Andrea Megela Simmons
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Richard R. Fay
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With 55 Illustrations

Acoustic Communication

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5
Selection on Long-Distance Acoustic Signals

MICHAEL J. RYAN AND NICOLE M. KIME

1. Introduction

The purpose of this chapter is to discuss the evolution of long-distance acoustic signals through the atmosphere (Bass and Clark, Chapter 2, address problems in underwater communication). We are especially interested in signals that are used in mate recognition. In most cases, these signals are produced by males to attract potential mates and repel male competitors, and they are evaluated by females when they make a mating decision. Although there are cases of females attracting males and males choosing females, we will tend to concentrate on the more typical case.

1.1. Long-Distance Signals, Selection, and Evolution

Sounds that have evolved to attract mates over relatively long distances are common throughout diverse taxa. These signals are often subject to strong natural selection imposed by the environment and by unintended receivers, such as predators and parasitoids, as well as sexual selection imposed by intended receivers, such as potential mates and competitors for those mates. The importance of these signals in reproduction implicates them in two processes central to evolutionary biology—speciation and sexual selection. These are the processes primarily responsible for increasing biodiversity through multiplying and diversifying species.

Long-distance communication signals occur in many taxa, such as mammals and fish, but are especially prevalent and well-studied in insects, frogs, and birds. Within each of these taxa, long-distance signals are better-studied than acoustic signals used in other contexts (see taxon-specific reviews cited below). There are several taxon-specific reviews of various aspects of long-distance communication (e.g., insects: Ewing 1989; Michelson 1998; frogs: Fritzsch et al 1988; Gerhardt 1994; Zelick et al. 1998; Ryan 2001; birds: Kroodsma and Miller 1982, 1996; Catchpole and Slater 1995) as well as reviews in more general texts on animal communication (Hauser 1996; Bradbury and Vehrencamp 1998; Owens and Morton

1998). In this chapter, we offer a general survey of various factors that influence the evolution of long-distance signals.

The focus by researchers on long-distance signals is due in part to the conspicuousness of these signals. Except for those secluded in the most urban and sterile environments, most of us have probably heard a dawn chorus of birds, the evening chirping of crickets, and the nocturnal serenading of frogs. In all of these cases, the sounds we hear are not merely random fluctuations in ambient pressure derived from some inconsequential movement of an animal's body parts, as if one happened to step in a puddle and caused a complicated and intricate but rather meaningless pattern of waves and troughs on the water's surface. These sounds are acoustic signals. Thus, by definition, they have evolved under selection to serve a communication purpose.

The purpose of long-distance signals, defined by Littlejohn (2001) as signals that function over a distance of more than several body lengths from the receiver, is to advertise the presence of the sender to a receiver. In many of the cases we consider, the sender is a male who is advertising his presence in a context linked in some way to reproduction, usually to receivers that are potential mates or potential competitors. The evolution of long-distance acoustic signals involves the modification of the animal's morphology and physiology to couple a mechanical displacement to pressure fluctuations in the external environment; the production of these signals sometimes stresses the physical and energetic limitations imposed on bioacoustic production. Furthermore, not all pressure fluctuations will be favored by selection. They must have the temporal and spectral properties that allow them to transmit over a functional distance; that is, to encounter the intended receiver. Nor is efficient transmission through the environment the sole criterion of selection. The signal must interact effectively with the receiver. At a minimum, it must be detected. Thus, the sounds are also constrained to function within temporal and spectral limitations relative to the intended receiver. But this pattern of pressure fluctuations emanating from the sender must have meaning; thus, it is also constrained by the higher-order neural processing and cognitive abilities of the intended receiver, and to complicate matters, evolution of these long-distance communication systems is not one-sided. Whether viewed as an intricate evolutionary dance or an arms race, the properties of the signal and receiver have the potential to influence each other's evolution—thus, the signals and receivers evolve but the communication system coevolves.

Only when all of these criteria are met do we have communication, and when we do, it is an amazing phenomenon. As Pinker (1994) eloquently stated for human language: "Simply by making noises with our mouths, we can reliably cause precise new combinations of ideas to arise in each other's minds. The ability comes so naturally that we are apt to forget what a miracle it is" (p. 15).

2. Morphological and Energetic Constraints

A number of different selective forces can act on any one morphological or behavioral trait, including long-distance communication signals (e.g., Wilczynski and Ryan 1999). These forces may act in unison or in opposition to one another. In addition, a trait may be restricted in its ability to evolve in response to selection either because of the constraints of physical laws. Consequently, the traits that we see are not always at a selective optimum with respect to one fitness component but instead reflect a compromise between a number of different selective forces and constraints.

The physical structures used for sound production play a large role in determining both the temporal and spectral characteristics of acoustic signals. Although these structures can certainly evolve in response to the various selective forces acting on long-distance communication signals, phylogenetic or physical constraints on their morphology can also impose limitations on the form of signals. In this section, we discuss how two such limiting factors, the low energetic efficiency of sound production and the body size of the sender, constrain the signals used for long-distance communication.

2.1. The Energetics of Signal Production

2.1.1. Energetics and Efficiency

One important element of natural selection is the energetic cost of an otherwise advantageous trait. The cost associated with the energy required to perform a display or behavior can outweigh the benefit of the trait, especially when it depletes resources necessary for basic maintenance or other activities. The energetic cost of acoustic signaling can be estimated in a number of ways, the best of which is probably the rate of oxygen consumption ($\dot{V}_{O_2}$) during a bout of calling. This measure is most easily procured for animals such as insects and frogs, which will call in a respirometer (MacNally and Young 1981; Ryan 1988). Less reliable methods must usually be applied to studies of birds and mammals (e.g., Brackenbury 1979; but see Eberhard 1994); for this reason, the most well-known studies of calling energetics have focused on anurans and insects.

These studies have repeatedly shown that acoustic signals are extremely costly to produce. The rate of oxygen consumption during calling can be 5–30 times that during rest (Stevens and Josephson 1977; MacNally and Young 1981; Prestwich and Walker 1981; Bucher et al. 1982; Taigen and Wells 1985; Taigen et al. 1985; Ryan 1988; Prestwich et al. 1989). Indeed, most studies on insects and frogs demonstrate that calling to attract mates is one of the most energetically expensive activities in which males engage

(Taigen and Wells 1985; Ryan 1988). For example, the energetic cost of advertisement calling for the gray tree frog, as measured by the rate of oxygen consumption, can be as high or higher than the amount of energy expended during forced locomotor activity, a measure commonly referred to as "$\dot{V}_{O_2}$ max" (Fig. 5.1; Taigen and Wells 1985).

One reason that these mating signals are so costly is that they are extremely inefficient to produce. The production efficiency of an acoustic signal is simply the amount of energy in the emitted sound relative to the energetic cost of its production. In most of the animals studied to date, the energetic efficiency of sound production is much less than 10% (Table 5.1 and references therein). Two factors are implicated in this low efficiency—the loss of energy as heat by the muscles used in sound production and the inefficiency of coupling acoustic energy from sound-production structures to the environment (Bradbury and Vehrenkamp 1998).

In animals that use internal sound-production structures (e.g., most birds, frogs, and mammals), the volume of air inside the vocal pathway is much smaller than the volume of air outside in the external environment. As a result, most of the sound energy that reaches the end of the vocal pathway is reflected at the boundary of the tube and will not be transmitted to the receiver.

One way to counteract this low efficiency is by the addition of radiating structures that decrease the acoustic impedance mismatch between the organism and its environment. The vocal sacs of male frogs and some pri-
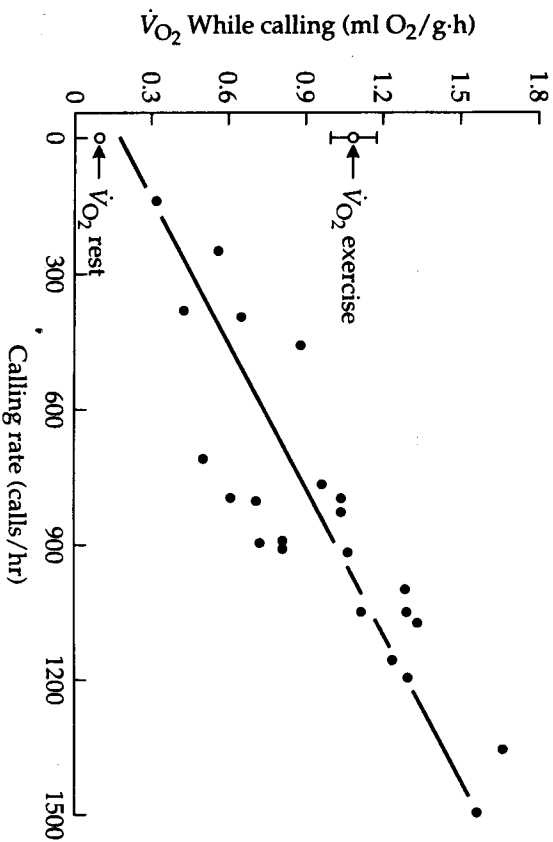

FIGURE 5.1. Rate of oxygen consumption during calling, rest, and forced locomotor activity in the gray tree frog. (From Taigen and Wells 1985.)

TABLE 5.1. Estimated efficiencies of acoustic signal production.

Species	Efficiency (%)	Reference
Insects		
Achroia grisella	0.008	Reinhold et al. 1998
Anurogryllus arboreus	0.09	Prestwich 1998
Cystosoma saundersii	0.82	MacNally and Young 1981
Gryllotalpa australis	1.05	Kavanagh 1987
Telogryllus commodus	0.5	Kavanagh 1987
Frogs		
Hyla cinerea	1.89	Prestwich et al. 1989
H. crucifer	4.9	Prestwich et al. 1989. Data from Taigen et al. 1985; Taigen unpublished
H. gratiosa	0.76	Prestwich et al. 1989
H. squirella	2.21	Prestwich et al. 1989
H. versicolor	3.6	Prestwich et al. 1989. Data from Taigen and Wells 1985; Wells and Taigen 1986
Physalaemus pustulosus	0.5–1.2	Ryan 1985
Domestic chicken, Gallus domesticus	1.6	Brackenbury 1977
Human	~1%	Wood 1962

2.1.2. Constraints on Signal Evolution

The high cost and low efficiency of calling can constrain the evolution of acoustic signals. Increasing either the length of individual calls or the rate at which calls are produced results in increased energy expenditures (Fig. 5.1; Taigen and Wells 1985; Prestwich et al. 1989; Wells and Taigen 1989). Call rates or lengths may thus be limited by an upper asymptote of energy availability. Furthermore, in some species, these two aspects of calling may be involved in an energetic trade-off. In gray tree frogs, males respond to the calls of other males by increasing call length, but they maintain calling

mates are examples of such radiators (Martin 1972; Schön-Ybarra 1988; Rand and Dudley 1993; Fitch and Hauser, Chapter 3). The sound frequencies that can be efficiently coupled to the environment via a radiator depend on its size—larger radiators allow lower dominant frequencies to be coupled to the environment with greater efficiency. However, even with such structures, the efficiency of sound production among animals is still very low, probably because the frequencies used for communication are below the effective cutoff frequency for the radiator (Ryan 1985a; Table 5.1). In the frog Physalaemus pustulosus, for example, if the entire male frog were conservatively assumed to radiate the call, its effective cutoff frequency would be 3,500 Hz. Male frogs produce calls that sweep from about 900 to about 400 Hz, far below the limits of maximum radiation efficiency (Ryan 1985b).

- effort at a constant level by decreasing the rate at which these longer calls are produced (Wells and Taigen 1986; Klump and Gerhardt 1987). This trade-off between call rate and length has been taken as evidence that overall calling effort is constrained by the energetic cost of signal production.

Energy limitations may also restrict calling behavior over a longer time scale, such as the amount of time that a male can spend calling over one or several nights. Some studies on the calling behavior of frogs have suggested that energetic demands limit male calling to a certain proportion of nights (Murphy 1994a; Marler and Ryan 1995) or to a restricted period during a given night (Wells and Taigen 1986; but see Murphy 1999). Male frogs usually call on less than 30% of available nights, and most males of species with prolonged breeding seasons appear in chorus only a few times during the season (Bevier 1997). Choruses usually do not last long after midnight, and large proportions of glycogen reserves of the trunk muscles can be depleted after only a few hours of calling (Wells et al. 1995; Bevier 1997).

The relative mating success of male frogs and toads is strongly tied to the number of nights in attendance at a chorus (Murphy 1994b; Wagner and Sullivan 1995). In addition, females often prefer to mate with males who produce longer mating calls or calls produced at faster rates (reviewed in Ryan and Keddy-Hector 1992). Such preferences can extend beyond the normal range of male variation (Gerhardt 1991). The origin for such preferences is unclear—it may be because of inherent sensory biases for greater neural stimulation or because the preference results in matings with males in better condition (Ryan and Keddy-Hector 1992). Whatever the cause of the preference, the response of male calling behavior to sexual selection may be constrained by the energetic cost of calling.

2.2. Body Size and Wavelength

The mass of the sound-producing structure plays a large role in determining the frequency of communication signals; structures with greater mass can produce lower-frequency signals more efficiently. Consequently, in many frogs, birds, and mammals, the frequency of communication signals is correlated with body size (Fig. 5.2). This relationship between body size and signal frequency often holds for comparisons among groups of species (e.g., frogs: Ryan 2001; birds: Morton 1977; Wallschager 1980; Bowman 1983; Ryan and Brenowitz 1985; Wiley 1991; mammals: Fitch and Hauser, Chapter 3). The same relationship holds among individuals within a single species or population for many frogs (e.g., Ryan 1985b; Gerhardt 1994; Howard and Young 1998). But Fitch and Hauser (Chapter 3) suggest that within species of birds and mammals, the expected correlation of body size and sound frequency is not as strong as expected.

One of the most comprehensive and enlightening studies on this subject was conducted by Martin (1972). He dissected various components of the
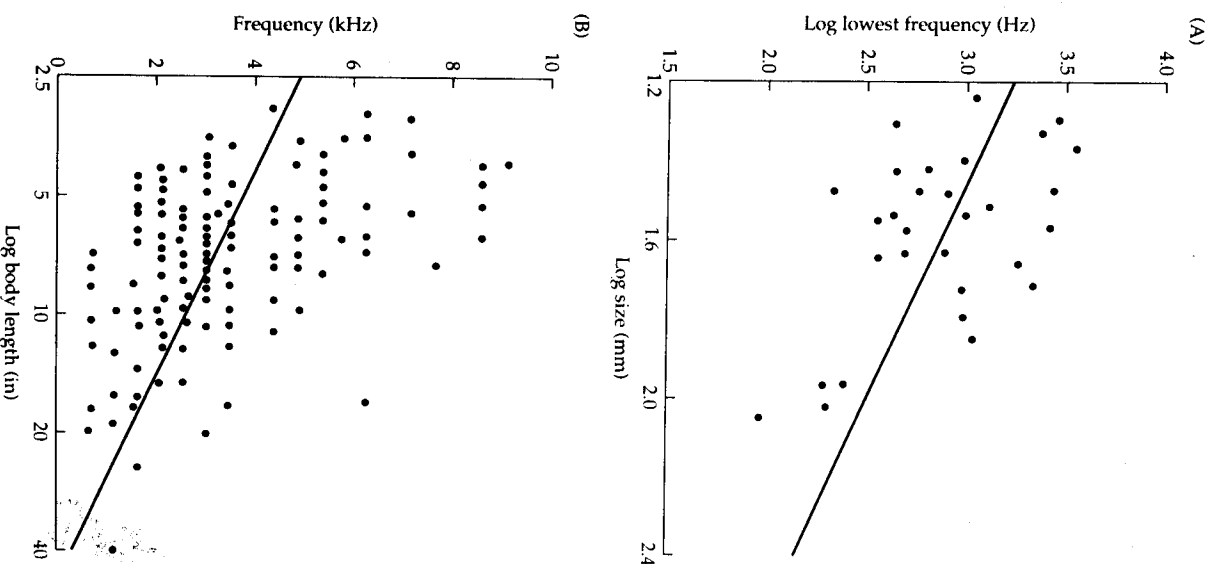
FIGURE 5.2. Relationship between body size and (A) the logarithm of the lowest frequency present in calls produced by leptodactylid frogs and (B) the emphasized song frequency of Panamanian birds. (From Bradbury and Vehrencamp 1998, modified from Ryan 1985; Ryan and Brenowitz 1985.)

toad vocal system, systematically altering them to study their effects on signal production. He showed that larger toads generally have larger vocal cords and that these larger vocal cords produce sounds with lower dominant frequencies. Of course, the relationship between body size and frequency is not perfect—Martin (1972) also showed that adding mass to vocal cords independent of body size can lower the dominant frequency of a call. In addition, call frequency can be changed by changing the tension on the vocal cords—the frequency-modulated calls of many frogs are an example of this process.

The interaction of calling efficiency and body size constrains the dominant frequency of acoustic signals. As the frequency of a signal decreases relative to the body size of the sender, the efficiency of signal production drops (e.g., Section 2.1 of this chapter; Bradbury and Vehrenkamp 1998). Taken together, the constraints of body size and energetic efficiency indicate that small animals should use the more efficiently produced higher frequencies for communication. However, as we will see in the following sections, natural and sexual selection can act on signal structure in ways that oppose this influence of sender morphology.

3. Environmental Constraints

During transmission, acoustic signals must travel through the external environment. Over distance, these signals will be altered in ways that can influence the response of receivers; all signals will eventually become so degraded that potential receivers fail to recognize them altogether. The temporal or spectral structure of signals, however, can influence the amount of change they experience and thus the distance over which they can be used. Selection can therefore act on the form of long-distance communication signals to decrease signal degradation and increase transmission distance. In this section, we will first review some of the basic properties of signal transmission in the atmosphere (see Bass and Clark, Chapter 2, for a discussion of underwater acoustics). We will then examine some of the evidence that long-distance communication signals have evolved in response to selection for increased propagation efficacy.

3.1. Signal Design for Maximum Range

The effects of transmission on acoustic signals have generally been partitioned into two main categories—loss of amplitude and loss of fidelity. Both contribute to the degradation of a signal's influence with distance. Because of spherical spreading alone, signal amplitude will decrease, or attenuate, by 6dB for each doubling of distance, even in an ideal environment. Absorption and scattering of sound waves by the air, ground, and vegetation cause additional, or "excess," attenuation in most natural environments (Wiley and Richards 1978). Attenuation of a long-distance communication

signal can reduce the chances that it will be detected by a receiver either because the amplitude of the received signal falls below the auditory threshold of the receiver or because the signal-to-noise ratio has decreased to a level at which the receiver no longer recognizes the signal.

The temporal and spectral structures of a signal will also be altered as it travels from sender to receiver (Wiley and Richards 1978; Richards and Wiley 1980; Michelsen and Larsen 1983). For example, reverberations from objects in the environment or irregular amplitude fluctuations caused by atmospheric turbulence can contribute to the degradation of a signal's temporal structure. Some frequencies attenuate more rapidly than others do; this "frequency-dependent attenuation" can alter the spectral form and thus the perception of a signal. Over long distances or in harsh environments, such loss of fidelity can render a signal unrecognizable to the receiver.

All sounds experience these changes during transmission, but the amount of change is partially determined by the spectral and temporal structures of the signal itself. Selection can therefore act on the form of a signal to increase the distance over which it can be heard and recognized (Morton 1975; Sorjonen 1986; Wiley 1991; Endler 1992). Endler (1992) described 12 "rules" for the design of communication signals, most of which were concerned with the effects of the environment on sound transmission. We present a modified list of design rules in Table 5.2. Although these guidelines are applicable to many communication signals, they should be especially important for calls that must travel over long distances.

The frequency of a signal has a large effect on its propagation distance. Sound-transmission experiments in various habitats have repeatedly demonstrated that lower-frequency sounds generally experience less attenuation than higher-frequency sounds (e.g., Morton 1975; Marten and Marler 1977; Marten et al. 1977; Waser and Brown 1986). This is because higher-frequency sounds are more susceptible to absorption by objects in

TABLE 5.2. Guidelines for acoustic signal production. (Modified from Endler 1992.)

1. Use frequencies lower than 2kHz in order to minimize reverberation, attenuation, and scattering during transmission.
2. For animals that must call near the ground, use frequencies above 0.5–1kHz to avoid ground attenuation.
3. Use species-specific frequency bands and tuned receptors to minimize interference from other species and abiotic sounds.
4. Use greater-amplitude signals to maximize the signal-to-noise ratio, increase transmission distance, and increase the probability of detection.
5. Use frequency modulation rather than amplitude modulation to encode information. Reverberations and air turbulence alter amplitude more than frequency.
6. Send signals from above the ground to minimize ground attenuation and the effects of vegetation and wind and temperature gradients.
7. Use redundant signals to offset the effects of discontinuous background noise and the effects of reverberations and amplitude fluctuations.
8. Call in locations or during times that minimize turbulence and/or background noise.
9. Use alerting signals to attract the receiver's attention before sending the main signal.

the environment and to disruption by atmospheric turbulence. Near ground level, however, sounds with very low frequencies will also experience increased levels of attenuation because of destructive interference between direct waves and waves reflected from the ground (Wiley and Richards 1978). Thus, near ground level in some environments, a "sound window" of minimal excess attenuation exists for frequencies in the range of about 1–3 kHz (Morton 1975; Marten et al. 1977; Waser and Brown 1986).

The temporal structure of a signal can also influence the amount of degradation it experiences (Richards and Wiley 1980; Ryan and Sullivan 1989; Mathevon et al. 1996). Reverberations and air turbulence can blur amplitude modulation contained within signals, favoring tonal signals over amplitude-modulated signals (Richards and Wiley 1980). The frequency of the signal also influences these effects—sounds between 2 and 8 kHz are less subject to reverberations from the vegetation and ground and are thus favored with respect to the maintenance of temporal fidelity (Wiley and Richards 1978).

3.2. Testing the Acoustic Adaptation Hypothesis

Like signals, all habitats are not equal with respect to signal transmission. Selection on call structure may be stronger, and thus elicit a stronger evolutionary response, in one type of environment versus another (Morton 1975; Ryan et al. 1990). Alternatively, the optimal call structure for long-distance communication can vary among habitats or microhabitats. For example, it has been shown that amplitude-modulated calls are favored for communication in open environments, whereas tonal calls are favored in forested environments (Morton 1975; Sorjonen 1986). Similarly, the presence and shape of the frequency sound window for low excess attenuation appears to differ among environments as well as between different heights within the same environment (Morton 1975; Marten and Marler 1977; Waser and Brown 1986). The frequency window may be present in some locations and absent in others, or the range of frequencies experiencing low excess attenuation may differ among habitats.

Given that different habitats can impose differing selection on the structure of calls used for long-distance communication, one might expect predictable divergence among the signals used by the species living in these habitats. These predictions can be used to test the hypothesis that long-distance communication signals have evolved in response to selection generated by habitat acoustics. Adaptation to the acoustic environment is one possible explanation when the observed trends in call characteristics match the predictions. Following this logic, a number of studies have used comparative methods to test the hypothesis that the signals used for long-distance communication have evolved in response to selection for decreased degradation and increased transmission distance within their home environment.

3.2.1. Community Studies

One of the first and most often cited tests of the acoustic adaptation hypothesis was performed by Eugene Morton, who compared the songs of birds that reside in open and forested habitats in Panama (Morton 1975). Morton first determined the amount of excess attenuation experienced by tones of varying frequency transmitted at different heights within different environments. In all locations, higher frequencies generally experienced greater attenuation than lower frequencies. However, near the ground in forest there was a "sound window" of low excess attenuation between 1,500 and 2,500 Hz. This sound window did not exist at higher heights within forest or in edge and grassland environments. Morton then compared the results of these transmission studies with data on the song frequencies of different species of birds living in these habitats. He found that birds that call in low forest, but not birds that call in grassland or above the ground in forest, have mean call frequencies in the range of the sound window. Morton concluded that the songs of these forest species have evolved in response to selection for decreased attenuation and thus increased transmission distance.

Since Morton's original study, a number of similar comparative studies have been conducted using the calls of birds and anurans. These studies evaluated a number of different aspects of temporal and spectral fidelity in addition to attenuation and frequency-dependent attenuation. Although there is some disparity in the details of the analyses, community-level studies in temperate and tropical birds generally support Morton's findings, at least for some signal characteristics (e.g., Richards and Wiley 1980; Sorjonen 1986), but community-level studies in frogs do not (Zimmerman 1983; Penna and Solis 1996; Kime et al. 2000).

The interpretation of multispecies comparisons such as Morton's can, however, be easily confounded by other determinants of call structure such as phylogenetic relationship or body size. As Ryan and Brenowitz (1985) pointed out, the frequency differences that Morton found in his original study could also be explained by differences in the body size of birds living in the different locations or by differences in the background-noise composition of the different environments. Correcting for body size in temperate birds, Wiley (1991) failed to find differences in dominant frequency among the songs of temperate-zone oscine birds in open and forested environments. For frogs, Zimmerman (1983) showed that the phylogenetic relationships among species in a community of tropical frogs were a better predictor of signal structure than was habitat acoustics.

3.2.2. Studies of Single or Closely Related Species

Some of the more convincing tests of the acoustic adaptation hypothesis compare signal structure among populations of a single species or among closely related species with habitat shifts. At this level, it is often easier to control for the effects of body size and other morphological or

phylogenetic constraints. Confounding variables are thus less problematic for studies of closely related species than for the community-level analyses described above.

The rufous-collared sparrow of Argentina can be found over a large altitudinal range. The song of males has a final trill, which varies in rate over its geographical range (King 1972; Nottebohm 1975). Although the trill rate remains constant over large areas of continuous habitat, it changes significantly with the habitat changes associated with increases in altitude (King 1972; Nottebohm 1975; Handford 1981, 1988; reviewed in Catchpole and Slater 1995; Fig. 5.3). Trill rate is generally higher in open areas and lower in forested areas because there is less scattering to mask patterns of amplitude modulation in the open environment.

In anurans, some evidence for acoustic adaptation becomes apparent when the phylogenetic scale of analysis is reduced from the level of the community to a single species. In the frog *Acris crepitans*, two subspecies
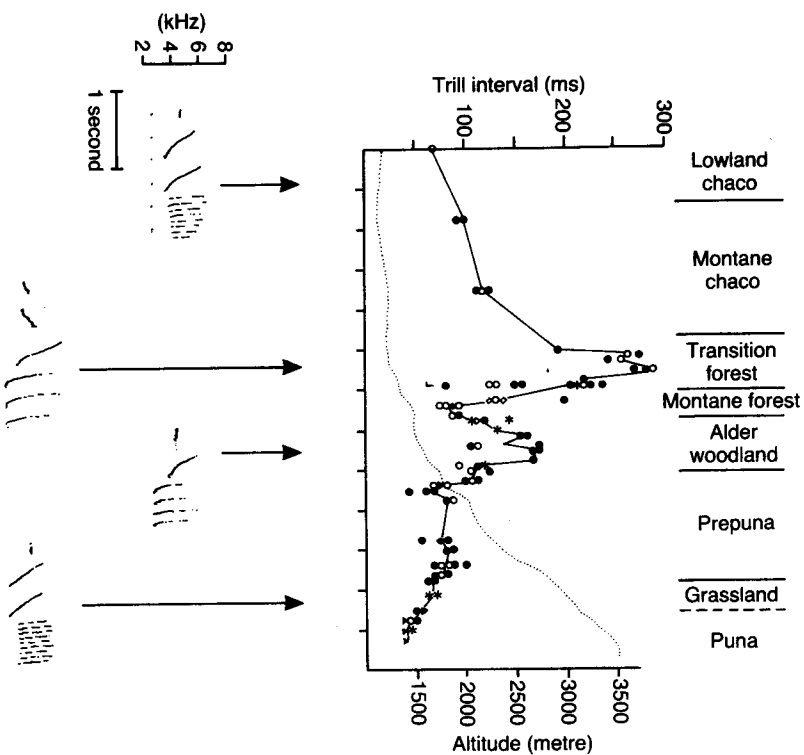

FIGURE 5.3. (Top) Changes in trill interval with vegetation type (noted on the upper *x*-axis) and altitude (dashed line, right *y*-axis) in rufous-collared sparrows. (Bottom) sonograms of song examples from four vegetation types. In each case, the trill is the last portion of the song. (From Catchpole and Slater 1995 after Handford 1988. Reprinted with the permission of Cambridge University Press.)

have slightly different mating calls. One subspecies, *A. c. blanchardi*, lives in open habitats in central Texas. The second subspecies, *A. c. crepitans*, resides in forested habitats to the east. For both subspecies, calls transmitted through an open environment experience less degradation than calls transmitted through forest. However, regardless of the environment, the calls of *A. c. crepitans* are always less subject to degradation than the calls of *A. c. blanchardi*. In addition, the difference in call degradation between the open and forested habitats is less for *A. c. crepitans* than for *A. c. blanchardi* (Ryan et al. 1990). Ryan et al. (1990) suggested that the calls of the forest subspecies, *A. c. crepitans*, have evolved in response to relatively strong selection for transmission efficiency in forest and thus transmit with less degradation in both environments. They further suggested that the calls of *A. c. blanchardi*, which lives in more open habitats, have not been under as strong environmental selection and have instead been more influenced by selection in other contexts.

Another convincing argument in favor of Morton's hypothesis comes from comparisons of short- and long-distance communication signals within species, especially in primates. As we have been discussing, long-distance communication signals should be under strong selection for increased transmission efficacy. But signals used over shorter ranges should not be under as strong selection and in some cases may be selected to degrade rapidly over distance in order to reduce eavesdropping by predators and other unintended receivers (Endler 1992). As predicted, the whoopgobble of mangabeys, a call used for intergroup communication, transmits farther and with less attenuation than calls used for intragroup communication. Three other primate species exhibit similar differences in attenuation between calls used for long- and short-distance communication (Waser and Waser 1977).

3.3. Environmental Selection on Signaling Behavior

For a given signal, both the location from which it is broadcast and the time of day during which it is transmitted can influence the amount of degradation it experiences. In addition to the temporal and spectral properties of acoustic signals, selection can also act on the behavior of the signaler.

3.3.1. Caller Height

Sounds transmitted from above the ground almost always experience less degradation than sounds transmitted near the ground (Marten and Marler 1977; Waser and Waser 1977; Henwood and Fabrick 1979; Brenowitz et al. 1984; Mathevon et al. 1996). Senders of long-distance communication signals can thus increase propagation distance simply by calling from above the ground. Likewise, the receivers of the signals can benefit from being above the ground regardless of the position of the sender (Dabelsteen et al. 1993). Birds are the most obvious example of how sound transmission

might influence behavior—males of most species broadcast songs from perches in trees or while in flight in spite of the energetic costs and the chances of increased predation (Mathevon et al. 1996). Many species of frogs and insects also call from well above the ground, although species of frogs that call from ground level across water often do not experience high levels of call attenuation, perhaps because the water acts as a waveguide (Venator 1999; Bass and Clark, Chapter 2).

3.3.2. Timing of Signaling

The dawn chorus of birds and evening choruses of insects and frogs are nearly ubiquitous. Why do these species restrict calling to certain times of the day, and why to early morning and evening? Meteorological conditions vary widely over the course of the day, causing variations in signal transmission. In addition, the composition of biotic and abiotic noise in the environment differs at different times of the day. Calling at times when the meteorological conditions favor sound transmission or when other species are not calling can increase the active space of a transmitted signal. In environments ranging from desert to tropical forest, early morning and evening hours usually have the best meteorological conditions for sound transmission (Waser and Waser 1977; Henwood and Fabrick 1979).

3.4. Acoustic Niche Partitioning

In addition to the effects of the physical environment, calling structure and behavior may be influenced by the other species within a community. Selection on individual species to match the transmission characteristics of their calling habitat would lead to convergence among sympatric species. However, we can easily hear that the calls of each species have distinctive features. Such differences among sympatric species can reduce the level of interference among the calls of different species, resulting in a partitioning of the "acoustic niche." In addition, when these signals are used for the recognition of conspecific potential mates over heterospecifics, differences among calls or calling behavior can be strongly advantageous, preventing costly mismatings among incompatible individuals.

Some anuran studies provide suggestive evidence for divergence in call structure or calling behavior among species that call in the same area. Frogs sometimes maintain different calling sites within a habitat, and these differences in location can reduce the chances of matings among heterospecifics (Duellman 1967; Hödl 1977). Temporal differences in calling behavior may also reduce interference and promote reproductive isolation (Duellman 1967). Even so, many species of frogs can often be observed calling at the same time and in the same place. In these cases, different species seldom have similar calls; some combinations of temporal or spectral properties of calls will differ among species, allowing for the discrimi-

nation of conspecifics from heterospecifics (Hödl 1977; Drewry and Rand 1983).

As with habitat acoustics, however, these community-level analyses are subject to a number of different confounds, such as differences in body size and evolutionary history. These confounds render the evidence for acoustic niche partitioning of frog and insect calls inconclusive.

4. Predator- and Parasite-Generated Selection

The most fundamental communication interaction is dyadic, involving a signal and a receiver. Most communication channels, however, are not private, and there can be eavesdropping from unintended receivers. When these unintended receivers are conspecifics, they can use the information gained to compromise the fitness of the communicators. When the eavesdroppers are parasites or predators, the fitness consequence can be even greater. The parasites are usually searching for a host on which their young can develop while predators are looking for food. Long-distance signals are the most risky because they are more likely to be detected by eavesdroppers than are close-range signals.

Zuk and Kolluru (1998) recently reviewed the literature on exploitation of sexual signals by predators and parasites. They list 19 known cases. In nine of the cases, the eavesdroppers are insects; seven of those cases involve a tachinid fly. In all but one case, the insect eavesdroppers are attracted to signals produced by other insects, usually crickets. The one exception is a chaoborid fly being attracted to a tree frog. Zuk and Kolluru (1998) cite ten examples of vertebrates that eavesdrop on signals. Often these are bats homing in on signals of frogs and insects, although turtles, lizards, birds, and other mammals do so as well. Acoustic cues are more likely to be used by parasites and predators to find a victim than are visual cues, although they are used less commonly than olfactory cues.

4.1.1. Acoustically Orienting Parasites and Calling in Crickets

The best-known example of parasite/predator-generated selection on acoustic signaling comes from the classic studies of Cade (1975, 1981) on a tachinid fly, *Euphasiopteryx depleta* (= *Ormia depleta*), that parasitizes the field crickets *Gryllus rubens*, *G. integer*, and *G. lineaticeps*. As do many crickets, males of these species use long-distance acoustic cues to attract females for the purpose of mating. Female crickets are not the only ones attending to these cues, however; the tachinid flies orient toward these calls and deposit larvae on the singing male. The larvae develop inside the male, use the male as a source of nutrition, and emerge in 7-10 days (Cade 1975).

Selection on male calling from these parasites has resulted in at least two adaptations by the crickets. The most dramatic is the evolution of variation

in the amount of time males spend calling. In many species, there are often alternative mating strategies in which one type of male signals for mates while the other does not and instead attempts to sneak copulations with females (Cade 1981). In crickets, these differences among males are attributable to genetic differences. Cade's studies of crickets are an illustration of how the costs of acoustic signaling can result in the evolution of genetically influenced variation in male mating behavior.

Risk of parasitism and predation does not only vary with the amount of signaling but with other environmental variables as well, and these are taken into account by female crickets when responding to calls. Hedrick and Dill (1993) showed that female response to attractive versus unattractive calls is influenced by the amount of cover in the environment. In situations that afford cover from parasites and predators, female crickets are more likely to respond to attractive calls perceived to be farther away. When the females are more exposed, they choose the closer, although what in other circumstances would be less attractive, call.

There are also adaptations on the side of the eavesdropper in this system. Robert et al. (1992) show that the tuning characteristics of the fly's hearing match the spectral energy of the cricket's call. Thus, there has been an evolutionary convergence between the fly's hearing and the cricket's call. The hearing sensitivity of the parasitoid fly appears to be an evolutionarily derived character that evolved because of the benefits derived by female flies in locating a host for their larvae.

4.1.2. The Frog-Eating Bat and Calling Frogs

A vertebrate analog to the fly–cricket system is that of the frog-eating bat and calling frogs. *Trachops cirrhosus* is a neotropical bat that feeds on a variety of frogs and uses the frog's advertisement call as a localization cue (Fig. 5.4; Tuttle and Ryan 1981). As with the fly–cricket system, *Trachops* has a number of effects on the communication system of frogs. Male túngara frogs (*Physalaemus pustulosus*) produce a whine-like advertisement call that is both necessary and sufficient to attract females. Males can add up to six chucks to the call; chucks are short duration (35 msec), harmonically rich (fundamental frequency of about 250 Hz, with up to 15 harmonics) sounds. The addition of chucks increases the call's attractiveness. Although *Trachops* are attracted to and able to localize calls without chucks, when given a choice they prefer calls with chucks. Thus, the interaction of sexual selection for calls with more chucks and natural selection for calls with fewer chucks seems to have resulted in the evolution of the túngara frog's advertisement call of facultatively varying complexity (Ryan et al. 1982).

Bat predation also influences how and when males call. Male túngara frogs exhibit more evasive behavior, such as submerging under the water, and are less likely to resume calling after the close approach of a bat (Tuttle et al. 1982). *Smilisca sila* males produce calls that overlap in time with one

FIGURE 5.4. A frog-eating bat, *Trachops cirrhosus*, about to capture a túngara frog, *Physalaemus pustulosus*. (Photo courtesy of M.D. Tuttle, Bat Conservation International.)

another and decrease bat predation risk relative to nonoverlapping calls (Tuttle and Ryan 1982). These frogs also modulate the number of syllables in the call in response to predation risk; they produce calls with more syllables under conditions of higher ambient light in which they can see an approaching bat (Tuttle and Ryan 1982). As do crickets and *S. sila* frogs, female túngara frogs assess risk when responding to male calls; they are more likely to approach attractive calls perceived as being farther away over less attractive calls perceived as being produced closer when ambient light levels are lower (Rand et al. 1997).

There was a surprising aspect of the finding that bats eavesdrop on frog calls. Bats are well-known for their reliance on the returning echo of ultrasonic (50–100 kHz in *Trachops*) signals for target localization (Barclay et al. 1981). Frog calls, on the other hand, are relatively low-frequency signals, with most of the spectral energy usually below 5 kHz (Ryan et al. 1983). *Trachops*, however, shows enhanced behavioral sensitivity (movement of the pinnae toward a sound source) to pure tones as they decrease from 15 kHz to 5 kHz; thus, they have heightened behavioral sensitivity to the frequencies that characterize frog calls relative to higher sonic (<15 kHz) frequencies (Ryan et al. 1983). Furthermore, these bats show what appears to

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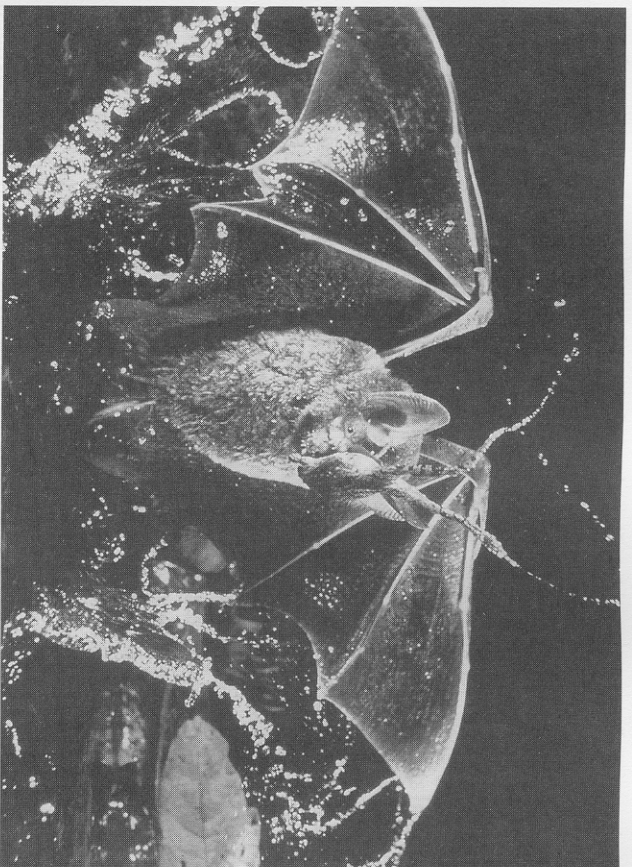
FIGURE 5.4. A frog-eating bat, Trachops cirrhosus, about to capture a túngara frog, Physalaemus pustulosus. (Photo courtesy of M.D. Tuttle, Bat Conservation International.)

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be a suite of neuroanatomical specializations for low-frequency hearing in the inner ear, which either increase sensitivity to low-frequency sounds or extend the range of hearing into the low frequencies. These include the largest number of cochlear neurons for any mammal, the second-highest density of cochlear neurons for any mammal, and three peaks of cochlear neuron density rather than the two peaks typical of other bats or the one typical of all other mammals. The third peak is in the apical portion of the cochlea, where low-frequency sounds are detected (Bruns et al. 1989).

Although there are a number of striking cases of predator- and parasite-generated selection on long-distance acoustic signals, the impression from being in the field with these calling animals is that we probably know of only a relatively small proportion of these cases. Furthermore, it seems that there will be many more cases of adaptations on the part of eavesdroppers to detect and localize long-distance cues of prey. We predict that many of these interactions between signalers and unintended receivers will be found in the tropics, where the diversity of predator–prey interactions tends to be greater.

5. Long-Distance Signals, Speciation, and Sexual Selection

It is not only the difficulties of production and transmission of long-distance signals that have made them a central focus of so many research programs. Their involvement in the reproductive biology of many species has made these communication systems critical to the development of evolutionary theories of speciation and sexual selection.

5.1. Speciation

The middle of the twentieth century saw a rebirth of Darwinism referred to as the Modern Synthesis. This synthesis combined research traditions from paleontology, systematics, population genetics, and behavior to accomplish a grand, unified theory of evolution by natural selection (Mayr 1982). A critical issue in accomplishing this synthesis was understanding the origin of species. It was in this realm that behavior made its most lasting contribution to evolutionary theory. If a biological species is defined as a group of potentially interacting individuals, then there must be mechanisms that draw conspecifics toward each other and away from heterospecifics when searching for mates.

Despite the large number of acoustically signaling insects, frogs, and birds, most of the species that produce long-distance signals produce a species-typical one. We make this statement without implying species typology and lack of meaningful geographic variation within a species (Foster 1999, Foster and Endler 1999). By classifying a signal as "species-typical," we are making a statement about how signal variation is partitioned within

species versus among species rather than implying unvarying species-specific stereotypy. It seems to us that in many if not all cases the variation in long-distance signals within the species is substantially less than the variation of the same kind of signals among closely related or ecologically sympatric species. Thus, the properties of the signal can be used for correct identification of the species producing it, as anyone who has tried to identify a bird, frog, or a cricket sight unseen might know. The females of the respective species are even more unerring in their identification, and it is this interaction of signal and receiver that has put long-distance communication at the center of research on speciation theory (e.g., Blair 1958; Alexander 1962; Andersson 1994; Howard et al. 1998).

Preferences of receivers for conspecific versus heterospecific signals lead to assortative mating, reduce the opportunity for reproductive interactions between incipient species, and contribute to the genetic divergence among populations that is critical for speciation. The preference for conspecific versus heterospecific signals is a species-isolating mechanism because it restricts reproduction among different species. The preference is also a premating isolating mechanism because the effect takes place prior to the act of mating, unlike a postmating isolating mechanism, whose effect on reproductive isolation takes place after the mating act; hybrid sterility would be an example of a postmating isolating mechanism.

5.1.1. Species Discrimination as an Incidental Consequence

The use of the term "mechanism" might imply that the function achieved, in this case preference for a conspecific versus a heterospecific signal, evolved under selection. Although there appears little doubt that selection can result in the evolution of such discrimination patterns (see Section 5.1.2), the preference for a conspecific signal versus many heterospecific signals may also be an incidental consequence of signal preferences already in place. For example, if an animal expands its range into a new area and encounters other species for the first time, it might have no problem recognizing the signals of its own species from that of the newly encountered heterospecifics. This particular set of preferences for conspecific versus heterospecific signals did not need to evolve; it was already present as a consequence of how this recognition mechanism—this interaction between properties of the signal and the receiver—happened to evolve in the past. It is *adaptive* (the current effect on fitness) to the animal to prefer the conspecific signal versus the novel heterospecific ones, but this particular preference is not an *adaptation* (the evolved function). The fact that a communication system results in effective species recognition need not mean it evolved for that purpose.

5.1.2. Reinforcement and Reproductive Character Displacement

A second possibility invokes direct selection in the evolution of mate-recognition signals. When two forms of a single species exist in sympatry,

mating signals can diverge as the result of lowered hybrid viability or fertility. Such a process is called reinforcement (Butlin 1989) and can eventually lead to complete reproductive isolation, or speciation.

As in the case above, in areas where species overlap, mate-recognition signals must be sufficiently different to prevent incorrect matings between heterospecific individuals. As a result, selection may favor divergence among the signals of different species where they occur in sympatry. The term "reproductive character displacement" describes the outcome of such a process (Butlin 1989), where traits used in mate recognition differ more among sympatric than among allopatric populations because of the divergence of these characters in response to selection to reduce the probability of heterospecific matings. Reproductive character displacement has proved to be difficult to demonstrate empirically.

The strongest evidence to date for reproductive character displacement comes from examples of call divergence within sympatric populations of related species of anurans. The tree frogs *Litoria* (*Hyla*) *ewingi* and *L. verrauxi* can be found in largely disparate areas of southern Australia but *verrauxi* can be found in largely disparate areas of southern Australia but do overlap in some regions. In allopatry, the advertisement calls of the two species are very similar. In sympatric populations, however, the calls of *L. ewingi* and *L. verrauxi* are quite different. In these populations, the pulse repetition rate and number of pulses per note in the calls of *L. verrauxi* are shifted away from the values for *L. ewingi* (Littlejohn 1965). There is evidence that these call characters are important in mate discrimination—females of these sympatric populations show strong preferences for pulse rates typical of conspecifics over pulse rates similar to those of heterospecifics (Loftus-Hills and Littlejohn 1971). Thus, the divergence of these call characters could result in a reduced number of hybrid matings.

5.1.3. Neuroethological Mechanisms of Species Recognition

The importance of communication in speciation not only involved behavior in evolutionary theory but also implicated neuroethology. The behavioral preferences so crucial to species recognition emerge from an interaction of stimulus variation and neural and cognitive processing. Understanding how auditory systems decode and process species-specific signals focuses the process of speciation on the nervous system. Studies on crickets (e.g., Huber 1990), frogs (Capranica 1972), and birds (Margoliash 1983) have identified features of the auditory system that bias behavioral responses toward the species' own signal. Although the neuroethologists' emphasis has been on the functional significance of these properties, they are the underlying substrates to the behavior that must evolve if speciation is to occur. Some neuroethological investigations, such as studies of neural pattern generators that could potentially link properties of the signal with signal recognition (Hoy et al. 1977), were motivated by evolutionary as well as neurobiological issues (Doherty and Hoy 1985).

5.2. *Sexual Selection*

Although the focus on the role of long-distance communication in speciation continues (e.g., Howard et al. 1998), even more interest has centered on its function in sexual selection (Andersson 1994). Although speciation is the process that gives us diversity through an increase in species numbers, sexual selection is a process that enhances diversity within species. It is primarily this process that makes males and females of the same species look so different from one another—humans included. It is also the process that makes some animals look so attractive and stunning, sound so charming, and behave in manners that are sometimes amusing to us.

Sexual selection favors traits that enhance reproductive success by enhancing one's ability to acquire mates. This can be achieved by a male becoming more attractive to a female, and often, but certainly not in all cases, this judgment of attractiveness is influenced by the male's long-distance signal. A large number of studies of acoustically advertising animals shows that receivers' preferences for long-distance signals will not only guide them to males of their own species but often to a subset of males within the species (Ryan and Keddy-Hector 1992; Andersson 1994). Thus, it is preferable to refer to these signals as mate-recognition signals rather than species-recognition signals or sexually selected signals (Ryan and Rand 1993). Sexual selection generated by these receiver preferences can cause the elaboration of mate-recognition signals. This has been most clearly seen in the elaborate plumage of many male birds but is no less extreme when one examines the variety of sounds that males use to coax a female into mating. The power of sexual selection is documented not only in the extreme signals that males have evolved but in the cost incurred to exhibit them. Metabolic rate can increase tenfold during calling in some frogs (Section 2 of this chapter; Wells 2001), and crickets (Cade 1975) and frogs (Tuttle and Ryan 1981) can attract deadly acoustically orienting parasitoids and frog-eating bats when signaling for females (Section 4 of this chapter).

Much of sexual selection involves communication. One is interested in a dyadic interaction between signaler and receiver, how signal variation is perceived and acted on by the receiver, and the reproductive consequences of such actions for both pairs of the communicating dyad. As with speciation theory, a major issue is how signal and receiver are functionally linked.

Behavioral studies of sexual selection have tended to concentrate on what information the signal conveys to the receiver about the sender. Some of this information might be useful in allowing a female to determine whether a male is of the appropriate species or is in control of resources critical to the female's immediate reproductive success. In such cases, selection should favor receiver preference for the signal variant that guides the female to the mate that maximizes her reproductive success. In other cases, it is suggested that females are not as interested in maximizing the number of offspring they birth but instead choose males whose signals suggest that

they will endow her offspring with genes to ensure future survival. Finally, it is possible that the relationship between signal and receiver properties might be due to males responding to selection to produce sounds that females already find appealing.

Acoustic signals have been repeatedly shown to be sexually selected, most often in birds, insects, and frogs, but also in fish and mammals (Andersson 1994). Andersson (1994) reviews a number of cases of sexually selected acoustic signals in all of these taxa. Across taxa, we often find that females prefer to mate with males that produce louder, longer, more rapidly produced calls (reviewed in Ryan and Keddy-Hector 1992). As noted above, such preferences could lead to matings with physically or genetically superior males and thus be directly or indirectly selected, or the preferences could result from the increased detectability of such signals or from females' preexisting biases toward certain types of signals. In Section 6, we discuss further the evolution of female mating preferences for male traits.

5.2.1. Neuroethological Mechanisms of Sexual Selection

Neuroethology has not played as crucial a role in explaining the behavioral mechanisms that contribute to sexual selection as it has in elucidating the role of behavioral isolating mechanisms in speciation. In some ways, the successes of neuroethology in identifying species-specific decoding mechanisms might have constrained it from similar success in sexual selection. In both speciation and sexual selection, it is crucial to understand how neural mechanisms allow the receiver to sieve through substantial signal variation to identify biologically meaningful signals. But the focus of the variation, and thus the focus of researchers, can be quite different in the two types of studies. In trying to understand species recognition, receivers and researchers alike confront the variation among species. Given signal variation at this level, how can the receiver identify a conspecific signal? In sexual selection, however, it is the variation within the species that is crucial, and one must ask how and why receivers are guided to one rather than another conspecific variant. This is not the type of question that neuroethologists originally set out to address about communication.

6. Signal–Receiver Coevolution

We have been discussing a variety of factors that cause and constrain the evolution of long-distance signals. But communication is a dyadic interaction, and signal evolution will proceed only if changes in the signal are meaningful to the receiver. This problem has been a major focus of interest in both speciation and sexual-selection studies. In the former, it is necessary to understand not only how mate-recognition signals evolve among incipient species but how the receivers evolve at the same time and

in the same direction to give these new signals meaning, resulting in two functional and different mate-recognition systems (Andersson 1994).

The problem in sexual selection has been a bit more complicated and controversial (e.g., Kirkpatrick and Ryan 1991; Andersson 1994; Ryan 1997). In some mating systems, the female's choice of a mate does not influence her immediate reproductive success. In these mating systems, the male signals evolve under selection generated by female mating preferences. But how can preferences, the neural and cognitive processes biasing receivers toward certain signal variants, evolve if all receivers are producing the same number of offspring?

Here, we review some of the hypotheses for maintaining congruence between the signal and the receiver during evolution. We use the term coevolution in the more general sense—when the evolution of one suite of phenotypic characters influences the evolution of another suite of characters. Evolution of the two sets of characters need not proceed simultaneously; there could be substantial lag. Furthermore, it must be remembered that not every change in a signal requires a change in the receiver. Receivers seem not to have highly tuned accept-reject filters but are more than capable of ample generalization (Enquist and Arak 1998). The three major factors we will consider that might contribute to the functional integration of signal–receiver systems are pleiotropy, genetic correlation, and sensory exploitation.

6.1. Pleiotropy

Pleiotropy is multiple phenotypic effects resulting from the same gene. This offers the simplest explanation for how signals and receivers remain functionally integrated during evolution. If signals and receivers are controlled by the same gene or tightly linked sets of genes, then genetic changes will simultaneously and similarly affect signal and receiver.

6.1.1. Scaling

Because mate-recognition functions are so important to both sender and receiver, we assume that selection plays an important role in bringing about the match between peripheral tuning and long-distance signal. But there might be other, more parsimonious processes at work.

There are two variables to which signal variation often scales in a predictable manner: body size and, in ectotherms, temperature. Dominant or carrier frequencies tend to decrease with larger size because the characteristic vibration pattern of the morphological substrate is negatively correlated with mass. This relationship has been especially well-documented in frogs (Martin 1972; this chapter, Section 2.2), birds (Bowman 1983), and mammals (Morton 1977). In many ectotherms, ambient temperature influences rates of behavior, and sound production is no exception. The

"temperature cricket" is so called because of the reliability of its pulse rate in predicting ambient temperature (Ewing 1989). How do receivers respond to such scaling effects in signals?

In anurans, the tuning of one or both of the two peripheral end organs that are sensitive to airborne sound tends to match the dominant spectral characteristics of the long-distance advertisement call (Fuzessery 1988; Zakon and Wilczynski 1988). The amphibian papilla (AP) tends to be most sensitive at threshold to frequencies below about 1,200 Hz, whereas the basilar papilla (BP) is most sensitive to frequencies above 1,200 Hz. Depending on the spectral distribution of call energy, either or both end organs will exhibit a match between the frequencies to which they are most sensitive and the spectral concentrations of call energy.

The AP and BP differ in a number of ways. The AP is thought to accommodate a traveling wave and has an array of hair cells that are tonotopically organized. The BP, on the other hand, has most of its hair cells tuned to similar frequencies, and the overall frequency sensitivity of the BP might result from its resonating properties, which will be influenced by size (Keddy-Hector et al. 1992; Wilczynski et al. 1992).

Cricket frogs, *Acris crepitans*, produce long-distance calls with most of the energy above 3,000 Hz. It seems clear that the BP rather than the AP is critical in the initial processing of the call. Calls exhibit a large amount of variation in dominant frequency across the geographical range of the species, but the auditory system tends to be tuned to frequencies characteristic of (Capranica et al. 1973; Ryan and Wilczynski 1988) or slightly lower than (Ryan et al. 1992) the local population. The geographic covariation of call frequency and auditory tuning might result from pleiotropic effects of changes in body size—both factors are negatively correlated with body size (Nevo and Capranica 1985; Ryan and Wilczynski 1991; Keddy-Hector et al. 1992; Wilczynski et al. 1992). It is assumed that the effect on tuning is derived from the effect of size on the resonating properties of the BP (Fig. 5.5). These results are consistent with patterns of frequency preference for call dominant frequency (Ryan and Wilczynski 1988; Ryan et al. 1992).

There are some cautions necessary, however. These scaling effects vary among populations (Keddy-Hector et al. 1992; Wilczynski et al. 1992), the relationships are not always very tight, and the preferences for call frequency appear to be statistically weak (although they could still generate strong biases in male mating success in the field). Nevertheless, dual scaling of signal and receiver to body-size variation does offer the potential for maintaining the functional integration of signal and receiver when size diverges among species or populations, and this will be true whether or not size has a significant heritable component.

A more short-term scaling problem involves temperature effects on signal characteristics. In most insects and frogs, temporal features of the call, such as pulse repetition rate, are drastically affected by temperature variation (Zweifel 1968; Gerhardt 1978; Bauer and Helverson 1987; Ewing 1989; Wagner 1989). In general, call rates increase with temperature. Tem-
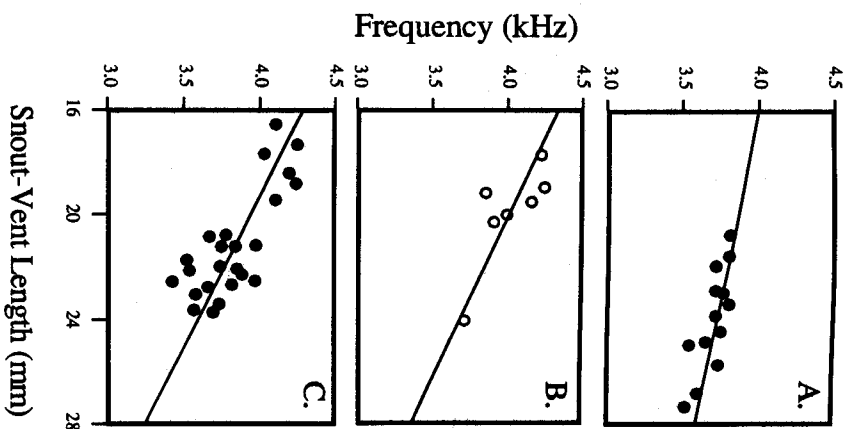

FIGURE 5.5. The relationship between body size (snout–vent length) and (A) the tuning of the basilar papilla in female and (B) male cricket frogs, *Acris crepitans*, and (C) the relationship between male body size and dominant frequency of the advertisement call within a single population. (Redrawn from Keddy-Hector et al. 1992.)

perature effects on spectral properties of the call are either not significant or less extreme—if there is an effect, frequency tends to be positively correlated with temperature.

One of the more interesting cases of temperature scaling involves study of the diploid-tetraploid species complex of *Hyla chrysoscelis* and *H. versicolor*. These are otherwise cryptic species that can easily be distinguished by the pulse rate of their call. *H. chrysoscelis* is diploid and has a faster pulse rate (~25–65 pulses/sec), whereas *H. versicolor* is tetraploid and has a slower pulse rate (~10–30 pulses/sec; Fig. 5.6). In both species, pulse rate is positively correlated with temperature. These two species can be sympatric, and if there is a wide enough range of temperature variation in the pond, it is conceivable that an *H. versicolor* male would have a higher pulse rate than an *H. chrysoscelis* male if, for example, the *H. versicolor* males were calling at 24°C while the *H. chrysoscelis* male was calling at 12°C (Fig. 5.6). Gerhardt (1978) showed that female preferences for pulse repetition rate scale to temperature similarly to that exhibited by conspecific calls. When challenged with calls that vary in pulse repetition rate, the female chooses that signal that would be produced by a male calling at her body tempera-
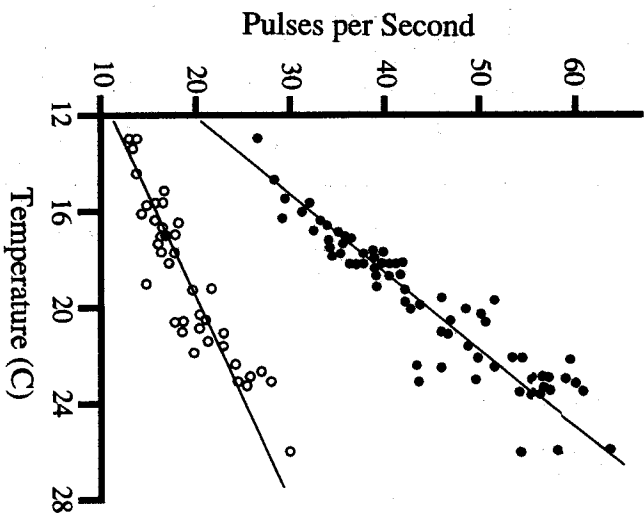
FIGURE 5.6. The relationship between pulses per second in the male advertisement calls of two species of gray tree frogs, *Hyla versicolor* (open circles) and *H. chrysoscelis* (closed circles). (Redrawn from Gerhardt 1978.)

ture. Brenowitz et al. (1985) showed that auditory neurons in the central nervous system that are sensitive to pulse rate show the same temperature scaling as the call and the preferences.

6.1.2. Pattern Generators

The dominant, or carrier, frequency of a signal is often determined by the mass of the primary vibrator that produces the sound and can be modified by radiating and resonating properties upstream from the vibrator. Temporal parameters of signals, on the other hand, are often actively regulated by behavioral-physiological properties, such as rate of stridulation or expiration. In such cases, there could be a neural oscillator that regulates the production mechanism to achieve the appropriate temporal characteristics of the signal. Receivers must decode these temporal signal characters. This could be achieved by comparing the pattern of auditory stimulation to a neural oscillator that acts as a template for temporal-pattern recognition. If the signal and receiver were both under control of the same neural oscillator or central pattern generator, any change in the temporal aspect of one component of the communication dyad would be immediately matched by the same change in the other component (Alexander 1962; Hoy et al. 1977).

A number of researchers have explored the possibility that signal–receiver systems maintain their functional integration through sharing a central pattern generator. If central pattern generators control signal–receiver variation, then hybrids should be intermediate relative to the two parental species in both temporal signal properties and response to these same properties. Studies of crickets and frogs both offered some qualified support for this hypothesis. Hoy et al. (1977) and Doherty and Gerhardt (1983) showed that in crickets and tree frogs hybrids tended to have intermediate pulse rates relative to the two parental species. Furthermore, in some but not all of the possible comparisons, hybrid females preferred the hybrid calls over the calls of at least one of the parental species.

The interpretation of these studies has been a challenge (Boake 1991). An alternative to the pleiotropy (central pattern generator) hypothesis is that signals and receivers are under separate and quantitative genetic control. If this were the case, one would still expect hybrids to be intermediate. This issue could be resolved through detailed quantitative trait locus mapping studies (Lynch and Walsh 1998). Another criticism of the central pattern generator hypothesis was offered by Bauer and Helverson (1987). If there is a single central pattern generator controlling the signal and receiver, then their response properties should be thermally linked. The authors showed, however, that if the head and thorax of a grasshopper are heated separately, the song and preference are decoupled.

One of the best-characterized genes controlling biological rhythms is the *period* locus in *Drosophila*. This locus is implicated in controlling a variety of rhythms, such as the circadian rhythms, as well as the fruit flies' love song (Hall 1994). The love song is produced by vibrating the wings, and mutants at the period locus vary in song rhythm. Previous studies had shown that mutant lines not only differed in love song pattern but in female preference for the same pattern (Kyriacou and Hall 1986). These results suggested that the female's preference for song pattern was one more rhythm under control of the *period* locus. More recent studies have suggested that this is not true, however. Greenacre et al. (1993) examined *Drosophila melanogaster* with mutations at the *period* locus, which predictably altered the rhythmic pattern of the song. Female mutants retained a preference for the wild type over the mutant song rhythm. This suggests that the song rhythm and the preference for song rhythm are under separate genetic control. Females from a *period* mutant stock that had been maintained for over ten years, however, did show preference for the mutant song rhythm. Thus, song and song preference are able to coevolve in *Drosophila*, but not through the pleiotropic effects of the period locus.

6.2. Linkage Disequilibrium

Signals and receivers could also maintain their functional integration if there were a statistical linkage between genetic variation influencing signal

and receiver properties. Linkage disequilibrium is a measure of the non-random assortment of alleles at different loci. It is a process that has generated considerable interest in sexual selection theory (e.g., Andersson 1994), but its generalities can be applied to the more general problem of signal-receiver evolution. As part of this theory of runaway sexual selection, Fisher (1930) was the first to suggest that linkage disequilibrium plays an important role in the evolution of sexually selected male signal traits and female preferences for traits. It has been more recently applied to "good genes" theories of sexual selection (Pomiankowski 1988; Grafen 1990).

The crux of linkage disequilibrium is that traits that are not under selection can evolve if they are genetically correlated with traits that are under selection. In the parlance of evolutionary genetics, the trait subject to selection is said to be under direct selection. If another trait variant is more likely to be associated statistically with the trait under direct selection than expected by random chance, the two traits are genetically correlated or in linkage disequilibrium. The second trait, not subject to direct selection, is under indirect selection by virtue of its genetic correlation with the first trait and can evolve as a correlated response to the trait under direct selection.

It is the observation that a trait can evolve even if it is not subject to direct selection that makes linkage disequilibrium especially relevant to sexual-selection studies. In lekking species of animals, males gather to signal for mates and provide them with few resources besides sperm. It is assumed that in many cases, regardless of with whom the females choose to mate, the number of offspring they birth will be the same. Yet—and this is the paradox—females sometimes assiduously choose their mates (in many cases, the signal parameters that influence mate choice are well-known (Ryan and Keddy-Hector 1992; Andersson 1994)), with only a few males on the lek gathering a majority of the mating success. How could such preferences evolve if there is no difference in the reproductive success of females exerting different preferences or, for that matter, no difference in the reproductive success of females exhibiting a preference or mating at random? Two major hypotheses, runaway sexual selection and good genes selection, have been offered as solutions to this paradox, and both are dependent on indirect selection and linkage disequilibrium. Even though this problem of evolution through linkage disequilibrium is usually addressed within the context of male trait/female preference evolution, in many cases the male trait is a long-distance signal and the female preference emerges from the interaction of this stimulus and the properties of her receiver.

6.2.1. Runaway Sexual Selection

Fisher's hypothesis of runaway sexual selection is best illustrated with an example. Suppose that there is heritable variation for a male signal, such as simple song or complex song, and a female preference, such as a preference for complex song or a lack of such a preference. The genes controlling trait

and preference are present in both sexes, but only the gene appropriate for each sex is expressed. For simplicity's sake, assume that the population is haploid. After the first episode of mating, males with complex songs will have garnered greater mating success. Furthermore, alleles that determine complex song will be in linkage disequilibrium with alleles that determine preference for complex song. As the frequency of complex song evolves in the population due to preference for complex song, the preference itself will "hitchhike" along with the complex song, and the preference will also evolve to be in a higher frequency in the population. The stronger the preference for complex song, the faster the rate of evolution of song and, through the genetic correlation of song and preference, the faster the rate of evolution of preference. The process can continue until the advantages of the enhanced male trait, song complexity in this example, are offset by the natural-selection costs of producing the trait, such as metabolic or predation costs, for example. At such a point, the forces of sexual selection and natural selection will be balanced, and trait and preference will reach an evolutionary equilibrium.

Although runaway sexual selection has been a popular hypothesis among population geneticists for a number of years, it has been difficult to marshal much empirical support for it (Andersson 1994; Ryan 1997). This might be because it is a transient process; once signal and receiver reach an equilibrium point, it is difficult to determine how they got there. One approach to testing the theory is to demonstrate the genetic correlation between signal and receiver either by conducting selection experiments or comparing populations of the same species that differ in trait and preference.

There are no good examples of studies in acoustic communication supporting the runaway hypothesis. But as a matter of illustration, consider an elegant study of visual signaling in stalk-eyed flies. The eyes are located at the end of long stalks in both sexes, but the stalks are much longer, and thus the eye span much greater, in males than in females. Females prefer males with greater eye spans. Wilkinson and Reillo (1994) conducted bidirectional selection experiments on male eye span and determined whether there was a correlated evolutionary response in female preference for eye span. After 13 generations, females from large eye-span lines and the unselected lines both preferred males with larger eye spans. Females in the lines for which short eye span was selected preferred males with shorter eye spans. Thus, the female preference evolved even though it was not under direct selection but instead because it was genetically correlated to the signal.

6.2.2. Good Genes Selection

Good genes selection has been viewed as an intuitively appealing and more utilitarian alternative to runaway selection. Under this scenario, females attend to signal variation to assess a male's genetic quality for survivorship. But what would keep signals honest? Why could males not cheat and evolve signals that falsely indicate high genetic quality? In some cases, signals

might be constrained from doing so. For example, Hamilton and Zuk (1982) suggested that plumage brightness and song complexity in birds indicate parasite load; parasites will directly influence plumage color and, it is assumed, the energetic potential to make complex songs. If there is a genetic basis to parasite resistance, then these signals are honest indicators of some genetic quality. An alternative means for enforcing signal honesty is the handicap principle (Zahavi and Zahavi 1997). This hypothesis suggests that males evolve signals that are costly in terms of survivorship; thus, only truly healthy males can afford the handicapping signal.

Early population-genetic models of the handicap principle did not support its internal logic (reviewed in Zahavi and Zahavi 1997). Later models, however, showed that the handicap principle could work through linkage disequilibrium. In this case, however, the preference genes become correlated with the "good genes" for survivorship that are being signaled. For example, let us assume faster call rate, which will be energetically more expensive than slower call rate, indicates healthier males because they are better foragers. Once some females begin to prefer faster call rate, the alleles determining that preference will become associated with the alleles for better foraging. Natural selection will cause an increase in better foragers, and the preference for faster call rate evolves as a correlated response.

All good-genes models, and especially the handicap principle, have been controversial and difficult to support empirically. Only recently have there been data to show that female preference for male signals influences the survivorship of their offspring. Most of these studies involve visual signals (reviewed in Ryan 1997), but data involving long-distance acoustic signals have recently become available. For example, molecular paternity analysis has shown that when female great reed warblers seek extra-pair copulations, they do so from males having larger song repertoires. Hasselquist et al. (1996) speculate that the female pairs with a male with superior territories, thus ensuring the resources necessary for immediate reproductive success, but seeks extra-pair copulations from males that have "good genes"; song repertoire size is correlated with survivorship.

One of the best studies comes from anuran communication and is similar to the hypothetical example given above. Gray tree frogs, *Hyla versicolor*, produce a pulse call that can vary among males in pulse rate and pulse duration. Males can increase the energy content of the call by increasing either call rate or duration; the former is an energetically more expensive option for the males. Klump and Gerhardt (1987) showed that when given a choice between a pair of calls varying in rate and duration but similar in overall energy content, females preferred longer calls. They speculated that this energy-independent preference might be indicative of selection for good genes. This hypothesis was supported recently by Welch et al. (1998). Female gray tree frogs were mated to two males, one that produced short calls and one that produced long calls; these crosses resulted in sets of maternal half-sibs. Tadpoles were raised through metamorphosis, and a number of

life-history parameters assumed to be predictive of higher survivorship were measured. The offspring of males with long calls performed significantly better than or not significantly differently from those of males with short calls. Although the data are too sparse to make any sweeping generalizations, the studies of gray tree frogs offer some of the best support for the notion that females can assess variation in long-distance acoustic signals to influence the genetic quality of their young.

6.3. *Sensory Exploitation*

Plants have evolved suites of adaptations to attract pollinators, much as males often use long-distance signals to attract females. In many cases, the attractions are mutualistic. The pollinator is attracted by various signals of the plant and inadvertently pollinates the plant while harvesting nectar. A number of plants, however, do not produce nectar. Orchids, for example, mimic the pheromones or the general body outline of insects; insects then attempt to mate with the flower, pollinating it during their mistaken sexual foray (Piji and Dodson 1966).

Although these interactions do not involve acoustic signals, they illustrate a relevant point. Congruence between the signal and receiver need not involve the sorts of genetic relationships within a genome envisioned in pleiotropy and linkage disequilibrium. Such phenomena cannot occur between species. In the orchid example, it appears that plants have evolved signals that exploit the insect's responses to conspecific sexual signals. The response of the insect to the orchid is not adaptive for the insect, but we assume that there is a net benefit to the receiver's biases; that is, the sum of costs and benefits of responding to plants and to sexually receptive conspecifics. Recent studies in sexual selection and communication have suggested that males evolve signals to exploit response biases of the females' receiver system (recently reviewed in Christy 1995; Endler and Basolo 1998; Ryan 1998, 1999).

6.3.1. Response Biases

Williams (1966) made a crucial point in distinguishing between an evolved function and incidental consequence in evolution. In the context of animal communication, the response properties of the receiver can be under selection to recognize the signal of a conspecific; if so, conspecific recognition is an evolved function. Depending on the recognition strategy, however, other stimuli might elicit strong receiver responses. For example, consider a receiver in an acoustic environment in which there is only one heterospecific using acoustic signals for mate recognition and its signal is much shorter in duration than the conspecific signal. A simple and effective recognition strategy would be to respond only to signals above a certain threshold in duration; this strategy, too, is an evolved function of the receiver. It seems that recognition strategies often involve such simple generalizations, as opposed

to more complicated ones having sharp multivariate filters that exclude all other possible signals but those of conspecifics (Enquist and Arak 1998). Such a simple recognition strategy might have some advantages of neural economy relative to a more complicated one that relied on a multitude of signal parameters, and in the simple environment of only one heterospecific, a more generalizing strategy would be as effective as a more specific one—effective, that is, until there appeared a new heterospecific with an even longer signal and the simple recognition strategy was foiled because the receiver now made recognition errors by responding to the longer heterospecific signal. Responses to this longer heterospecific signal would be an incidental and maladaptive consequence or response bias of the original, and adaptive, mate-recognition strategy. This is bound to happen because selection cannot anticipate future situations but can only judge among alternative phenotypes in a current context. But if the costs of making a recognition error toward longer signals exceeded the benefits of such a simple recognition strategy, we assume that the recognition strategy would evolve further under selection (Dawkins and Guilford 1996; Ryan 1999).

Such response biases are the basis of another exploitative, interspecific interaction similar to the orchid–insect example reviewed above. Cuckoos do not raise their own young. They place their eggs in the nests of other species, where their young are raised by the host, often to the detriment of the host's own young. Reed warblers are one such host. Even though the host young produce begging calls to elicit feeding from their parents that are quite different from the begging calls of the cuckoo (Fig. 5.7), reed warblers feed cuckoos preferentially to their own young. The begging call of the cuckoo does, however, mimic the sounds of a group of begging reed warblers (Fig. 5.7). In a series of elegant experiments, Davies et al. (1998; see also Kilner et al. 1999) showed that it is this cuckoo signal that exploits the receiver system of the reed warbler.

In many other cases, we might not expect response biases that emerge from recognition strategies to be maladaptive. Ryan and Keddy-Hector (1992) reviewed numerous cases of female preferences based on long-distance signals. If female preference deviated from the population mean, it was usually in the direction of greater signal energy—more intense, longer signals produced at higher repetition rates. If such preferences represent general response biases of many auditory-recognition systems, they might still continue to guide females toward conspecific males and, incidentally, toward males that are in better physical condition, being able to marshal more energy to support calling. An alternative is that the general pattern of bias toward greater signal content is an evolved response to choose such males in the first place.

6.3.2. Habituation and Song Preference in Birds

Songs of many oscines are characterized by their signal complexity. One explanation for such complexity, the antimonotony hypothesis, is based on
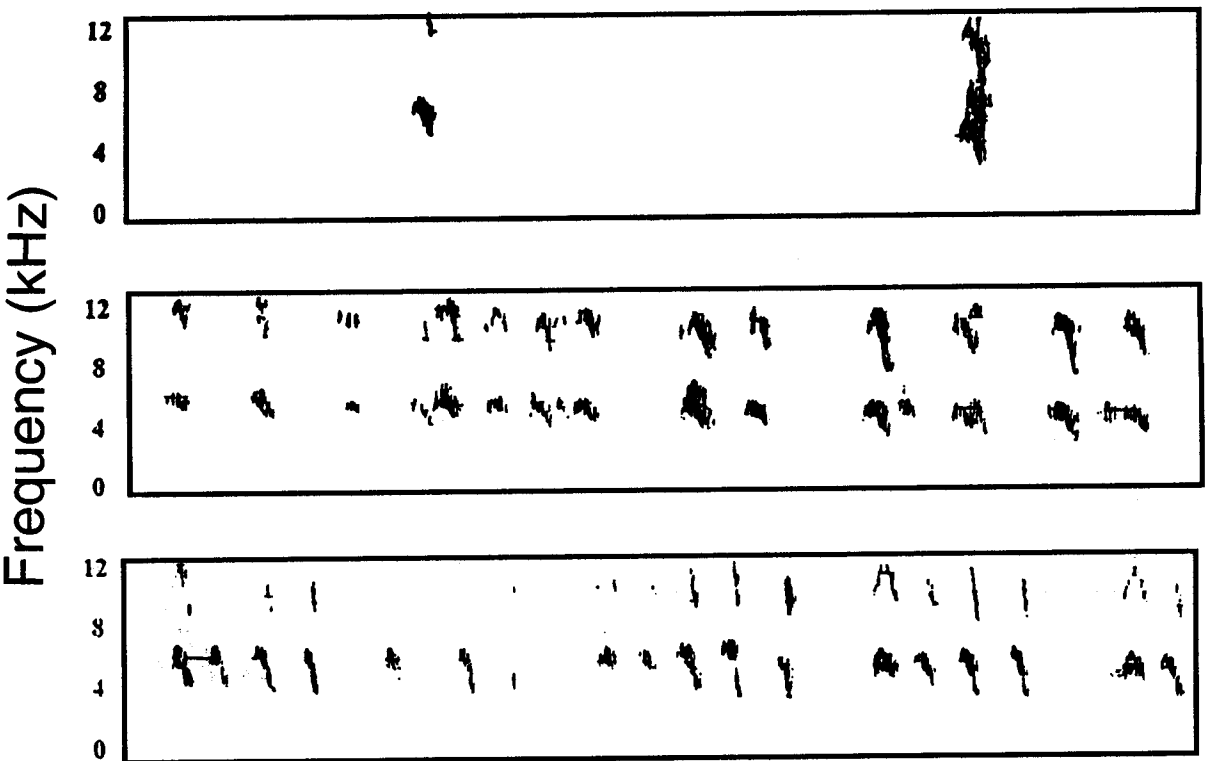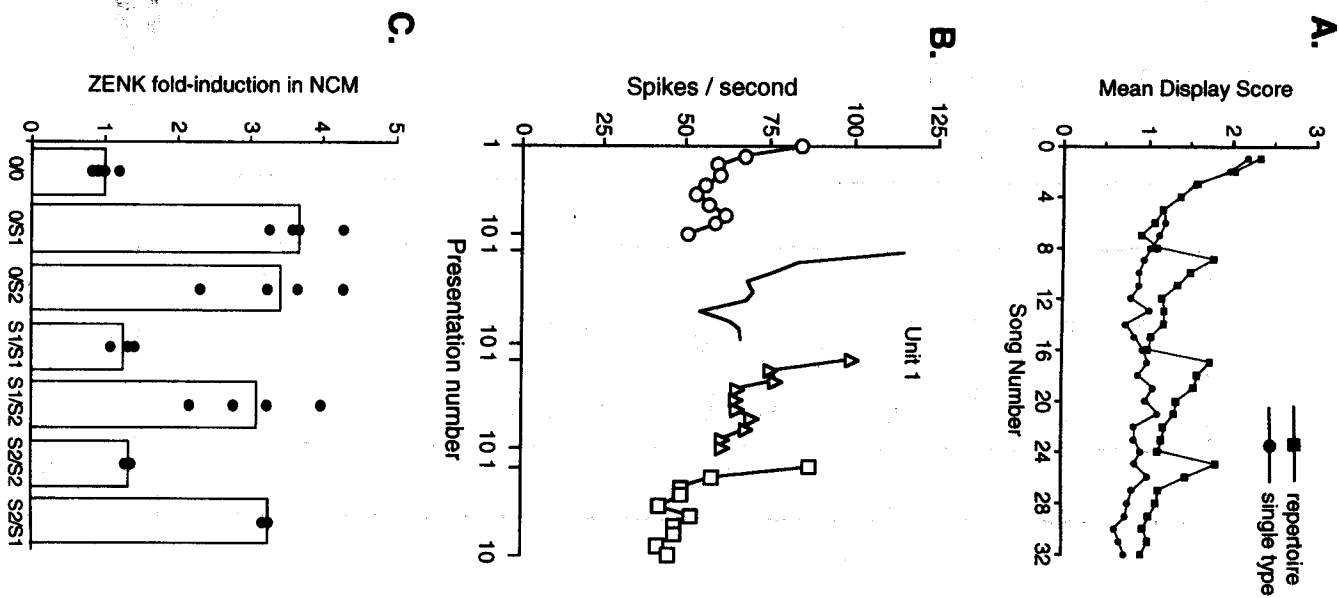
FIGURE 5.7. Sonograms (2.5 sec) of the begging calls of (top) a single reed warbler chick, (middle) a brood of four reed warblers, and (bottom) a single cuckoo chick. Note the similarity between the begging call of the single cuckoo and an entire brood of their reed warbler host. (Redrawn from Davies et al. 1998.)

A.

Mean Display Score

repertoire
single type

Song Number

B.

Spikes / second

Unit 1

Presentation number

C.

ZENK fold-induction in NCM

0/0 0/S1 0/S2 S1/S1 S1/S2 S2/S2 S2/S1

a general response bias of auditory systems (Hartshorne 1956; Searcy 1992). This hypothesis suggests that song complexity per se is selected, rather than any message encoded in different song syllables, because it reduces habituation in neighboring males and courting females. Searcy presents some evidence supporting this hypothesis in studies of grackles (Fig. 5.8). These birds do not have complex repertoires, but females are attracted preferentially to artificially enhanced repertoires compared to the more monotonous song of their conspecifics. When females were presented with a song of 32 syllables, they showed more courtship solicitation displays to the song that contained eight successive repetitions of four different syllables to a song of 32 identical syllables. Interestingly, the female response decreased within the repetition of the same syllable but increased during transition between syllable types, suggesting a pattern of habituation in response to the simple song but habituation and release from habituation in response to a more complicated song (Fig. 5.8, top).

Studies of zebra finches and canaries point toward some of the underlying mechanisms of this preference for more complex songs. Both electrophysiological responses (Stripling et al. 1997) of auditory neurons and expression of an early gene, *zenk*, implicated in auditory function (Mello et al. 1992), also show decreased response to repeated song stimuli and enhanced response during transition between stimulus types (Fig. 5.8; reviewed in Ryan 1998).

To the extent that habituation to signal monotony was a general phenomenon, we would expect response biases to generate selection for more complicated signals. The manner in which signal complexity could be enhanced would be constrained by the types of sounds that are efficacious in that particular system. For example, although swamp and song sparrows learn each others' song in the absence of their own, there is a strong bias to learn their own song type (reviewed in Marler 1997). Such genetic pre-

FIGURE 5.8. **(A)** Female courtship displays to complex song in grackles show higher levels in response to multiple-song repertoires than to single-song types. The single type (circles) contains 32 repeats of the same song. The repertoire (squares) contains four different song types repeated in groups of eight (e.g., 1–8, 9–6, etc.). The response to repertoire songs shows that there is habituation to repeated songs within each song type (e.g., 1–8,9–16, etc.) and release from habituation at transition between quartets (song 9, 17, etc.; Searcy 1992). **(B)** Electrophysiological responses of units in the zebra finch's caudomedial neostriatum, which borders the song-control nucleus, shows decreased spike rates to repeated presentation of the same song and enhanced spike rates in response to a new song (Stripling et al.1997). **(C)** Expression of an immediate early gene, *zenk*, is higher during transitions from no song to song (0/S1), or from one song to another song (S1/S2; S2/S1), than during absence of song (0/0) and repeated stimulation of the same song (S1/S1; S2/S2; from Mello et al. 1992). (Reprinted with permission from Ryan 1998. Copyright © 1998 American Association for the Advancement of Science.)

dispositions could bias the types of sounds incorporated into signal complexity; some species, such as mockingbirds, might be less constrained. This view of signal complexity, in general, and bird song repertoires, specifically, shifts the focus from any message that might be encoded by parts of the song to the value of complexity per se. Marler (1998), for example, has recently suggested that "... the song functions as affective rather than symbolic signals, and the variety is generated, not to diversify meaning, but rather to maintain the interest of anyone who is listening, and to alleviate habituation" (p. 12). Music rather than language might be the preferred analog for some types of animal communication. Such a view is consistent with the ideas of sensory biases and sensory exploitation discussed here. In fact, some recent studies in musicology have considered the proposition that characteristics of the human cochlea might dictate some aspects of music appreciation (Zentner and Kagan 1996).

6.3.3. Sensory Exploitation in Túngara Frogs

The call of the túngara frog, *Physalaemus pustulosus*, has two components: a whine and a chuck. The whine initiates the call, is always present, and may be followed by one or several chucks or can be produced alone. When chucks are added to the call, they are appended near the end of the whine. Up to six chucks can be added, although one to three chucks is the more common occurrence. In controlled laboratory experiments, a whine is both necessary and sufficient to elicit phonotaxis in female frogs. When females are given a choice between a whine only and a whine with chucks, females prefer the latter. Thus, the túngara frogs exhibit both chucks and preference for chucks (reviewed in Ryan 1985b; Ryan and Rand 1999).

Phylogenetic analysis combined with behavioral experimentation can sometimes provide insights into the historical pattern by which signals and receivers evolved. Pleiotropy and the genetic correlation hypotheses suggest that signals and receivers evolve in concert, whereas sensory exploitation suggests that signals exploit preexisting biases. These approaches were used to investigate the manner in which the chuck and the preference for chuck evolved.

The species group to which the túngara frog belongs is the *Physalaemus pustulosus* species group. This group consists of two smaller monophyletic groups, one west of the Andes mountains and the other in Middle America and east of the Andes (Cannatella et al. 1998; Fig. 5.9). Only species in the eastern group add suffixes to the call; they are lacking not only in the species in the western group but also in the more than 20 species of the genus that have been studied. This suggests that the chuck evolved after the two smaller groups within the species group diverged; examination of laryngeal correlates of the chuck support this interpretation (Ryan and Drewes 1990).

If females in the western group preferred chucks added to their conspecific whine, even though their males are incapable of producing them, it would suggest that preference for chucks was a preexisting bias exploited
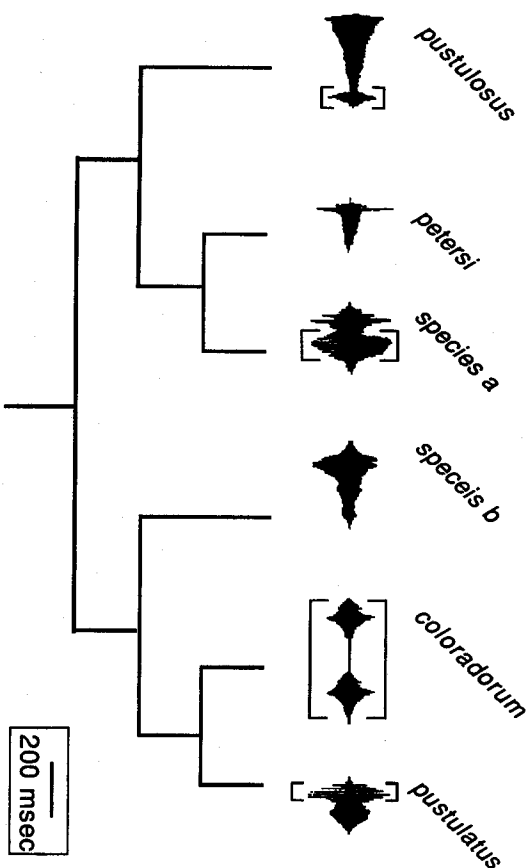
FIGURE 5.9. The phylogenetic relationships within the *Physalaemus pustulosus* species group, as determined by analysis of DNA sequences, allozymes, and morphological traits (see Cannatella et al. 1998 for details). The brackets over the calls of *P. pustulosus* and *species a* indicate call suffixes that are facultatively added. Such suffixes are absent in the sister clade and in the rest of the genus *Physalaemus*. *P. coloradorum* is the only species in the group to produce calls in doublets, while only *P. pustulatus* has an extreme amplitude-modulated component in the beginning of all its calls.

by male túngara frogs. This hypothesis would be favored over the less parsimonious one that the chuck was lost in the western group or that the preference for chucks evolved twice independently. When a chuck from a túngara frog call was digitally added to the whine call of *P. coloradorum*, a species in the western clade of the *Physalaemus pustulosus* group, females preferred calls with chucks to the normal species call, which lacks chucks (Ryan and Rand 1993). The fact that *P. pustulosus* and *P. coloradorum* both prefer calls with chucks suggests that this preference is shared through a common ancestor as opposed to the hypothesis that *P. coloradorum* females happened to evolve the same preference for traits not existing in their own males. Because the common ancestor of *P. coloradorum* and *P. pustulosus* existed before the Middle American–Amazonian and western–Andes groups diverged (Fig. 5.9), this suggests that the preference for chucks existed prior to the evolution of the chucks themselves. This supports the contention that males evolved chucks to exploit a preexisting preference for chucks.

Analogous results in a variety of other taxa suggest that sensory exploitation is not restricted to this taxon (reviewed in Ryan 1998). However, one must assume caution in interpreting these phylogenetic analyses because

the most parsimonious conclusion is only a bit simpler than the alternative of multiple losses or gains of a character (Ryan 1996).

6.4. Historical Effects on Receiver Biases

Although we have concentrated on the receiver's role in long-distance communication, hearing or, more generally, sensing ambient vibration patterns plays a more general role in the behavior and ecology of many species. Auditory receivers can partition their functions among different tasks. As discussed above, for example, the frog-eating bat, *Trachops cirrhosus*, exhibits a suite of neuroanatomical specializations that enhance hearing of the relatively low-frequency calls of frogs while still maintaining their ability to utilize ultrasonics for echolocation (Bruns et al. 1989). Alternatively, adaptations of a receiver for a noncommunication task might bias the types of signals that can be used for communication. Two examples, one involved in finding prey and the other in avoiding predators, illustrate this point nicely.

6.4.1. Evolution of Communication from Prey Localization and Predator Avoidance

Water mites do not "hear" in the sense that the vibrations they sense are borne on the water's surface rather than through the air. The vibratory patterns to which they are cued are produced by copepods, one of their main prey items, and a number of species of water mites use this information for prey localization. In one species, however, males mimic these vibrations and use them to lure females. Females approach the source of this vibration and then are courted by the male producing it (Proctor 1991). To show that the female's response appears to be incidental to courtship, Proctor (1991) showed that females deprived of food were more likely to approach and encounter courting males than were females who were satiated. The courtship communication system seems to have evolved in an exploitative process. Although many species of mites use copepod vibrations to hunt, only one of those species is known to mimic food for sex (Proctor 1992).

Animals use their ability to sense ambient vibrations to avoid becoming food as well as in finding food. In some moths, evolution of adaptations to avoid bat predation seems to have dictated some aspects of the acoustic courtship communication that has evolved.

Bats are major predators on moths, and many moths have responded to this selection force by evolving the ability to detect ultrasonics, and a subset of these moths also produce ultrasonics that seem to deter predation either because they are aposematic signals (the moths are distasteful) or because they interfere with the bats' echolocation system (reviewed in Fullard 1998).

There are at least two groups of moths in which these predator-avoidance adaptations also serve the purpose of acoustic communication.

Ultrasonic courtship signals, in the same range as the hearing of bats, increase mating success in both ctenuchid (Sanderford and Conner 1995; Simmons and Conner 1996) and wax moths (Jang and Greenfield 1996), and in some ctenuchids the males and females conduct an ultrasonic dialog. It seems probable that the use of ultrasonics has nothing to do with the precise message being sent but was a convenient channel to use because it already existed, albeit for another purpose.

6.4.2. Neural Networks and Response Biases

The examples above illustrate that if an auditory receiver is adapted for one function, this can bias how it then becomes adapted for another function. A similar effect could also occur across time but within the same function. As we have been discussing, long-distance cues are often important components of a species' mate-recognition system. When an ancestral species splits into two daughter species, the two daughter species have different recognition systems: the mate-recognition signals will differ between the species, and each species will be biased toward responding to the conspecific signal. Thus, at a minimum, one daughter species evolved a new recognition system (i.e., signal plus receiver properties) and the other maintained the ancestral recognition system, or both diverged from the ancestral signal and receiver.

There are probably a large number of computational strategies by which a receiver can bias its response to the conspecific signal. The strategy it chooses might be dependent on how ancestors of this receiver achieved the same task. For example, if within a lineage of animals the mate-recognition signals of species could always be discriminated by signal duration or by a more subtle multivariate comparison of a multitude of spectral parameters, we might expect the receiver to be biased toward using temporal parameters for recognition, much as the moths discussed above utilized ultrasonics for communication. This should be true as long as such a strategy could achieve the task.

Phelps and Ryan (1998) recently addressed this issue of historical biases of receivers by combining studies of artificial neural networks with their empirical studies of mate recognition in túngara frogs. Initially, they trained recurrent artificial neural networks to recognize a túngara frog call in 20 replicate populations. In each population, they retained the network that best discriminated between the call and noise. They then determined their responses to a variety of signals, such as heterospecific calls and purported ancestral calls, with which túngara frogs had been tested. Neither the networks nor the frogs had any previous experience with these signals. The responses to these signals therefore are considered response biases because they are incidental rather than being the target of selection. There was a strong correlation between the response biases of the frogs and the networks. Thus, whatever computational strategies these two systems were

employing to achieve signal recognition, they were producing similar response biases.

In a subsequent study, the authors examined the effect of history on response biases. Ryan and Rand (1995, 1999b) had used phylogenetic techniques to estimate what the calls of ancestors of túngara frogs might have sounded like. The correlation between evolutionary relationship (estimated as similarity in DNA sequences) and call similarity was not statistically significant—calls of close relatives were not more likely to sound alike than calls of more distant relatives. Nevertheless, female responses to the calls were predicted by phylogenetic relationship as well as, and independent from, overall call similarity. These results suggested that the history of the receiver can influence its response biases.

Phelps and Ryan (2000) trained neural networks along three distinct histories. In the first, the mimetic history, networks were trained to the call at the root of the phylogenetic tree (Fig. 5.10). Once the networks reached recognition criteria, they were trained to the call that was the next most immediate ancestor to the túngara frog. This procedure was continued on the line of descent to the túngara frogs until the networks were trained to the calls of the three direct ancestors of túngara frogs before being trained to the target call, the túngara frog call. This was replicated 20 times, and the most discriminating net in each replicate was later tested. The authors conducted the same procedure for two control evolutionary histories. For one, the random history, three cells were picked at random from the sample of heterospecific and ancestral calls. The nets were trained to these calls prior to being trained to the túngara frog calls. There were 20 random histories, and the most discriminating net in each was later tested. In another control, the calls used in the mimetic history were rotated 180° in principal component space and the new calls synthesized. The path length among these "mirror" calls was identical to the path length among the calls in the mimetic history; both of these path lengths were longer than that of the random histories. There were 20 replicates and, as with the other histories, the most discriminating net in each was saved.

The best nets from the mimetic, random, and mirror histories were tested against the same set of heterospecific and ancestral calls as with the ahistoric nets. Only the networks that were trained along the mimetic history significantly predicted the response biases of the túngara frog females. These results suggest that the past history of tasks a receiver needs to accomplish influences the computational strategies it uses to accomplish current tasks.

6.5. Summary and Conclusions

Long-distance acoustic signals are prevalent as mate-recognition signals in a number of diverse taxa and are accessible for studies by behaviorists,

a. mimetic history networks

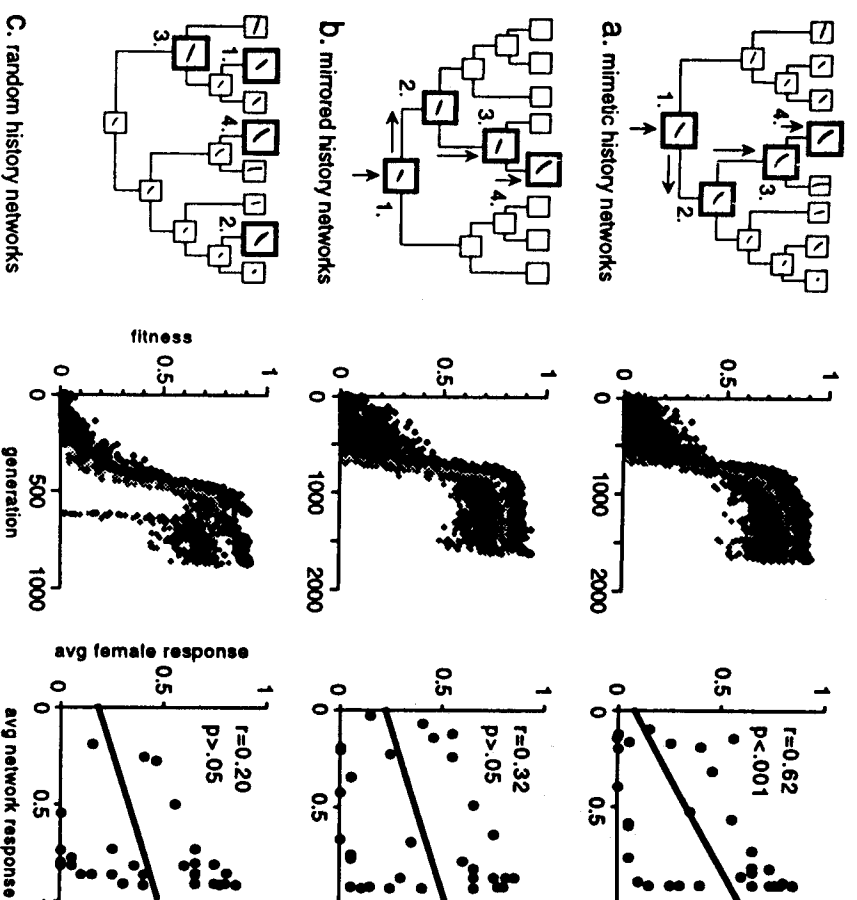**b. mirrored history networks**

c. random history networks

FIGURE 5.10. The left-hand columns show the various sequences of calls, or "evolutionary histories," to which artificial neural networks were trained. In all cases, the networks were trained to three calls prior to being trained on the túngara frog call. The middle column shows the relative fitness of the networks as a function of generation time. The right-hand column shows the relationship between the responses of networks and real female túngara frogs to an assortment of acoustic stimuli. Note that only networks trained along the mimetic history significantly predict the responses of real females (S.M. Phelps unpublished).

evolutionary biologists, and neuroethologists. As such, there is a wealth of information on their function, underlying morphological and physiological control, and how they might be influenced by selection. Most generalizations, however, are pieced together from data gathered in different systems. There are no model systems for which all of the issues we review here have been addressed. The advantage to such an approach is that we have a very good understanding of some of the diversity of long-distance communication systems. The disadvantage is that it is more difficult to appreciate how

different constraints and selection forces that are documented in different systems might interact in a single species. The underlying theme of this chapter is that long-distance acoustic signals are subject to a variety of selection forces and constraints and that the evolutionary history of a taxon can influence the manner in which it responds to such forces. Thus, a true understanding of long-distance communication will inevitably require an increase in both breadth and depth of studies.

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