this species on the mainland). Selection against banded patterns on the islands is very strong and would eventually eradicate the dark forms entirely were it not for the immigration of banded individuals from the mainland.

Good examples of disruptive selection among vertebrates are hard to find, although it must have occurred many times. Disruptive selection must be involved in the evolution of sexual differences in size, color, or pattern that are observed in many species of vertebrate. Small male and large female house sparrows were especially vulnerable in Bumpus' winter-storm sample (Johnston et al., 1972). This differential in survival maintains the sexual differences in body size.

Opposing selection forces favor two color types in some populations of the three-spine stickleback (*Gasterosteus aculeatus*). By implication, intermediate color forms are at a selective disadvantage (Fig. 1–4). Three-spine stickleback males typically develop a bright reddish throat during their breeding season. Males of populations in many areas are monomorphic ("one form") for this characteristic—that is, all males develop red throats.

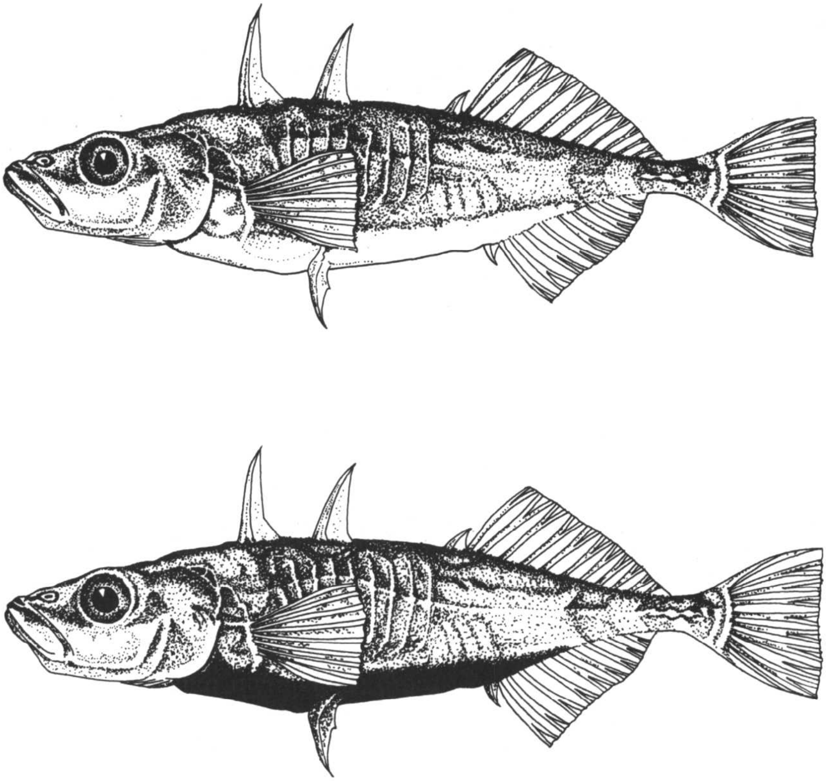


Figure 1–4 A male three-spine stickleback, *Gasterosteus aculeatus*. The common name derives from the three spines located anterior to the dorsal fin proper. The formal name of the genus denotes the series of bony plates found along the flanks, at least in some populations. Two color morphs are shown here.

But in certain streams in western North America, several populations have polymorphic ("several forms") males: Some have red throats, others (the majority) have silver or black throats. Females prefer to mate with red-throated males, thus giving this morph a reproductive advantage (Semler, 1971). Red-throated males also may have a higher success in defending their eggs and young against cannibalism by other sticklebacks, especially other males. On the other hand, the prevalence of nonred males in certain populations suggests that something in those areas must be selecting against red males. Cutthroat trout (*Salmo clarkii*) attacked red males more frequently than they did nonred males, and trout predation was particularly successful in well-lit waters where the red color was conspicuous. Thus, we would expect to find nonred males primarily in clear waters with an abundance of predatory trout. Males with pinkish (intermediate-colored) throats were apparently unobserved; presumably, they would have neither the reproductive nor the antipredator advantage and thus be disfavored by selection. This example is complicated by the existence of at least two nonred morphs, the probable existence of other conditions affecting the maintenance of the polymorphism (Hagen et al., 1980; Hagen and Moodie, 1979), and the fact that selection against the intermediate form is inferred and not demonstrated directly. Nevertheless, the idea of disruptive selection and the resulting population of two (or more) major forms is adequately illustrated.

Both stabilizing and directional selection tend to reduce existing variation by eliminating certain types. On the other hand, disruptive selection tends to increase the total amount of variation in a population, although variation around each peak may be reduced in each generation. Variation is continually reconstituted in sexual organisms by mutation and by recombination of chromosomes, however.

Fitness

We use the term "fitness" to describe the relative genetic contribution of different individuals to future generations. Individuals producing the most offspring that in turn reproduce successfully are the most fit, and the fitness of other members of the population is measured relative to the most fit. Thus, if individual A produces 100 surviving offspring and individual B produces only 90, clearly the second kind has produced only 90 percent as well as the first and is at a 10 percent disadvantage. It is customary to set the fitness of A at 1.00; then the fitness of B relative to A is 0.90. The difference in the fitness of A and B (10 percent in this case) is called the selection coefficient, which measures the relative disadvantage of the type disfavored by selection or the intensity of selection against the inferior kind. It is important to realize that fitness is defined in this relative way. A certain constellation of phenotypic characteristics may be most fit in one set of circumstances, but a new constellation in the next generation may then