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evolution of behavior
Michael J. Ryan
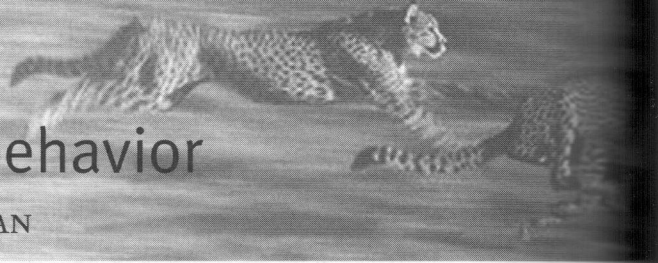
INTRODUCTION: WHAT IS THE EVOLUTION OF BEHAVIOR?

As we have seen in Chapter 1, Tinbergen (1963) summarized the four main "questions" of **ethology** as **causation**, ontogeny, **survival value** (or **function**), and evolution. It is the last question we will explore here – evolution. In much of animal behavior, and especially **behavioral ecology**, the term "evolution" encompasses two subjects. One is the process of selection that gives rise to the evolution of **adaptations**. The other is the historical pattern by which biological diversity has come about. Such an approach to evolution encompasses two of Tinbergen's questions, survival value and past evolutionary history. The functional aspects of behavior have been addressed in Chapter 9. This chapter will focus on its historical patterns, what Tinbergen meant by "evolution."

Evolutionary thinking has been applied to behavior for several reasons. Humans are obsessed with historical roots, whether it be their own genealogies, the derivation of Roman mythology from that of the Greeks, or the possibility that the American game of baseball might be a descendant of the English sport of cricket. It is this same interest that motivates some behavioral biologists' pursuit of evolution. Charles Darwin (1872), the first evolutionary biologist, analyzed the evolution of emotions in animals, including humans. There are striking similarities in the facial expression of humans and some of their closest relatives. Did such expressions come about in each species separately or can their similarities be best explained by being inherited from a common ancestor of humans and other primates? Thus behavioral biologists have always been interested in explaining the history by which behavior evolved.

Some of the early behavioral biologists were trained in the traditions of **comparative** morphology and taxonomy. Characters that are shared through common descent give some indication of how species are related

to one another. During the development of ethology, morphology provided the primary data used to derive **phylogenetic** relationships, much as genetic methods today provide the bulk of data used in phylogenetics. Konrad Lorenz (1967, 1971) thought that the analysis of differences and similarities in behavior might also provide useful information for taxonomy and phylogeny, as well as being used to understand the historical patterns of behavioral evolution. In fact, Lorenz's emphasis on comparing **homologous behaviors** among species to understand patterns of behavioral evolution presages the current trend in studies of behavioral evolution.

Besides describing historical patterns and using behavior for taxonomy, behavioral biologists have more recently been using historical information to test hypotheses about the adaptive function of behavior (reviewed in Brooks & McLennan 1991; Harvey & Pagel 1991; Martins 1996). For example, consider how variation in a species' **mating system** might drive the evolution of a species' morphology (as discussed in Chapter 12). One might hypothesize that large testis size is an adaptation for **sperm competition** in **promiscuous** mating systems, as opposed to having small testis size in **monogamous** mating systems. This hypothesis can be tested by reconstructing the evolution of these two traits, testes size and mating system, and determining how often the predicted correlation between the traits evolves (see Fig. 12.5).

When we ask questions about history we are asking about the past. Unlike the three other areas of Tinbergen's ethology, experimentation and observations in the wild are usually not sufficient tools for glimpsing what has already happened. In this chapter we will be exposed to a different logic and a different set of tools for exploring behavior, those of historical analysis.

Behavior, Taxonomy, and Phylogenetics

In biology, one uses the phenomenon of descent with modification to reconstruct the phylogenetic relationships among organisms. Many behavioral biologists have asked whether behavioral characters, like morphological and genetic characters, can be used for taxonomic assignment of individuals to species. Others have used these same data to gain insights into the historical relationships among species.

The premise underlying the first question is that there are species-specific behaviors that can act as diagnostic characters in assigning species status. This is true for an obvious reason. Species are often operationally defined as a group of potentially interbreeding individuals. Individuals will only interbreed if they recognize each other as mates. Most sexually reproducing species have evolved species-specific behavior, such as courtship displays, calls, songs, and **pheromones**, that one sex (usually females) uses to judge the appropriateness of other individuals as mates (usually males). There is strong selection

to mate only with conspecifics since mating outside the species rarely produces viable and vigorous offspring. This is why species-specific courtship is usually dimorphic, with the males being the more elaborate. More specifically, this is why the plumage of birds and the songs of insects, frogs, and birds often allow one to correctly identify species (see Chapter 11). In fact, in many cases researchers first note differences in courtship signals that then lead them to describe populations as new species.

The second question, whether behavior provides insights into the historical relationships among species, is more complicated. The logic underlying this question is that similarities in traits among species result from either inheritance from a common ancestor or independent evolution under similar selection regimes. Traits that are similar among species because they were present in the common ancestor are called homologous. Traits that are similar but which evolved independently are called **homoplasious**, and the particular pattern of similarity is called convergence. The pattern of shared homologous traits is the footprint of evolution; if this pattern can be distinguished correctly from convergence, then we should be able to reconstruct the branching pattern or **phylogenetic tree** by which species diverged from one another. The challenge is distinguishing between homologous and homoplasious traits. Under the assumption that evolution is a conservative process, many scientists rely on the **principle of parsimony**, which is that the simplest explanation is more likely to be correct than a more complicated one. For an example of the logic of parsimony, consider that there are approximately 5000 species of mammals and they all have four-chambered hearts. We can ask, did this trait evolve 5000 times independently or is it present in all mammals because it is shared through a common ancestor? Parsimony favors the latter explanation. This exercise in logic is applied only to the evolutionary origin of the trait. It does not make any judgment as to whether the trait has current survival value, i.e., whether it is maintained by selection.

When phylogeneticists assess species relationships, they analyze the similarities of traits among species and present the results as species arranged on a phylogenetic tree. This tree is a representation of the way the species have diverged from one another over time. For any given number of species there are many possible trees. Phylogeneticists usually attempt to find the tree that explains the distribution of data by invoking the fewest number of evolutionary changes under the principle of parsimony. In principle, any traits can be analyzed but those subject to strong selection are more likely to evolve similarities through convergence than are traits that are selectively neutral. One way to avoid the effects of misleading data is to analyze a variety of types of characters, especially traits that are somewhat different from those of immediate interest. This is one reason why current phylogenetic studies often use DNA sequences in addition to morphological and behavioral traits. Although there are noteworthy exceptions, many studies have shown that phylogenetic analyses of behavioral traits yield hypotheses about relationships that are similar to analyses based on molecular characters (Wimberger & de Queiroz 1996).

Patterns of Behavioral Evolution

Deduced from strong inference

In some cases a detailed understanding of an animal's behavior in the wild combined with a basic understanding of evolution is sufficient to allow one to propose likely scenarios for how behaviors have evolved. A simple and stunning example concerns the star orchid of Madagascar. In his book on how orchids are fertilized, Darwin (1862) described this flower as having its nectar in the bottom of a flower spur almost a third of a meter in depth. Such nectar could only be accessed by a very special pollinator, one with a tongue at least as long. No such beast was known from Madagascar at the time, but Darwin predicted one would be found. And it was, a hawkmoth with the longest known tongue in the Old World (*Xanthopan morganni praedicta*; Fig. 13.1). In this case, a simple observation about a plant yielded a specific and testable prediction about a behavioral adaptation of an animal that was not even known to exist at the time.

Understanding the evolution of behavior is usually not as simple as in the case of the hawkmoth. Darwin's theory of natural selection suggests that complex traits arise by small incremental changes from more simple traits. The evolution of complex traits can thus present a challenge (Dawkins 1996). One could argue that behavioral traits are among the most complex of phenotypic traits. They did not arise out of whole cloth. So we can ask: what is their evolutionary history and how do we go about studying it?

As mentioned at the outset of this chapter, closely related species often share similar behaviors, and it seems likely that these behaviors are shared through a common ancestor. Consider the following quote from Darwin's book *The Expression of the Emotions in Man and the Animals* (1872, p. 91):

> When male animals utter sounds in order to please the females, they would naturally employ those which are sweet to the ears of the species; and it appears that the same sounds are often pleasing to widely different animals, owing to the similarity of their nervous systems, as we ourselves perceive in the singing of birds and even in the chirping of certain treefrogs giving us pleasure.

In this passage Darwin is suggesting that similar behaviors, in this case acoustic signals used by males to court females, result from a variety of species sharing the same properties of the nervous system that deem such sounds attractive. He even suggests, quite boldly, that female animals and humans might share the same esthetic preferences for animal song due to such evolutionarily shared properties. Thus ever since Darwin it was thought that some of the similarities in behavior among species might be due to descent with modification.

Sometimes there can be striking similarities between behaviors associated with different activities within the same species. Julian Huxley (1914) pondered the complicated courtship patterns of the grebe *Porpodiceps cristatus*. In one part of the grebe's courtship, the penguin dance, the birds exhibit **stereotyped behavior** patterns that bear a striking resemblance to other behaviors associated with nest building. It seemed to
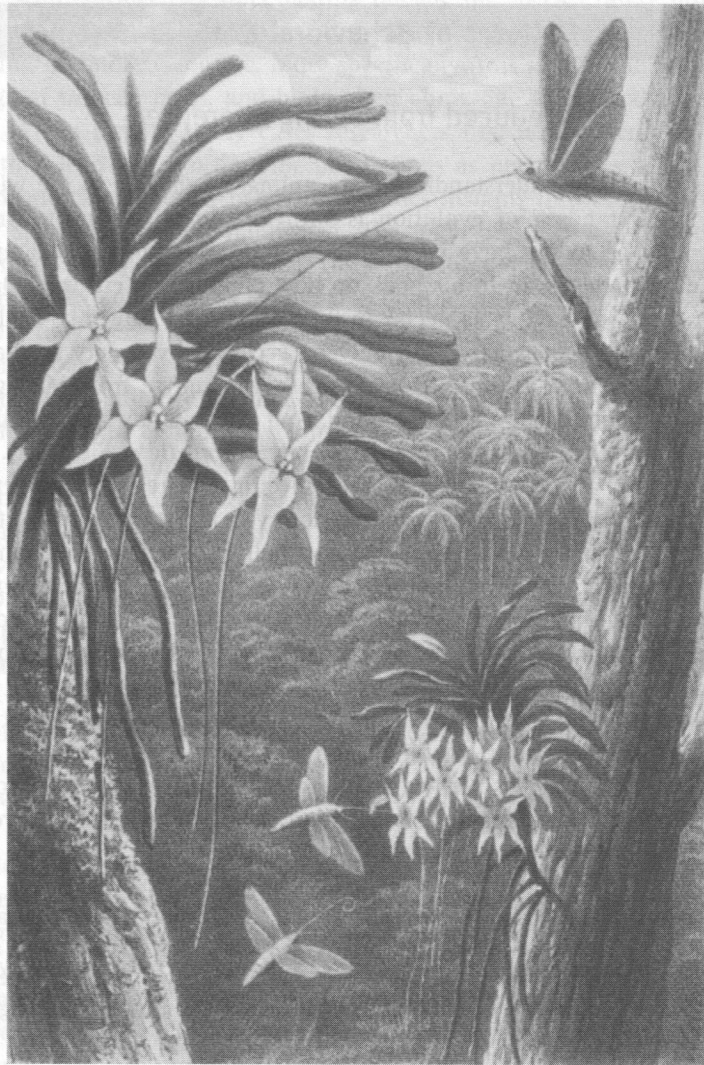
Fig. 13.1 Darwin predicted that the Madagascar star orchid *Angraecum sesquipedale* would require pollination by an insect with an exceptionally long tongue. Later, the hawkmoth *Xanthopan morganni praedicta* was discovered. (From *Trends in Ecology and Evolution* 1998, 13, 259.)

Huxley unlikely that such complex motor patterns, so gracefully coordinated between mates, arose de novo and just happened to resemble behaviors used in other contexts. Instead, Huxley thought such display behaviors were derived or "**ritualized**" from more simple motor patterns that served other functions. How does ritualization take place?

Here is a simple example. When a dog is about to attack an opponent it must open its mouth; thus the open mouth becomes a cue of an impending attack. The open mouth may then evolve into an exaggerated and stereotyped behavior that evolves into a threat

signal. Tinbergen (1952) summarized the ways in which an original behavior can become ritualized into a display behavior: the original behavior becomes more intense, is performed more slowly, is repeated **rhythmically**, is combined with other behaviors, and is no longer directed toward the stimulus that originally elicited it. A bird squatting and pointing its beak skyward prior to flight evolved from behaviors associated with preparation for flight and is one example of a ritualized behavior. Another example is the rhythmic courtship drumming that woodpeckers evolved from their behavior of hunting insects. Thus similarities in behavior within as well as among species can give us clues as to how they evolved.

One sort of behavioral evolution that is a little more complicated is when the behavior of one species influences the behavior of another and vice versa. Fireflies have species-specific patterns of flashing that are used in conspecific mate choice (summarized in Lloyd 1984). Male fireflies search for a mate by signaling with a flash, the female responds with her own flash, and the male approaches the female and mates with her. Or at least that is usually how it happens. Fireflies in the genus *Photuris* prey on other fireflies, including those in the genus *Photinus*. Female *Photuris* sometimes **mimic** the flashing signal of female *Photinus*. When the male *Photinus* approaches he is not mated by a female of his own species but eaten by the female *Photuris*. This game of deceit is continued by the male *Photuris*. Male *Photuris* will sometimes mimic the flash of the male *Photinus* as a way to locate their conspecific female *Photuris*. The female *Photuris* mimics her prey, female *Photinus*, in replying to the flashes of what appears to her to be a male *Photinus*, but instead when the male approaches she finds it is a potential mate rather than a potential meal.

How did all this come about? By what pattern did this sequence of deceitful behaviors evolve? Strong logic suggests what seems to be the most likely hypothesis. First, each species has its own species-specific flash pattern; then female *Photuris* evolves to exploit male *Photinus*; then male *Photuris* evolve to exploit female *Photuris*. Although we cannot prove that this scenario is the correct one, none of the alternatives seems to be as feasible. If there were no species-specific signals, there would be nothing for the female *Photuris* to exploit; if female *Photuris* did not try to lure their prey by mimicking the flashes of *Photinus* females, they could not be exploited by *Photuris* males. The logic seems tight, the scenario seems right. Of course, the scenario is just a hypothesis which could be wrong.

This type of logic has also been applied to a more complicated pattern of evolution, the widely cited courtship behavior of a group of empidid flies known as balloonflies, described by Kessel (1955). In some species males form **leks**, areas where males aggregate solely for the purpose of displaying to females (see Chapter 11), and present females with large empty balloons of silk. Females choose mates as if they are evaluating the size of the balloons. Can we possibly understand how something like this might evolve? Kessel studied other species of empidids and found an interesting range of courtship behaviors. Some species hunt small insects which they use as **nuptial gifts**, and some but not all of these species with nuptial gifts gather in leks. Furthermore, the presentation of these gifts to females varies among species: some partially wrap the nuptial gifts in a single strand of silk, others totally wrap the gift in silk, whereas the males of other species suck the juices out of the gift before wrapping it. Even empidids that feed on

nectar instead of insects buy into this gift-giving scheme, but instead of hunting down a prey item they wrap the balloon around dead insects they find. And finally, back to where we started, some species present the female with a large empty balloon.

Given the behavior of the various species of empidids, there is a very logical series of behavioral transitions. Among insect-hunting empidids there is first the evolution of nuptial gift giving, and then the adornment or "packaging" of the gift. Once packaged, males cheat either by sucking the juices out of the prey or by not even putting a gift in the package. An alternative explanation is that females, for some reason, evolve to be more impressed by the package itself than what it contains. Thus, males are free to devalue the gift (sucking out the juices) or just give an empty package. In addition, it also appears that when at least some of these flies shift from an insect to a nectar diet they are still "stuck" with the ancestral gift-giving tradition. Again, the logic seems tight, the scenario seems right. As Cumming (1994) points out, however, these scenarios are drawn from a few species of balloonflies in different genera of the subfamily Empidinae and range from seemingly simple to more complicated behaviors. The subfamily contains more than 1500 species and this popular scenario still needs to be verified using some of the more rigorous phylogenetic tools we discuss below.

Deduced from phylogenetic comparisons

In the above examples, variation in behavior among species was examined and a logical scenario of how such behaviors might have evolved was proposed. A more rigorous approach is to propose such logical scenarios in a phylogenetic context, in the knowledge that phylogeny could eliminate certain explanations of patterns of evolution as being unlikely.

Such an approach was taken in a study of song evolution in fruit flies of the *Drosophila repleta* group of species (Ewing & Miyan 1986). Fruit flies produce low-**frequency** love songs by flapping their wings. The researchers analyzed the courtship songs of 22 species. All the songs had either one of two components, labeled A and B, or both components (Fig. 13.2a). The authors surmised that component A was important in **species recognition** whereas component B evolved under **sexual selection** (see Chapter 11). They used a phylogenetic tree of the species relationships that was derived from an analysis of chromosome variation. They then mapped the songs onto the phylogenetic tree (Fig. 13.2b). The challenge is to derive major patterns of evolutionary changes in the song from this combined dataset of behavior and phylogeny.

Ewing and Miyan proposed that the ancestral call type contained both A and B components. Figure 13.2(c) shows how the substantial variation in song can be explained by a relatively small number of evolutionary changes, including loss of A song in one group, loss of B song in another, and elaboration of the B song in a third. This analysis is similar to those above in that it is based on strong inference, but it does so in a phylogenetic context. Without having an independent hypothesis of phylogenetic relationships, one might have assumed, for example, that the three species with only A-song components (*D. martensis*, *D. repleta*, and *D. limensis*) must be each others' closest relatives. This might have resulted in a quite different interpretation of the pattern of song evolution. Thus unlike some of the previous examples that were based
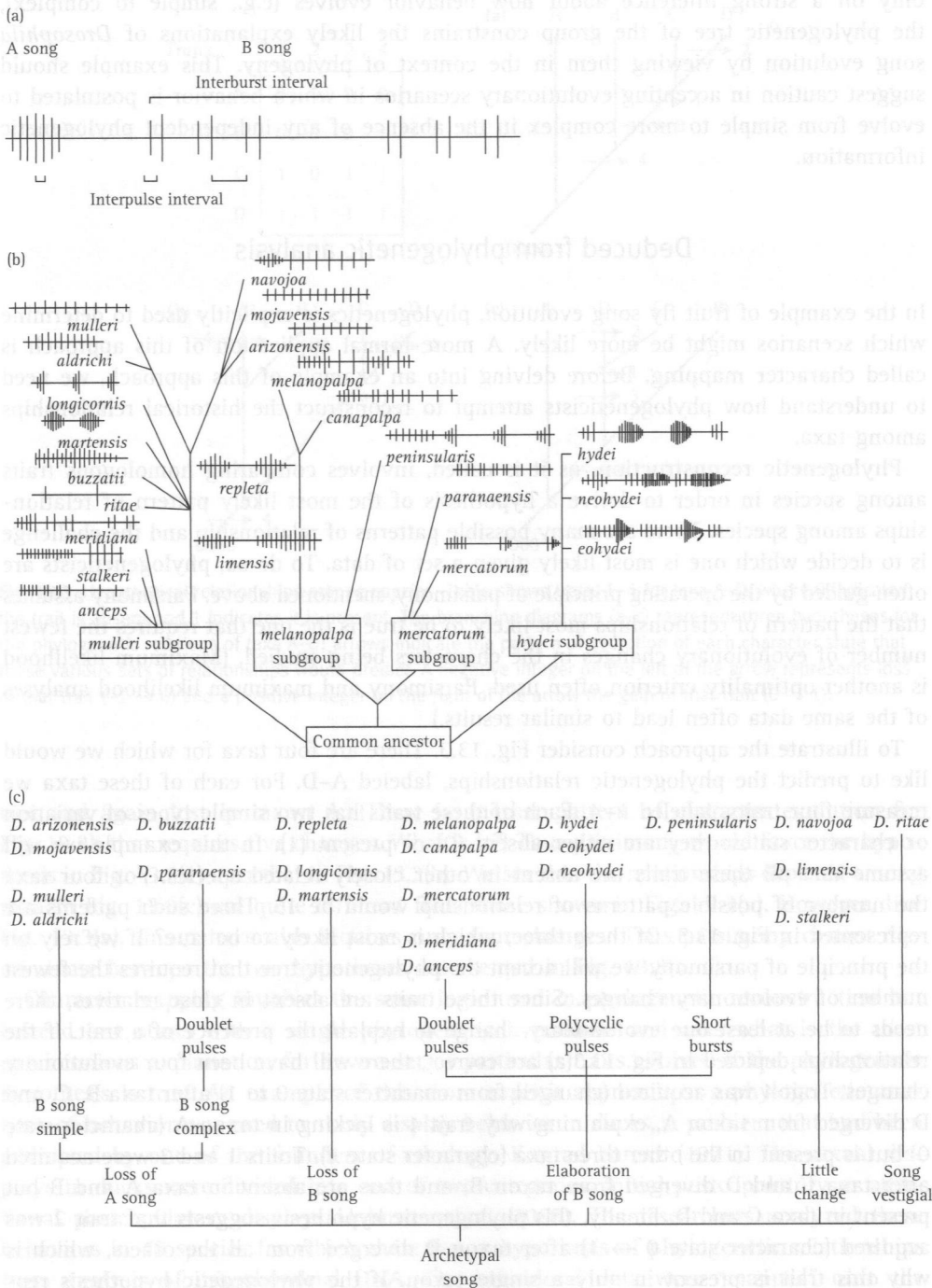
Fig. 13.2 (a) Oscillograms illustrate the A and B song types in the *Drosophila repleta* group. (b) Songs of the different species on a phylogeny of the species group. The phylogenetic relationships were determined from cytological data and not data from songs. (c) Interpretation of song evolution by the researchers. (Redrawn from Ewing & Miyan 1986.)

only on a strong inference about how behavior evolves (e.g., simple to complex), the phylogenetic tree of the group constrains the likely explanations of *Drosophila* song evolution by viewing them in the context of phylogeny. This example should suggest caution in accepting evolutionary scenarios in which behavior is postulated to evolve from simple to more complex in the absence of any independent phylogenetic information.

Deduced from phylogenetic analysis

In the example of fruit fly song evolution, phylogenetics is explicitly used to determine which scenarios might be more likely. A more formal application of this approach is called **character mapping**. Before delving into an example of this approach, we need to understand how phylogeneticists attempt to reconstruct the historical relationships among taxa.

Phylogenetic reconstruction, as it is called, involves comparing homologous traits among species in order to derive a hypothesis of the most likely pattern of relationships among species. There are many possible patterns of relationship and the challenge is to decide which one is most likely given a set of data. To do so, phylogeneticists are often guided by the operating principle of parsimony, mentioned above. Parsimony assumes that the pattern of relationships most likely to be true is the one that requires the fewest number of evolutionary changes in the characters being studied. (Maximum likelihood is another **optimality** criterion often used. Parsimony and maximum likelihood analyses of the same data often lead to similar results.)

To illustrate the approach consider Fig. 13.3. There are four taxa for which we would like to predict the phylogenetic relationships, labeled A–D. For each of these taxa we measure four traits, labeled 1–4. Each of these traits has two simple types of variation or character states: they are either absent (0) or present (1). In this example we will assume that all these traits are absent in other closely related species. For four taxa the number of possible patterns of relationship would be 15. Three such patterns are represented in Fig. 13.3. Of these three, which is most likely to be true? If we rely on the principle of parsimony we will accept the phylogenetic tree that requires the fewest number of evolutionary changes. Since these traits are absent in close relatives, there needs to be at least one evolutionary change to explain the presence of a trait. If the relationships depicted in Fig. 13.3(a) are correct, there will have been four evolutionary changes. Trait 4 was acquired (changed from character state 0 to 1) after taxa B, C, and D diverged from taxon A, explaining why trait 4 is lacking in taxon A (character state 0) but is present in the other three taxa (character state 1). Traits 1 and 3 were acquired after taxa C and D diverged from taxon B, and thus are absent in taxa A and B but present in taxa C and D. Finally, this phylogenetic hypothesis suggests that trait 2 was acquired (character state 0 → 1) after taxon D diverged from all the others, which is why this trait is present in only a single taxon. If the phylogenetic hypothesis represented by the tree in Fig. 13.3(a) were true, then parsimony predicts that there would have been four evolutionary changes in the characters under study. The phylogenetic hypothesis in Fig. 13.3(b) posits five changes, as character 4 is gained at the root of the
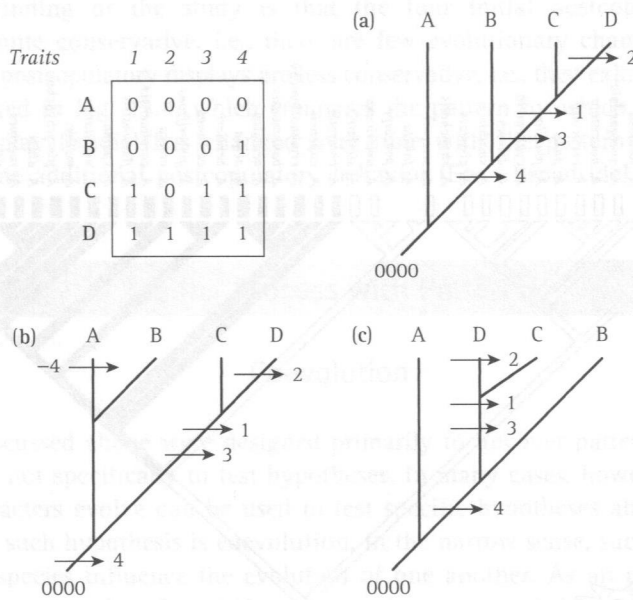
Traits	1	2	3	4
A	0	0	0	0
B	0	0	0	1
C	1	0	1	1
D	1	1	1	1

Fig. 13.3 Hypothetical relationships among species. Table shows traits 1–4 for taxa A–D, where 0 indicates the trait is absent and 1 indicates it is present. The branching diagrams (a–c) represent three hypotheses for the phylogenetic relations of taxa A–D; arrows indicate the pattern of evolution of each character state that these various sets of relationships would predict. A negative integer on the left of the arrow represents loss of that trait (−1 → 0) and a positive integer on the right of the arrow the gain of that trait (0 → 1).

tree and again lost in taxon A. (There is another pattern of character evolution for Fig. 13.3b that requires five changes. What is it?) Thus parsimony would favor the hypothesis in Fig. 13.3(a) over that in Fig. 13.3(b). We see that the relationships depicted among taxa in Fig. 13.3(c) are quite different from those shown in Fig. 13.3(a). However, like Fig. 13.3(a), this pattern also requires only four changes. Thus parsimony cannot discriminate between the two hypotheses represented in Fig. 13.3(a, c).

Character mapping involves the same logic used in phylogenetic reconstruction but instead one starts with a single phylogenetic hypothesis and asks what is the most parsimonious explanation for how a set of particular traits evolved if the phylogenetic hypothesis is true. An example of this more explicit approach to a phylogenetic analysis of behavior was used to study display behavior in ducks, a problem that had been addressed by one of the founders of ethology, Konrad Lorenz (1971). The sexual displays in ducks were divided into one of two categories, initial postcopulatory or additional postcopulatory displays (Johnson et al. 2000). The researchers analyzed these behaviors in 48 species for which there was a hypothesis of phylogenetic relationships from analysis of mitochondrial DNA. The behavioral data were "mapped" onto the phylogeny. What this means is that the character states of the displays (present/absent in this study) were assigned to the species. Given that information, the researchers mapped onto the phylogeny when evolutionary changes for each character took place.
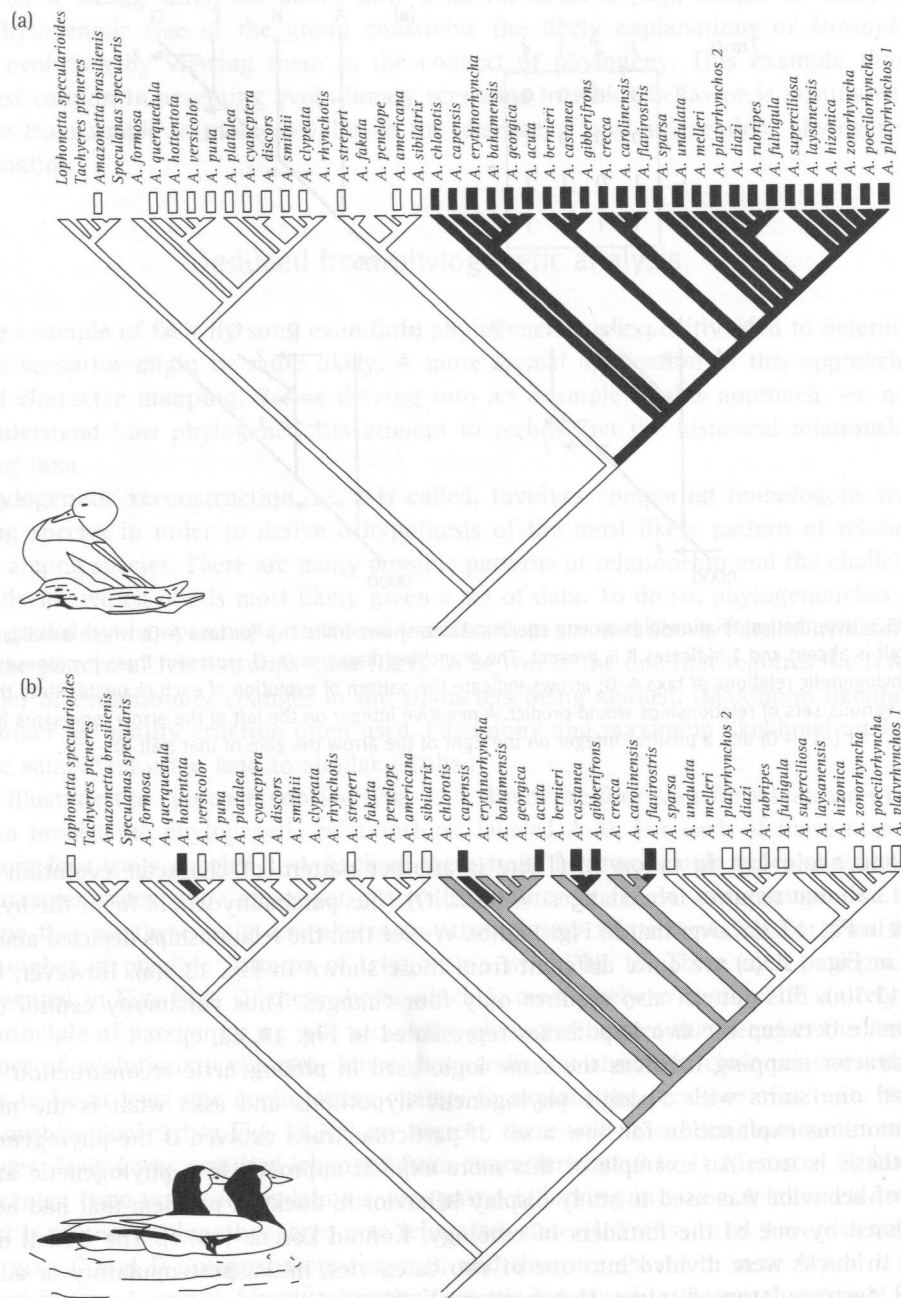
Fig. 13.4 Duck displays. (a) Bridle display of the mallard *Anas platyrhynchos* and depiction of a hypothesis of its evolution. (b) Erect broadside display of the Chiloe wigeon *Anas sibilatrix* and depiction of a hypothesis of its evolution. Open branches indicate the display is absent, closed branches that it is present, and gray branches that assigning the state is equivocal. (Modified from Johnson et al. 2000.)

A general finding of the study is that the four initial postcopulatory displays analyzed are quite conservative, i.e., there are few evolutionary changes, whereas the four additional postcopulatory displays are less conservative, i.e., they exhibit more changes. This is illustrated in Fig. 13.4, which compares the pattern by which one initial post-copulatory display (Bridle) has changed over time with the pattern deduced for the evolution of one additional postcopulatory behavior (Erect Broadside).

Testing Process with Patterns

Coevolution

The studies discussed above were designed primarily to uncover patterns of behavioral evolution, and not specifically to test hypotheses. In many cases, however, the patterns by which characters evolve can be used to test specific hypotheses about evolutionary processes. One such hypothesis is **coevolution**. In the narrow sense, such studies address how multiple species influence the evolution of one another. As an analogy, consider the "coevolutionary" cycles of pesticide resistance by insects and the use of new pesticides in agriculture, and the evolution of drug resistance by bacteria and the development of new antibiotics by pharmaceutical companies (Bull & Wichman 2001). These examples are not true cases of coevolution in the Darwinian sense, as new pesticides and anti-biotics do not evolve but are produced by humans. Furthermore, in these cases, the coevolutionary cycle is sometimes easy to document as there are human records of the new innovations in pesticides and antibiotics. So how does one test the hypothesis of coevolution between species in the wild?

A particular type of coevolution that has seen widespread interest is that of **cospecia-tion**. This phenomenon has often been suggested as an explanation of the patterns of herbivore diet specialization and plant defense one sees in the wild. Ehrlich and Raven (1964) postulated the following scenario:

1 the diet of an insect is determined by chemical plant defenses known as secondary compounds;

2 selection generated by an insect feeding on a plant will cause the species of plant to evolve new defenses;

3 the evolution of an especially effective innovation in defense will allow the plant lineage to diversify in the newly found herbivore-free "adaptive zone";

4 insect species specializing on other plants will eventually adapt to the defenses of the newly radiating plant species, which will result in the diversification of the insect taxa.

Futuyma and Mitter (1996) compared the phylogenetic relationships of several species of leaf beetles (*Ophraella*) to that of its host plants to test the hypothesis of cospecia-tion. As Fig. 13.5 shows, there is little evidence in this system for cospeciation. Instead, it is argued that when insects change the plant species on which they feed they are
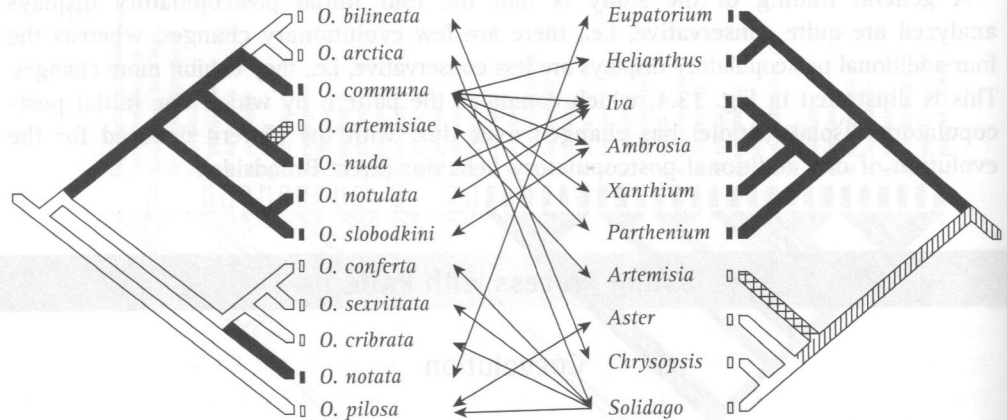
Fig. 13.5 Phylogenies of the leaf beetle genus *Ophraella* (left) and its host plants (right). The lines indicate the host plants used by each species. The shading on the beetle phylogeny illustrates when host shifts took place.

likely to change to a closely related species, as opposed to the scenario of cospeciation proposed by Ehrlich and Raven.

A convincing case of cospeciation is provided by studies of figs and the wasps that pollinate them. In general, each species of fig is pollinated by a single species of wasp, and each fig-pollinating wasp will pollinate only that species of fig. This is one of the most extreme cases of obligate pollination known. A female wasp will enter a fig, which has its flowers enclosed within the fruit. The female will pollinate some of the flowers, lay eggs in others, and then die inside the fig. After her offspring hatch, the male and female offspring mate, the females gather pollen from some of the flowers and then leave to find another fig in which they can oviposit, die, and thus continue the life cycle (Machacado et al. 2001). A detailed phylogenetic analysis of the relationships of figs and wasps shows that there are 20 genera of fig-pollinating wasps and, with a few exceptions, each wasp genus is restricted to pollinating the same fig subgenus, as predicted by the hypothesis of cospeciation.

Sexual selection and sensory exploitation

In a broader sense, coevolution can also encompass patterns of character evolution within a species lineage. This is expected to be important when the function of one aspect of the phenotype depends on other aspects of the phenotype. Since much of the phenotype appears to be a larger integrated unit rather than a series of unrelated modules, we might expect coevolution within lineages to be critical. A prominent example might occur in communication systems associated with reproduction.

In many sexually reproducing species, males produce advertisement signals specific to the species; females are attracted preferentially to males producing the conspecific signal in contrast to males producing signals of other species. The evolution of such

mate-recognition systems is a critical part of the **speciation** process. In one simple scenario of how speciation comes about, it is supposed that the range of an ancestral species becomes split by a geographic barrier, resulting in two isolated populations. Reproductive interactions are constrained to individuals on either side of the barrier. These populations become different in various aspects of their phenotype, including the mate-recognition system, due to random genetic drift or local adaptation. Eventually the populations differ to a degree that they no longer recognize their former conspecifics as appropriate mates. Speciation has occurred (Mayr 1942).

During the process of speciation there is often evolution of a new communication system that recognizes mates. For this to happen, it is thought, there must be a change not only in the signal used by males but also in females' perception of that signal. Many studies have shown that various aspects of the **receivers'** neural systems are tuned or biased to properties of the species-specific signal, whether it be in the auditory, visual, chemosensory, or electrical modality (see also Chapter 2).

Sexual selection is responsible for the evolution of exaggerated male, and sometimes female, traits that enhance an individual's ability to acquire mates even if the exaggerated traits reduce survivorship. Sometimes the exaggerated traits give the bearer tools that are used in combat, but in many cases the elaboration involves signals that males use to attract females (see Chapter 11). Although sexual selection can be important in driving evolution of traits used in species recognition (Lande 1982; West Eberhard 1983), much of the interest in sexual selection is in trying to explain the evolution of exaggerated traits within a lineage.

A central focus in the study of sexual selection is understanding why females would prefer males with traits that reduce survivorship, especially in mating systems in which males offer no resources to females but their sperm. Two hypotheses have received most of the attention: the "**good genes**" theory and Fisher's theory of **runaway sexual selection** (see Chapter 11). Both hypotheses posit that the variation in the genes underlying the male trait and the female preference become correlated, and that evolution of the male trait in response to female preference generates correlated evolution of the preference itself. Thus tight coevolution of the trait and preference should be apparent. A third hypothesis is **sensory exploitation**. This hypothesis states that females will have general sensory or perceptual biases, as detailed by the more general theory of sensory drive, and that males who evolve traits that exploit these biases will be favored by sexual selection.

The two hypotheses of coevolution can be distinguished from that of sensory exploitation if one can reconstruct the evolution of sexually selected traits and female preferences for those traits. If the trait is restricted to one lineage but the preference for that trait encompasses not only the lineage with the trait but others without it, then the most logical interpretation is that the preference existed prior to the trait. However, if the preference is restricted to the lineage in which the trait is present, then the coevolution hypotheses are more tenable.

This approach to sexual selection was initially taken in two groups of animals, swordtail fishes (*Xiphophorus helleri*; Basolo 1990) and túngara frogs (*Physalaemus pustulosus*; Ryan et al. 1990; Ryan & Rand 1993). Female swordtails prefer males with longer swords, an elaboration of the bottom rays of the caudal fin. At the time of the
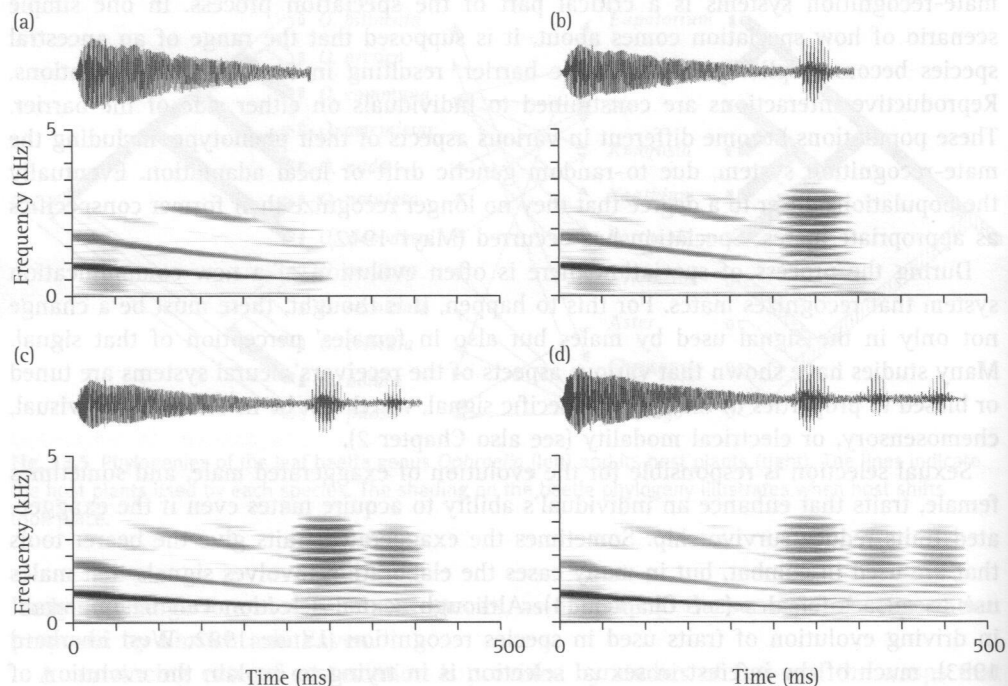
Fig. 13.6 Example of the call complexity series of the túngara frog *Physalaemus pustulosus*. Each diagram shows a waveform (top) and a spectrogram (bottom). (a) Whine with no chucks; (b) whine with one chuck; (c) whine with two chucks; (d) whine with three chucks.

experiments, swordtails were thought to be a **monophyletic** group consisting of two smaller groups, northern swordtails and southern swordtails. A third group, the platy-fish, is a monophyletic group belonging to the same genus. Male platyfish lack swords, but Basolo showed that if she appended a plastic sword to a male platyfish his own females found him more attractive. Later, there was some debate as to the origin of the sword within *Xiphophorus*, and whether southern swordtails and platyfish were indeed separate groups (Meyer et al. 1994). Although the phylogeny of these fish is not fully resolved, Basolo's interpretation of sensory exploitation seems to hold, as she repeated the experiments with another fish, *Priapella olmacae*. This fish is in a genus closely related to *Xiphophorus* but which, like platyfish, has swordless males. And like platy-fish, they have females that prefer swords (Basolo 1995).

A similar result was found in a very different mating system that relies on acoustic rather than visual cues. Male túngara frogs produce a call consisting of a whine and a number of chucks (zero to six) (Fig. 13.6). Females prefer males with chucks, and particularly the larger males that make lower frequency chucks. Except for its sister species *P. petersi*, all other known *Physalaemus* species (> 30) lack chucks, so the chuck seems to have been derived from the ancestor of these two species. Females of a closely related species, *P. coloradorum*, prefer the whines of their own species; however, when a túngara-frog chuck is appended to the normal call of a *P. coloradorum* male, females

prefer this more than the normal chuckless whines. Thus it appears that among some *Physalaemus* species there is a preexisting bias for chucks and male túngara frogs evolved chucks to exploit that bias (Ryan & Rand 1993). There is also a more subtle exploitation occurring. The relationship between the tuning of one of the frog's two inner-ear organs and the frequencies in the chuck results in female túngara frogs preferring the lower frequency chucks of larger males. However, other species of *Physalaemus* in the same species group all have similar tuning properties (Ryan et al. 1990; Wilczynski et al. 2001). Thus it seems that the properties of the chuck evolved to match what is a very conservative feature of this animal's neurobiology.

Correlations of variables with independent contrasts

Hypotheses about how behavior evolves are often tested using a comparative approach by determining if two variables are correlated as would be predicted by independent convergent evolution of traits. For example, as we saw in Chapter 12 and especially Fig. 12.5, males should have larger testes in more promiscuous mating systems, primates that eat fruit should have larger brains than those that eat leaves, and birds that are more susceptible to parasites should have brighter plumage than birds that reside in parasite-free zones. The two variables for a number of species are compared to determine if these variables exhibit the predicted correlation. If so, the hypothesis is supported; if not, it is rejected.

Using the species as the unit of comparison implies that the relationship between the variables in question evolved independently in each species, as if the species had no evolutionary connection to each other. But this may not be the case. Consider one of the predictions just mentioned: males should have larger testes in more promiscuous mating systems, a prediction from sperm competition theory (see Chapter 12 and Fig. 12.5). For example, assume that we have data on testis size and mating system of a group of primates. The variation in the mating system is quantified as the number of males per group. The more males in a group, the greater the possibility of sperm competition due to females mating multiple times. Assume that when we examine these two variables there is a strong correlation: males of species with more promiscuous mating systems have larger testes. These data would seem to support the sperm competition hypothesis. However, such an interpretation depends not on the number of species that have the predicted relationship between testis size and mating system, but the number of times this relationship evolved.

Assume that the mating system of the common ancestor was monogamous (one male per group) and that the males had small testes. This common ancestor then gave rise to a large number of descendant species, and in each species independently there was an increase in both testis size and the number of males per group. This pattern would support the sperm competition hypothesis because the two variables have changed in concert a large number of times. Alternatively, assume that the same common ancestor, monogamous with small testes, gave rise to two descendants, one with testes and a mating system like itself and the other with larger testes and a more promiscuous mating system. Each of these two species then gave rise to many descendant species
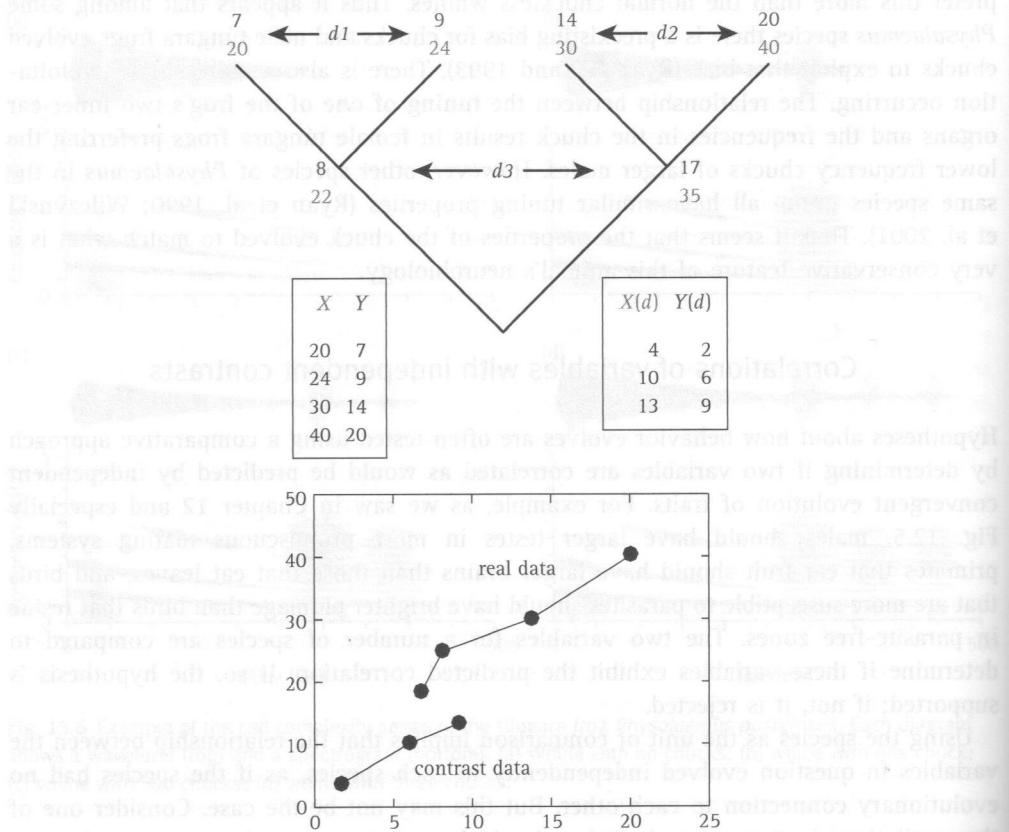
Fig. 13.7 Example of independent contrasts. The distribution of two variables, X (blue) and Y (red), are shown for four extant taxa (tips of the branches). The relationship between these two variables is shown on the graph (real data). The estimates for X and Y for the two ancestors of the four extant species is shown at the two nodes. The three independent contrasts are shown indicated on the tree as d1–d3 and the values listed in the table on the left and the relationships of the contrasts of X to the contrasts of Y are plotted on the graph (contrast data).

but there was no further evolution of testes size or mating system. Although in this scenario there are many species with the predicted relationship between testes size and mating system, there is only one independent evolutionary event, the initial evolution of larger testes and more promiscuous mating system. All the other species exhibit their values of these two variables because they inherited them from a common ancestor rather than by independent evolution.

How can we estimate the degree to which associations between traits within species have evolved independently? A popular method is called **independent contrasts** (Felsenstein 1985), and this approach is illustrated in Fig. 13.7. Again, one must begin with a hypothesis of phylogenetic relationships. Here one is not interested in the actual values of the variables of interest for each species, but in how much these variables have changed between species since they have diverged from a common ancestor. Thus the first step is to estimate the variables of interest for the ancestors or the nodes on

the phylogenetic tree. The second step is to determine the degree to which the two variables differ between sister taxa, be they on the tips or the nodes of the tree. It is these differences or independent contrasts that are tested for the predicted relationships. As Fig. 13.7 indicates, the relationships between the variables of the extant species and their contrasts can be quite different.

There is somewhat of a consensus among behavioral biologists that the comparative approach needs to control for history. Many studies that predated this consensus have been reevaluated. For example, the data first presented by Harcourt et al. (1981) showing the predicted relationship in primates between testis size and mating system did not control for phylogenetic relationship. When this hypothesis was tested with a larger taxonomic range of species with appropriate phylogenetic controls, the data still supported the sperm competition hypothesis (Harvey & May 1989). Alternatively, Hamilton and Zuk (1982) predicted that species of birds that were more exposed to parasites would have brighter plumage, and a comparison of species without considering phylogeny supported this hypothesis. This support, however, withered when the data were reanalyzed with the appropriate phylogenetic corrections (Read & Harvey 1989).

Brain, Behavior, and Evolution

When selection favors the evolution of traits needed to face environmental challenges, such as survival in harsh temperatures, there could be the evolution of an optimal solution that would be stable over time. For example, animals in arctic climes might evolve an optimal degree of fat and fur given the various tradeoffs of such an adaptation. As long as the temperature and other aspects of the environment are stable, we would not expect to see further evolution of these traits. In many social situations, however, evolution is best characterized as an arms race in which the traits of organisms drive the evolution one another. A predator evolving more efficient hunting tactics and a prey evolving greater ability to evade those tactics is one example. An arms race can also take place within a species. A signaler might evolve the ability to be deceptive and a receiver the ability to detect such deceptions, even though a single individual can act as both signaler and receiver depending on the social situation (Dawkins & Krebs 1978; see also Chapter 10).

It has long been known that the neural and cognitive mechanisms by which signals are processed by a receiver can lead to the evolution of elaborate or exaggerated signals without concomitant change in the receiver. This is amply illustrated by Tinbergen's notion of the supernormal stimulus, where a stimulus with certain properties exaggerated relative to the normal stimulus elicits a greater response (see Chapter 2). Two examples from the early ethological literature include male sticklebacks in their bright-red nuptial coloration rushing toward a large red postal van driving past their aquarium (Tinbergen 1952), and oystercatchers preferentially retrieving a large model of an egg in preference to the smaller real egg that has been removed from their nests (Tinbergen 1951). There are other types of stimulus–response patterns that suggest that internal biases of animals can drive evolution in certain directions.

In a more artificial setting, pigeons exhibit a well-known psychological phenomenon called **peak shift displacement**. In such an experiment a bird receives positive **reinforcement** to one wavelength of light, say 550 nm, and negative reinforcement to another, say 555 nm: if it pecks the keys in its box in the presence of one wavelength, it is rewarded with food; if it does so in response to the other wavelength, the lights in the box are turned off. After **conditioning**, the strength of the pigeons' responses are measured across a variety of wavelengths. One might predict that the most vigorous key-pecking would be to 550 nm, the wavelength at which the bird was rewarded. But no, the peak of responsiveness is shifted away from that wavelength to one more different than the wavelength associated with the negative reward, i.e., to wavelengths less than 550 nm (Staddon 1975).

Humans show similar directional biases in how they recognize faces. Enquist and Arak (1998) reviewed experiments by Brennan (1985) in which subjects were given several line drawings of faces. One was a "prototypical" face derived from an average of a large number of faces. One was a realistic drawing of the face of former US president Ronald Reagan, and another a caricature of Reagan. The caricature, almost by definition, exaggerated the traits of Reagan that made it distinctive from the face of others in general and from the prototypical face specifically. When asked to choose the true rendition of Reagan, most subjects chose the caricature rather than the more accurate rendition of Reagan.

Enquist and Arak (1993) showed how these perceptual biases can even be instantiated in some artificial intelligence systems known as artificial neural networks. These networks are arrays of computational units that respond to digital inputs of stimuli, such as visual patterns. These networks can be trained with an evolutionary **algorithm** to recognize patterns. To do so, a large number of networks are constructed, they are all given the same target stimuli, there is selection in which the networks that respond best to some criterion are chosen to be represented in the next generation, and some of these networks are mutated by changing details of the algorithms that govern their response. This procedure is conducted until the networks achieve the specified recognition criterion. In their experiments Enquist and Arak selected networks to respond positively to a cross in which one of the arms was longer than all the others, and to respond negatively to a cross in which all of the arms were of equal length. Once the networks evolved the ability to make such a discrimination, they were tested with novel stimuli. Although most novel stimuli elicited a smaller response than the positive-training stimulus, some novel stimuli elicited an even greater response. In the language of ethology, these seemed to be supernormal stimuli. In the language of some animal communication workers, these were stimuli that exploited the response biases of the receivers.

In all the above examples (sticklebacks, oystercatchers, pigeons, humans, and artificial intelligence), recognition decisions have directional biases. We assume that those biases would generate selection for certain signal traits if they were to evolve. This might be the explanation for some, although certainly not all, of the examples of sensory exploitation that have been offered.

In the above examples, the animal's brain influences the evolution of signals it needs to process. But the alternative could be true. It could be that the problems a brain needed to solve in the past might influence how it solves current problems. A good analogy is

Luchin's (1942) water jug problem. Subjects were given a large jug of water and measuring cups of three sizes: 3, 23, and 49 ounces (1 ounce is equivalent to ~ 29 mL). They were asked to remove a given volume. One group was trained on a simple problem that could be solved in two steps. They were told to measure 20 ounces of water. Most subjects filled the 23-ounce cup to the brim and then used the other cup to remove 3 ounces. A second group was given a problem that could be solved with a minimum of three steps. They were given cups of 3, 21, and 127 ounces and asked to measure out 100 ounces. They filled the 127-ounce cup and emptied it once with the 21-ounce cup and twice with the 3-ounce cup. This second group was then asked to solve the two-step 20-ounce problem. Instead of solving it in two steps (see above), they solved it in three steps: they filled the 49-ounce cup and emptied it once with the 23-ounce cup and twice with the 3-ounce cup. Their solution was no less correct than that of the group initially trained with the simpler problem, but it was different and it was more complex. And, more importantly, their previous experience influenced their solution.

There appears to be an evolutionary analog to the water jug experiment in that the evolutionary history of the brain influences which solutions the brain will use to achieve various functions. Or at least that is what is suggested by some studies of túngara frogs. We mentioned above that these frogs produce whines for species recognition and that some species add chucks to make the call more attractive. The female preference for chucks did not coevolve with the chucks, but appears to be a preexisting bias that was exploited by males that evolved chucks. On the other hand, it appears that the details of the whines that needed to be recognized by ancestors influenced how túngara frogs decode this species-specific character.

Ryan and Rand (1995, 1999) used the independent contrast approach to estimate calls at ancestral nodes of the phylogenetic tree of the *Physalaemus pustulosus* species group. They determined the probability that females would approach a speaker broadcasting a heterospecific call, but these calls could be of extant species or the estimated calls of ancestors. They then asked if the phylogenetic relatedness between the túngara frog and the heterospecific/ancestor would predict any of the variation in the female's behavior independent of the overall acoustic similarity between the túngara frog call and the target call. The answer was yes; phylogenetic relatedness, or more generally, history, explains a substantial proportion of variation in female responses. It seems that indeed "evolution leaves a footprint on the frog's brain." This conclusion was critically borne out by Phelps and Ryan (2000) using artificial neural network simulations. These networks were used to simulate brain evolution. A population of networks was trained to recognize calls at the root of the phylogenetic tree using an evolutionary algorithm somewhat similar to the one described by Enquist and Arak. Once the networks recognized this call, they were trained to recognize the immediate ancestor of this call on the direct path of descent to the túngara frog. This continued until the networks reached the end of the path, the túngara frog itself, and were selected to recognize the túngara frog call. The same procedure was conducted in which the history of the neural networks was randomized. In these cases, the networks were trained with three calls chosen at random before finally being trained to recognize the túngara frog call. After the networks evolved to recognize the túngara frog call, their ability to predict the behavior of real females was measured. This was done by testing real frogs and the networks

with all the heterospecific and ancestral calls and computing the correlation between the response strength of females and networks. Only the networks with the real histories significantly predicted the response of the real frogs. Even though past history does not constrain the ability to evolve the adaptation of species recognition, it does influence how the artificial networks, and presumably the frogs, go about doing it.

SUMMARY AND CONCLUSIONS

Tinbergen considered understanding the past evolutionary history of behavior as one of the four major aims of ethology. We have seen that in some cases sufficient knowledge of the animal's natural history can suggest how behavioral adaptations have come about. However, arguments based only on strong logical inference, especially when making a priori assumptions about how behaviors should evolve (e.g., from simple to complex), might be more prone to error than arguments that are framed in the context of the animal's phylogenetic relationships. Furthermore, it is becoming clear that knowledge of the mechanisms underlying behavior, what Tinbergen called causation, is also critical since such mechanisms can bias the direction of evolution. Although we have concentrated on the evolution of behavior, a deep understanding of behavior must involve all Tinbergen's four questions.

FURTHER READING

Lorenz (1967) provides some instructive examples of how the early ethologist explored patterns of evolution of homologous behavior, whereas Greene (1994) offers a more recent as well as insightful synopsis of the general issue of establishing behavioral homology. Felsenstein's (1985) independent contrast method was critical for promoting the use of phylogenetic data to test hypotheses of adaptation. Thornton et al. (2003) use phylogenetic information to reconstruct ancestral characters of hormone receptors and test the functionality of the ancestral receptor. Finally, Autumn et al. (2002) argue that incorporating information about phylogenetics is critical to understanding the evolution of complex phenotypes.

ACKNOWLEDGMENTS