In my view, *Mechanisms of Animal Behavior* (Marler and Hamilton 1966) still stands as a model of how to approach the study of animal communication. Signals should be described objectively in terms of their physical properties, and their production and recognition examined in terms of the underlying mechanisms. Of equal importance, however, are questions about the biological function and evolution of communication.

In this paper, I discuss some environmental factors that account, at least in part, for evolutionary change in communication systems. I focus on geographical variation in acoustic communication and, in particular, on reproductive character displacement, wherein divergence in two species is driven by mistakes in signal identification. This topic was discussed in *Mechanisms of Animal Behavior* in a thorough and balanced way. Examples that did not support the hypothesis were discussed along with other results, including original work comparing the songs of island and mainland birds (Marler and Boatman 1951), which were consistent with the patterns expected from reproductive character displacement.

Mixed results are common in studies of evolution, which, by its very nature, is opportunistic. For any population, group of populations, or species, the forces of evolutionary change—mutation, selection, drift, and gene flow—vary in time and space. Thus, in principle, one cannot expect to find that some particular environmental variable always plays a major role in promoting or constraining evolutionary change in communication systems. For example, some mutations affecting signal structure, female preferences, or both are subject mainly to sexual selection, while the environment plays only an indirect role. In this sense, changes in communication systems caused by sexual selection can be thought of as intrinsic. One example of an indirect role for the environment in this context is the distribution of resources required for reproduction, which determines their defensibility and can therefore influence the dominant mode (intrasexual or intersexual) of sexual selection. By contrast, other environmental factors—both biotic and abiotic—can also serve as more direct sources of selection on communication systems by influencing signal transmission or the detectability of signals. These external factors interact with sexual selection: senders whose signals most effectively propagate in a given environment, for example, have an advantage over their sexual competitors.

**Intrinsic Change in a Communication System**

One example of intrinsic change involves the advertisement calls of four species of myobatrachid frogs found in southwestern Australia. As shown in figure 18.1,
Figure 19.1
(A) Sonograms of the advertisement calls of four species of myobatrachid frogs of the genus *Gevaertia*. The arrows in the sonogram of *G. lutea* indicate the pulses produced by a second individual in the background. (B) Map showing the allopatric distributions of the four species in southwestern Australia. Notice that the species pairs with nearly contiguous distributions have the most similar calls. Modified from Roberts and Wardell-Johnson 1995.
Geocrinia alba and G. vitellina occur in the west and have shorter calls with slightly higher pulse rates than the calls of Geocrinia rosea and G. lutia, which occur in the east (Roberts and Wardell-Johnson 1995). Within each species, there is a high degree of genetic differentiation, maintained by extremely low rates of migration. Substantial differences occur even between some populations that are separated by only a few kilometers (Drisoll et al. 1994). Driscoll et al. (1994) suggest that these differences and, by extension, speciation within this complex have resulted from range contraction and local extinctions, divergence in isolated populations, and subsequent range expansion. So far, no significant ecological differences—in habitat, climate, or the acoustic community—have been documented that could reasonably be invoked to explain the call differences (Wardell-Johnson and Roberts 1993).

Thus, in my opinion, the most parsimonious view is that after establishment of the isolated populations that gave rise to the four recognized species, their calls diverged gradually by random mutation and drift. These changes would then be subject to sexual selection. The differences between the calls of the species with nearly contiguous ranges (G. alba and G. vitellina in the west and G. rosea and G. lutia in the east) are so trivial that they are unlikely to be discriminated by females; random mating would be expected if these geographically adjacent taxa become sympatric. The more substantial differences between the calls of the two eastern species vis-a-vis the calls of the two western species might reflect the initial fragmentation of an ancestral species. One scenario assumes that changes in calls arising by mutation are tested by females; very large changes might result in a call’s not being perceived as a conspecific signal. Another scenario involves random changes in female preference that serve as preexisting biases for particular changes in calls that later arise by mutation (Ryan and Rand 1993). Changes in female preference should not, however, be so large that existing signals become ineffective in mate attraction.

Sources of Environmental Selection

In many systems, environmental factors must interact directly with intrinsic processes to bias evolutionary change in sexual signals and responses. Besides mistakes of signal identification that might lead to reproductive character displacement, which is discussed in detail below, there are two other sources of environmental selection.

First, local habitats can affect transmission so that signals with particular acoustic properties are distorted less or suffer less attenuation than signals with other properties. Individuals whose signals have such favorable properties should have increased success in attracting mates or repelling rivals. There are good examples of
environmental effects on signal structure from comparisons of populations within wide-ranging species of anurans (Ryan and Wilczynski 1991) and songbirds (Nottelbohm 1975; Handford 1981), although in both systems habitat acoustics do not explain all of the geographical variation. Moreover, we badly need studies of how such changes in signals affect the responses of receivers.

Second, acoustically orienting predators and parasites can also serve as sources of natural selection, favoring signal variants that are less likely to be detected or localized (Marler 1955; Klump and Shalter 1984). Recent comparative studies of the songs and singing patterns of different populations of the cricket Teleogryllus oceanicus are particularly informative. Males in populations where an acoustically orienting parasitoid occurs produce shorter, simpler songs than males in parasite-free populations (Zuk et al. 1993). Predators can also affect the evolution of hearing in their prey. For example, the ultrasonic sensitivity of many species of moths almost certainly evolved to detect the orientation signals of their bat predators (review by Fullard and Yack 1993).

Reproductive Character Displacement

Mistakes in the identification of conspecific signals because of confusion with those of other species have negative effects on the fitness of signalers, receivers, or both. Such mistakes are the driving force for reproductive character displacement. The processes that result in preferences for the signals of a particular conspecific mate or rival are, in principle, the same as those that result in preferences for the signals of conspecific individuals over those of heterospecific individuals. Except for certain hybrid zones, however, the consequences of mistakes involving heterospecific individuals are generally far more severe than mistakes involving choices between conspecific individuals. Responses to heterospecific signals result at least in increased assessment costs (e.g., loss of time and energy, risk of predation), and there might be a loss of gametes, which will almost always be a severe consequence for the female.

This form of selection should lead to patterns of geographical variation in which differences in the acoustic signaling system (including response selectivity) will be accentuated in areas of overlap between closely related species compared with differences in areas where only one of the two species occurs. In principle, interspecific masking, of which there are good examples from insects and anurans (see, e.g., Schwartz and Wells 1983; Römer et al. 1989), could have the same result by effectively decreasing the signal-to-noise ratio and hence increasing the chances of misidentification of signals (intra- and interspecific) used in mate choice. I am unaware.
however, of any comparisons of the acoustic communication systems of different populations of a species based on whether or not masking species are present.

I apply the term reproductive character displacement to the pattern of enhanced divergence of signals, receiver selectivity, or both in sympathy and to the process (selection against mistakes in signal identification), but other definitions and terms (e.g., reinforcement) are also widely used (see, e.g., Butlin 1987; Howard 1993; Littlejohn 1997). Character release is another aspect of this phenomenon: in areas where other species with similar signals are absent, greater variance in signal structure or the dominance of some other form of environmental selection might be expected (Miller 1983).

Why Is Reproductive Character Displacement Rare?

There is a great deal of skepticism about the evolutionary significance of reproductive character displacement. One reason for this is that the conditions favoring the process and its documentation are restrictive. First, not only must there be areas of sympathy between the two taxa, but also areas of allopatry, which are required to calibrate the differences observed in sympathy (Grant 1972). Second, there must be some initial difference in signals, and yet some mistakes of identification, which are costly to the signaler, receiver, or both, must also occur, at least when sympatric contact is first established. Character displacement would not be expected if the communication systems of the interacting species have diverged so much in disjunct allopatry that individuals hardly ever interact when sympathy is achieved. Indeed, one extreme view is that species can become sympatric only if they have diverged to such an extent (Paterson 1985). Character displacement based on acoustic signals alone might be expected to be rare in birds because many species rapidly learn to discriminate between appropriate and inappropriate signals on the basis of subtle acoustic differences; moreover, birds make extensive use of visual cues to identify prospective mates and rivals (Miller 1983; Lynch and Baker 1991). Third, character displacement is favored when genetic incompatibility of the interacting taxa reduces or eliminates gene exchange and hence recombination (Butlin 1987). Recombination can break down associations between the genes that promote assortative mating and those responsible for hybrid unfitness, thus requiring strong selection to cause divergence in the area of overlap (Barton and Hewitt 1981). Fourth, the conventional view is that restricted migration and hence limited gene flow from allopatry to sympathy will favor character displacement. That is, divergence caused by selection in sympathy could be diluted when individuals in lineages established within the zone of contact mate with naive individuals that move into he zone from
outside. However, according to a recent model by Liou and Price (1994), gene flow may sometimes increase the likelihood of character displacement by rescuing from extinction the taxon with a lower population size or growth rate.

The second reason for skepticism about reproductive character displacement logically follows from the first: good examples are rare. Here there is a range of opinion about what are "good examples." On the one hand, Paterson (1985) would deny that there is any robust demonstration of reproductive character displacement, whereas Howard (1993) provides a long list of examples (see also Otte 1989). Miller (1983) offers a balanced and critical view that includes limited supporting evidence from some studies of birdsong, especially in the context of territorial defense. The following examples, which I consider the best available for acoustic signals, also serve to illustrate the difficulties of robustly demonstrating reproductive character displacement.

Two Examples of Sympatric Divergence in Acoustic Signals

Fouquette (1975) studied geographical variation in the pulse rate of advertisement calls, an acoustic property that reliably distinguishes two species of chorus frogs, *Pseudacris nigrita* and *P. feriarum* found in the southeastern United States. In *P. feriarum*, there is an abrupt increase in pulse rate at the transition between allopatry and the overlap zone with *P. nigrita*. There is little evidence for such a shift within *P. nigrita*. This pattern, and the fact that *P. feriarum* may be expanding its range southward along the Appalachee River system, supports the view of Littlejohn (1993, 1997) that changes in calls might be more likely in an invading species than in a species with an established range of distribution.

One strength of this study is that Fouquette (1975) extensively sampled areas of allopatry, thus providing baseline information about variation in pulse rate that might be expected in the noninteractive state. However, there are no estimates of the extent of mismating between the two species, nor are there experimental data concerning the minimum differences in pulse rate required for discrimination by females.

In another contact zone involving *P. nigrita* and *P. triseriata*, extensive interbreeding occurs in a narrow hybrid zone, and there is no evidence of reproductive character displacement (Gartside 1980). Gartside (1980) and Littlejohn (1997) suggest that the difference in the outcome of interactions in the two zones of contact might be caused by ecological factors. This counterexample underlines my caveat about the variability of evolutionary processes in time and space.

Littlejohn (1965) documented a striking divergence in sympatric areas between the pulse rates of the calls of *Litoria ewingii* and *L. verreauxii*, which are two treefrogs found in southeastern Australia. While the hypothesis of reproductive character displacement could be improved by additional sampling in areas of allopatry, addi-
tional studies provided critical information about the salience of the observed differences in calls to receivers. Littlejohn and Loftus-Hills (1968) showed that females of both species from the western part of the overlap zone discriminated between the calls of a conspecific male and a heterospecific male recorded in the same area; females did not, however, discriminate between local conspecific calls and heterospecific calls recorded in allopatry. Moreover, females of *L. verreauxii* from western sympathy preferred the call of a local conspecific male to that of a conspecific male from allopatry.

More recently, Littlejohn et al. (1993) provide evidence for character release (an increase in variance) in pulse rate in *L. ewingii* introduced from Tasmania to New Zealand. Additional details concerning these and other examples of reproductive character displacement of acoustic signals in anurans are provided by Littlejohn (1997).

**Sympatric Divergence in Receiver Selectivity for Acoustic Signals without Divergence in Signals**

Waage (1979) pointed out that reproductive character displacement might be more common than is generally accepted because most studies have focused only on signals and not on receiver selectivity. Enhanced divergence of signals is not always a necessary consequence of interspecific interactions in sympathy if, for example, the signals of two taxa were to become different enough to be discriminated during the noninteractive period of geographical separation. Selection on receivers should generally be strong because receivers usually have more to lose than signalers from a mating mistake in the case of females, or from unnecessary aggression in the case of territorial males. Data consistent with this view are available for several species of *Drosophila*, a katydid, and some songbirds (review in Gerhardt 1994). A particularly well-studied example is the subject of the rest of this chapter.

**The Gray Treefrog Complex: A Model System**

The gray treefrog, *Hyla chrysoscelis*, is a diploid species; there are two or more sibling species that are biparental tetraploids currently designated as *H. versicolor* (Patek et al. 1994). Mismatings result in sterile triploid offspring with reduced viability (Johnson 1963). Here I focus on geographical variation in the advertisement calls and female phonotactic selectivity of the diploid species.

Mate choice in these treefrogs is based solely on a single type of long-range acoustic signal, the advertisement call, which is produced only by males. Females
approach a speaker from which conspecific calls or appropriate synthetic calls are played back, and there is no evidence of any kind of close-range assessment by either sex prior to mating. There is only one mating by a female on any given night, and usually only one mating per season (Ritke and Seghier 1991). Finally, males do not displace other males from mating pairs, nor do males defend territories containing resources used by females. These are important attributes for testing for character displacement. If other sensory cues were used, say, at close range, as they are in many insects and birds (Miller 1983; Ewing 1989), then the selection for divergence in acoustic signals would be weakened. Similarly, mating mistakes are potentially more costly when there is only one chance for fertilization, as compared with insects, for example, in which multiple matings might occur over short periods of time. If males were to compete physically for females, or if females were to assess territorial quality, then selection on signals and response selectivity would also be considerably weakened.

As shown in figure 18.2, the calls of the two species have the same basic temporal and spectral structure. They differ in two stereotyped properties: pulse rate (after temperature correction), and the shape (= amplitude-time envelope) of the pulses. On the one hand, females of both species discriminate between synthetic signals that differ only in pulse rate by the average magnitude existing between the calls of the two species in nature at the same temperature. On the other hand, females of both species often show phonotactic approaches to a source of heterospecific advertisement calls when conspecific calls are unavailable (Gerhardt and Doherty 1988). That is, females treat the calls of the other species as signals, and females sometimes make mistakes in nature. The frequency of mispairing at sympatric breeding sites in Missouri can be as high as 5% (Gerhardt et al. 1994), although some mistakes probably do not involve misidentification of calls but rather a female’s inadvertently moving too close to a male of the wrong species. Again, some misidentification of signals that reduces the fitness of signalers, receivers, or both favors reproductive character displacement and is a requirement for its initial stages.

As shown in figure 18.3, there are widespread areas of stable sympatry with H. versicolor; within these areas, the two species frequently breed synchronously at the same breeding sites, although there may be some differentiation of calling sites within such ponds (Pracek 1992). As pointed out by Littlejohn (1993), the processes leading to the establishment of sympatry are poorly understood, and the outcome of interactions between species (or groups of populations that are not formally recognized as separate species) is often indeterminate, especially when there has been limited divergence of the ecology and communication systems during the period of disjunct allopatry. The widely separated areas of sympathy provide the opportunity to generalize
Figure 18.2
Oscillograms of (A) advertisement calls and (B) representative pulses from those calls of *Hyla versicolor* (top trace) and *H. chrysoscelis* (bottom trace) (C) power spectra of calls of *H. versicolor* (top) and *H. chrysoscelis* (bottom). The recordings were made at about 18°C at the same locales in Missouri. From Gerhardt 1952.
Figure 18.3
Map showing the geographical distribution of the diploid species of the gray treefrog (*Hyla chrysoscelis*) and its tetraploid sibling species (*H. versicolor*). There are likely to be areas of sympatry within some poorly sampled regions where the presence of only one species has been established.
about differences in the communication system of *H. chrysocelis*, if any, that are associated with the presence of *H. versicolor*. The large areas of allopatry in the southeastern United States allow us to assess the degree of geographical variation in *H. chrysocelis* that can occur in the absence of tetraploid species.

Finally, there are also data, based on chromosome polymorphisms (Wiley et al. 1989), allozymes (Rafin and Selander 1979), and mtDNA sequences (Ptacek et al. 1994), that bear on genetic differentiation within both species. Thus strong tests of character displacement can be made by comparing sympatric and allopatric populations that show, by other criteria, minimal genetic divergence. Otherwise, differences between the communication systems of such populations could be interpreted as historical effects of past evolutionary divergence. For example, analyses of mtDNA sequences indicate that tetraploids have arisen independently multiple times from *H. chrysocelis*, and the calls of all of the different lineages are very similar in pulse rate and shape (Ptacek et al. 1994). Moreover, females from the two lineages of *H. versicolor* that have been studied show preferences based on pulse shape; such preferences are absent in females of *H. chrysocelis* (Gerhardt and Doherty 1988; Diekamp and Gerhardt 1995; Gerhardt, unpubl. data). These call differences, the new preference, or both could have arisen, in part, as a consequence of polyploidization. Bogart and Wasserman (1972) first proposed this hypothesis, and Ueda (1993) showed that artificially produced polyploids of the treefrog *Hyla japonica* produced calls with lower pulse rates than those of diploid controls. Preliminary results from similar experiments with *H. chrysocelis* also show that autotriploid males produce calls with significantly lower pulse rates than diploid controls (Keller and Gerhardt, unpubl. data).

**Geographical Variation in Pulse Rate**

I focus on variation in pulse rate in *H. chrysocelis* because females of this species show strong preferences based solely on differences in this acoustic property and because the extent of geographical variation in pulse rate is much greater than in *H. versicolor*. Advertisement calls were recorded along three major east-west transects, and mean pulse rates, corrected to a common temperature, are shown for many of these populations in figure 18.4. Mean pulse rates in sympatric populations are not consistently higher than those in populations in adjacent allopatry; indeed, greater differences in mean pulse rate are found among populations in remote allopatry along the southern transects (up to 12 pulses/s) (statistical analyses in Gerhardt et al. in preparation). These data indicate that, in terms of the current distributions of these frogs, geographical patterns of variation in mean pulse rate are inconsistent
with the patterns expected from the operation of reproductive character displacement on the calls of *Hyla chrysoscelis*.

These data do not rule out the possibility that reproductive character displacement played a role in signal divergence in the past. Besides changes in the ranges of distribution that would obscure the expected pattern of geographical variation, interactions at the time that the tetraploids arose and became established could have caused major shifts in pulse rate in the diploid or the tetraploids. If call differences occurred as a consequence of polyploidization, for example, then strong selection against infertile hybrids could have rapidly enhanced the differences. In a theoretical
analysis of reinforcement by Liou and Price (1994), for example. complete isolation could be achieved within 60 generations under some conditions, such as low recombination. An interesting feature of their model is the assumption that genetic correlations arise between signals and preferences, as in models of indirect sexual selection (Fisher 1930). Once started, further divergence could occur even in the absence of additional mating mistakes, being driven instead by Fisherian sexual selection.

Geographical Variation in Female Selectivity

If indirect sexual selection did play a role in the initial divergence of the communication systems of the diploid and tetraploid species, then present-day geographical variation in female preferences would be expected to parallel patterns of variation in male signals. Thus present-day sympathy with H. versicolor would not be expected to explain geographical differences in the pulse-rate selectivity of females of H. chrysoceles, just as it explains little, if any, of the differences in pulse rate.

At one level of analysis, the expected correlation between variation in pulse rate and female preferences based on this property occurs in H. chrysoceles. In figure 18.5, I summarize the results of experiments in which females were given choices between synthetic calls that differed only in pulse rate. Females from both sympatric and allopatric areas usually reject alternatives that have pulse rates that are about 50% higher or 20% lower than a standard call, defined as having a pulse rate equal to the mean value in the calls of males in the population from which the females were collected (Gerhardt 1994). Thus, all things being equal, even females from remote allopatric populations would be expected to discriminate against the calls of H. versicolor. Females should also discriminate against the calls of some males in their own population and against the calls of many males from some other populations (figure 18.4).

In nature, however, not all things are equal or average. First, many conspecific and heterospecific calls will differ by less than the average difference in some behaviorally relevant acoustic property (see also Littlejohn 1997, who derives a measure of differentiation between interacting taxa that considers the gap in the ranges of variation of call properties). Second, in the experiments just mentioned, not only were all other attributes of the synthetic calls held constant, but the pulse rate of the standard call corresponded to the mean value of a local male at 20°C, and females were tested at the same temperature. Temperature variation of the order of 5°C on the same night is common in breeding ponds (Gerhardt 1994). Thus, because pulse rate and female preferences for a particular pulse rate in both species are temperature-dependent (Gerhardt 1982; Gerhardt and Doherty 1988), females must often be confronted with choices of conspecific and heterospecific calls that are effectively
Figure 18.5
Current estimates of pulse-rate selectivity in females of *Heliothis zea* from throughout the range of geographic distribution. The points at the top of the figure show the average percentage of females that chose a standard synthetic call (ω = mean pulse rate of males from the same population at 20°C) which was also the test temperature: the points at the bottom of the figure show the average percentages of females that chose alternatives to the standard call that were either 20%, lower or 50% higher in pulse rate. Females did not prefer the standard call over alternatives that were 10% lower or 25% higher. See Gerhardt (1994) for details concerning the playback experiments.

much less different in pulse rate than the average, temperature-corrected difference. Third, conspecific and heterospecific calls encountered in nature also vary in carrier frequency, duration, call rate, and sound pressure level (SPL), and variation in each of these properties also affects female preferences (Gerhardt 1975, 1994; Gerhardt et al. 1996). For example, the average call duration among males of both species varies by a factor of 300% or more in many populations (Gerhardt 1994), and females of both species prefer long calls to short calls, sometimes even when the source of short calls is closer and of greater amplitude (Gerhardt 1994; Gerhardt et al. 1996).

Fourth, the relative amplitudes of the first conspecific and heterospecific signals that are detected by a female will obviously depend on where it enters a mixed-species chorus.

These considerations led me to design experiments that reflected the more difficult choices that some females would experience in nature. First, I reduced the difference
in pulse rate between synthetic calls from the usual 40–60\% to about 30\%, a difference that has been documented in mixed-species choruses (Gerhardt 1994). Second, I either increased the duration of the alternative with the lower pulse rate (the “H. versicolor” stimulus) or lowered the SPL of the standard call. My strategy was, within the limits observed in nature, to favor the stimulus with the lower pulse rate to the extent that some females from sympatric populations chose the longer or louder calls. I could then compare the pulse-rate selectivity of females from these and other sympatric populations with the selectivity of females from allopatric populations in these more difficult and realistic choice-tests.

Earlier, I presented data showing that females from three sympatric areas were much more selective than females from two allopatric regions in experiments in which the standard call was shorter than the alternative stimulus of lower pulse rate (Gerhardt 1994). Since then, additional females from the same and different populations (one sympatric and two allopatric) have been tested, and the results for all sympatric and allopatric populations are summarized in figure 18.6a. The new data corroborate these earlier results. The highest proportion of females choosing these standard call from an allopatric population for which there were reasonable samples was about 65\%, and the lowest proportion from a sympatric population was about 85\%.

The proportions of allopatric and sympatric females that chose the standard call rather than the alternative with a higher SPL and lower pulse rate are also summarized in figure 18.6a. The results parallel those for the unequal-duration experiment, except that, as shown in figure 18.6b, about 75\% of the females from allopatric areas in the southeastern part of the range chose the standard call. By contrast, only about 30\% of the females from an allopatric population in Kentucky chose the standard call. This difference serves to reemphasize that multiple factors (including historical ones), and not just the presence or absence of another species, are likely to affect the evolution of communication systems.

These results have implications outside the context of character displacement. First, the data show differences in the potential for directional change in pulse rate. That is, the strength of stabilizing selection acting on pulse rate is weaker and more easily confounded by other acoustic variables in allopatric populations than in sympatric populations. Second, the existence of geographical variation in the strength of preferences and the relative importance of different acoustic properties means that neurobiologists interested in the underlying mechanisms must be concerned with the collecting sites of the animals they study. Findings from only one or two populations or from randomly sampled individuals from throughout an extensive geographical range are unlikely to be general for the whole species. For *H. chrysocelis*. 
Figure 18.6
(A) Histograms summarizing the results of two-speaker playback experiments with females of *Hyla chrysoscelis* from areas of sympatry and allopatry. The percentages of females choosing the standard synthetic call are shown. The alternative stimulus had a pulse rate that was approximately 50% lower, and either its sound pressure level (Unequal SPL) was 12 dB higher than that of the standard call (85 dB versus 73 dB) or its duration (Unequal Duration) was three times longer than that of the standard call (1.2 versus 0.4 s). The numbers on the histograms indicate the numbers of frogs tested from either allopatric areas (Allop) or sympatric areas (Symp). These data include previously published results (Gerhardt 1994) for the Unequal Duration experiments, plus additional unpublished data for these experiments and the Unequal SPL experiments (Gerhardt, in preparation). (Bi Histograms showing the data for three allopatric regions of
for example, we might expect to see geographical differences in the tuning properties ("best" pulse rate and cut-off values) of bandpass neurons in the midbrain (Rose et al. 1985).

This research is ongoing. Sample sizes need to be increased for some populations that have already been studied in order to improve our estimates of female selectivity, and, of course, additional populations must be studied. These additional populations should be chosen to increase the number of within-lineage comparisons, that is, pairs of sympatric and allopatric populations, which by other independent criteria show little genetic divergence. Moreover, because most comparisons of female selectivity have been between animals collected from sympatric areas and animals from remote allopatry, it will also be important to study females from populations that are intermediate in their geographical location in order to assess the possible effects on receiver selectivity of gene flow.

Summary

1. Intrinsic changes in communication systems may be subject mainly to sexual selection, with the environment (physical and biotic) playing only an indirect role of influencing the dominant mode of sexual selection.

2. Environmental sources of selection that can interact with intrinsic changes and sexual selection include: (a) habitat effects on signal structure and attenuation; (b) acoustically orienting predators and parasites; (c) reduced efficiency of communication caused by masking interference generated by the signals of other species; (d) negative consequences (loss of fitness) of misidentifying and responding to the signals of other species.

3. Good examples of reproductive character displacement are rare, reflecting the restrictive conditions favoring this process and the difficulty of documenting this phenomenon. In particular, additional divergence of signals in sympatry is unlikely to occur in taxa that use multiple cues (modalities) for mate identification or whose signals diverge sufficiently during allopatric disjunction to be readily discriminated.

Figure 18.6 (continued)

populations that were lumped in figure 18.6a. The data from the southeastern United States (SE US) included females collected at two localities in Florida, one in Georgia, two in South Carolina, and one in Alabama. The data from Central Kentucky (K.Y.) were derived from females collected at a single locality, and the data from Central Texas (T.X.) were obtained from females collected at two localities (Gerhardt, in preparation).
4. One new perspective, exemplified by studies of the gray treefrog complex, emphasizes a multivariate approach to analyzing both the signals of the entities and the mate-choice criteria used by receivers.

5. Gray treefrogs show patterns of geographical variation expected from reproductive character displacement in female preferences but not in male advertisement calls. However, the effects of sympathy on selectivity were detected only by offering females biologically realistic choices of acoustic stimuli.

6. There appear to be differences in selectivity between allopatric populations as well as between sympatric and allopatric ones, suggesting that generalizing from one or two populations is risky.

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