

Geographic Variation in Animal Communication Systems

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Intraspecific communication is fundamental to most social behavior. It is also a special problem in animal behavior because it necessarily involves the interaction of two systems within a species, a sender and a receiver (Walker 1957, Blair 1964, Capranica 1966, Schneider 1974, Hoy et al. 1977, Hopkins and Bass 1981, Gerhardt 1988, Brenowitz 1994). Sender and receiver components are almost always separable morphologically, physiologically, and behaviorally. Each may be under different mechanistic and developmental control, and, especially in those cases in which the senders and receivers are segregated by sex, the impact of selection pressures and constraints can be very different (Brenowitz 1986, Ryan 1986, 1988; Wilczynski 1986, Endler 1983, 1993). The presence of two different but necessarily interacting components make the evolution of communication systems a particularly challenging problem in behavioral biology.

In any communication system, the interaction between senders and receivers dictates some degree of matching such that the signal emitted by one member of the communicating pair is effectively received, recognized, and assessed by the other member (Blair 1964, Gerhardt 1982, 1988; Capranica and Moffat 1983, Littlejohn 1988, Ryan 1988, 1991; Endler 1993). Effective coupling of senders and receivers is crucial when communication underlies mate choice. Communication systems that accurately discriminate between heterospecifics and conspecifics, while effectively linking conspecifics to each other, are important for ensuring mating with genetically compatible conspecifics. As such, communication systems can be integral parts of speciation and the maintenance of species isolation (Blair 1958, Mayr 1963, Paterson 1985, 1993; Littlejohn 1981, 1988; Butlin 1987, Coyne and Orr 1989, Claridge 1993, Moore 1993, Wood 1993).

The natural variation among and within species in both signals and receivers provides a means for examining the factors contributing to the evolution of com-

munication systems (Templeton 1981, Ryan and Keddy-Hector 1992, Paterson 1993). Among the different levels of variation observed, geographic variation provides the best material for disentangling the myriad factors shaping the evolution and divergence of communication systems and for testing fundamental ideas about the evolution of behavior (Endler 1983, Baker and Cunningham 1985, Nevo and Capranica 1985, Ryan and Wilczynski 1991, Loftus-Hills and Littlejohn 1992).

Heterospecific and Conspecific Variation

The obvious function of communication signals in separating conspecifics from heterospecifics has led to examination of species-specific characteristics of communication systems (e.g., Wells 1977, Hopkins 1980, Capranica and Moffat 1983, Walkowiak 1988, Penna et al. 1990, Wilczynski et al. 1993). For example, both sensory systems and signals used by frogs have been shown to be species-specific, and, on average, sensory systems have proven to have areas of expanded representation (Narins and Capranica 1976) or enhanced sensitivity (reviewed in Walkowiak 1988, Zakon and Wilczynski 1988) that match important features of the signal. The species-typical characteristics of signals and receivers, important for the recognition functions critical to reproduction, should tend to constrain the evolution of intraspecific diversity. Although the magnitude of this effect is difficult to quantify, phylogenetic relationships predict the maintenance of some degree of behavioral similarity (Ryan 1986, Ryan and Rand 1993a, 1995; Brenowitz 1994, Cocroft and Ryan 1995). Thus, intraspecific change should be constrained to occur within a species-typical framework.

Even above the species level, many features of vertebrate sensory systems are shared and may thus constrain or channel the evolution of call diversity. The discovery of such common sensory characteristics has led to the suggestion that some operations apparently specialized for communication may in fact be generalized neural processing operations coopted for recognizing conspecific signals. Rose (1986) suggested that midbrain feature detectors for amplitude modulation rates characteristic of many acoustic communication signals are no different from the neurons sensitive to temporal patterns in sound that are found in many vertebrate auditory systems, regardless of the use of such sounds in intraspecific communication. Similarly, Wilczynski and Capranica (1984) noted that the two-tone suppression apparent in the peripheral auditory system of amphibians, while clearly important for bullfrog call recognition, is a common feature of all terrestrial auditory systems. Similarly, multiple syllables in bird song may have evolved to counteract habituation common to all sensory systems (Searcy 1992), and peripheral auditory system tuning characteristics common among species of *Physalaemus* may have channeled the evolution of calls toward features that better stimulate the ear's receptors (Ryan and Rand 1993a).

Despite potential constraints on diversity, the communication signals and receiver characteristics of species do vary geographically. The diversifying effects of variation in habitat, in pleiotropic effects brought on by evolutionary changes

in noncommunication characters of organisms, and in selection due to interactions between species and among conspecifics may interact in different ways in different parts of a species' range, leading to significant differences among populations and among species occupying different habitats.

Environmental Effects and Variation in Communication Systems

Ecological factors can have direct effects on the evolution of geographic variation within a species and can account for some of the differences among species in different habitats. Signals must be transmitted through the environment from sender to receiver. Therefore, habitat characteristics can impose selection on the form of a communication signal (Lythgoe 1979, Brenowitz 1986, 1994; Endler 1991, Dusenbery 1992, Fleishman 1992, Narins 1995). Studies of acoustic signals have demonstrated adaptation to local environmental conditions enhancing transmission (Wiley and Richards, 1978, 1982; Gish and Morton 1981, Bowman 1983, Ryan et al. 1990a). In visual communication, variation in background clutter, ambient light, and, in aquatic environments, clarity of the transmission medium, can similarly influence a signal's effectiveness (Endler 1983, 1991, 1992; Fleishman 1992). Studies of both interspecific (Marchetti 1993) and intraspecific (McKenzie and Keenleyside 1970, Endler 1983, 1991; Reimchen 1989) signal variation have suggested that geographic variation in habitat characteristics can indeed affect the evolution of visual signals.

Environmental factors might also shape communication signals indirectly by acting on morphological traits correlated with aspects of the communication system (Ryan 1988). The most obvious of these is body size. For example, Nevo and Capranica (1985) suggested that in cricket frogs (*Acris crepitans*), dry conditions in western parts of their range favor larger body sizes that decrease desiccation (Nevo 1973). As call frequency and body size are negatively correlated in frogs (Ramer et al. 1983, Ryan 1985, Wagner 1989a, Keddy-Hector et al. 1992), western cricket frogs would have lower-frequency calls than eastern cricket frogs on this basis alone (Nevo and Capranica 1985). Narins and Smith (1986) made a similar suggestion to explain altitudinal variation in call frequencies in some tropical frogs. Tuning of the auditory system is also negatively correlated with body size in frogs (Wilczynski 1986, Zakon and Wilczynski 1988, Keddy-Hector et al. 1992), so environmental selection acting on body size might also affect the receiving portion of the communication system in these vertebrates.

Habitat differences in predation can also lead to geographic variation in communication systems. Endler's (1980, 1988) studies of guppies demonstrate that the presence of visually-hunting predatory fish in some areas provides a strong selection pressure on the color patterns male guppies use to attract females. Although there have been no studies of habitat differences in predation effects on acoustic communication systems as thorough as those of coloration in guppies, Ryan (1985, Ryan et al. 1982) demonstrated that bats prey on Túngara frogs by locating their calls and that the frogs' calling behavior was influenced by this

predation. Presumably, geographic variation in bat predation could lead to geographic variation in calling in these frogs.

Social Behavior and Variation in Communication Systems

Heterospecific interactions and interference that occur as each species engages in its own mating behavior can influence the form of another species' communication behavior (Blair 1958, Walker 1974, Schwartz and Wells 1984, Butlin and Hewitt 1985, Gwynne and Morris 1986, Gerhardt 1988, Littlejohn 1988, Coyne and Orr 1989, Otte 1989, Loftus-Hills and Littlejohn 1992, Ryan and Rand 1993a,b). Where species breed together using acoustic signals, one often observes an apparent partitioning of communication channels (Drewry and Rand 1983, Duellman and Pyles 1983, Wilczynski et al. 1993). Such interactions could, in principle, lead to geographic variation if the mix of interacting species varies across a species' range, although there is little documentation of this.

One evolutionary issue that directly relates heterospecific interactions to geographic differences in a species' communication system is the phenomenon of "character displacement." In areas of its range where a species or population is sympatric with another having a similar communication system, there can be increased selection to limit mate choice "mistakes" (Brown and Wilson 1956, Littlejohn this volume). This can result in an accentuation of the differences in the courtship signals of the two groups. This idea has been applied to zones of overlap between subgroups within a species (i.e., pairs of subspecies or "incipient" species), as well as between pairs of genetically incompatible species (Nevo and Capranica 1985, Butlin 1987, 1989; Littlejohn 1988, Otte 1989). Butlin (1987) suggests that the term "character displacement" be used to describe this phenomenon where the sympatric groups are historically separate species producing infertile hybrids if mated, and that "reinforcement" be used where interacting species or sufficiently (genetically) different populations within a species may produce fertile hybrids with reduced fitness. In either case, the result in terms of geographic variation in the communication system within a species is the same: a shift in signal or receiver characteristics away from those of the interfering signal at points in the geographic range where groups interact. Because selection leading to this shift is absent at points in the range where only one population exists, differences between sympatric and allopatric populations within a species are expected.

Reproductive character displacement and reinforcement remain controversial (see also Littlejohn this volume, Verrell this volume). They have been challenged theoretically (Templeton 1981, Butlin 1987), and there have been few unequivocal empirical demonstrations of these phenomena. Most searches for character displacement have targeted the signals rather than the receiver portions of communication systems. The best examples occur in the calls of some frogs (Littlejohn 1965, Fouquette 1975, Ralin 1977, Loftus-Hills and Littlejohn 1992) and insects (Otte 1989, Benedix and Howard 1991). There is also some evidence that female discrimination can change geographically in ways that suggest character

displacement (Wasserman and Koepfer 1977, Waage 1979, Gwynne and Morris 1986, Gerhardt 1994).

Intraspecific social interactions also drive the evolution of communication systems, although in a way less clearly predictive of particular patterns of geographic variation. Sexual selection induced by a bias among females for particular male signal characteristics is the primary example of a social factor that can drive the evolution of male communication signals. There is abundant evidence in many species that females not only prefer the signals of conspecifics to heterospecifics, but that they find some conspecific signals more attractive than others (Kirkpatrick 1982, Ryan 1985, Bradbury and Andersson 1987, Rand et al. 1992, Ryan and Keddy-Hector 1992, Endler and Houde 1995, Tokarz 1995, Wilczynski et al. 1995).

Disagreements exist about why female mating preferences are expressed (see reviews in Bradbury and Andersson 1987, Kirkpatrick and Ryan 1991, Andersson 1994, Tokarz 1995). Adaptive hypotheses posit that female preferences evolve either because females exerting those preferences produce more offspring due to immediate benefits provided by the male (e.g., parental care, nuptial gifts, or greater fertilization efficiency) or because the genes controlling signal characters become genetically correlated with a male's "good genes," and the preference then evolves via indirect selection. A hypothesis of "arbitrary" female mate preference is Fisher's theory of runaway selection (Fisher 1958), which suggests that female preferences evolve due to a genetic correlation with a male trait. A third hypothesis, "sensory exploitation" (and its more general form, "sensory drive"), suggests that there are preexisting biases in the female's sensory system, which may or may not be adaptive in the context of mate choice or other aspects of the animal's life such as foraging, and that males evolve traits that are more attractive to females given these sensory biases for particular stimulus configurations (Ryan 1990a, Ryan and Rand 1990, Endler 1992, Ryan and Keddy-Hector 1992, Enquist and Arak 1993).

Several authors (e.g., Fisher 1958, Ringo 1977, Lande 1981, West Eberhard 1983, Eberhard 1985) suggest that sexual selection driven by mate choice can have diversifying effects on communication systems, and others (Endler 1980, 1983; Eberhard 1985, Ryan and Keddy-Hector 1992) provide evidence that mate choice can provide strong directional selection on male signals. Sexual selection, when not mediated by "good genes," is unpredictable, which means that its expression in different conspecific populations could in principle lead to geographic variation in the characteristics of the communication system (Fisher 1958, Ringo 1977, West Eberhard 1983, Ryan 1990a,b). If mate choice has evolved under the influence of "good genes" or some instances of "sensory drive," the direction of evolutionary change might be more predictable but might still lead to geographic variation in communication signals if factors that influence fitness vary geographically (Endler 1993).

Ecological and social factors are obviously not mutually exclusive in their influence on communication systems. They, plus other factors such as genetic drift in isolated populations, and patterns of gene flow across a species' range, likely interact in complicated ways to yield the geographically changing profile

of communication characteristics seen in many species. The interaction among various factors can be seen in one model system, the acoustic communication system of the cricket frog, *Acris crepitans*.

Geographic Variation in the Communication System of Cricket Frogs

Cricket frogs, *Acris crepitans*, are members of the family Hylidae. This species occupies much of eastern and central United States and is the only representative of the genus in the western part of its range across Texas and northeastern Mexico. Male cricket frogs produce a short, clicklike advertisement call, which they repeat in rapid bursts referred to as "call groups" (fig. 11-1, Nevo and Capranica 1985, Wagner 1989b, Ryan and Wilczynski 1991). The call serves as a mate recognition signal (Nevo and Capranica 1985, Ryan and Wilczynski 1988, Ryan et al. 1992) and also mediates aggressive interactions among males (Wagner 1989a,b,c). Therefore, the communication system in this species, as in most anurans, consists of a vocal signal (produced by males) and the auditory system (in females and males) receiving it.

Like other anurans, cricket frogs have two inner ear organs sensitive to sound (see Wilczynski and Capranica 1984, Zakon and Wilczynski 1988, Wilczynski 1992 for reviews of the amphibian auditory system). Each receptor structure, and each of the eighth nerve fibers connected to them, can be described in terms of its tuning. Tuning is the range of sound frequencies that will stimulate its receptors and the frequency to which it is most sensitive (its "best excitatory frequency"). In cricket frogs, as in many small anurans, the advertisement call stimulates only the basilar papilla (Capranica et al. 1973, Ryan and Wilczynski 1988). The amphibian papilla, which is larger and tuned to a wider range of lower frequencies, is not used for the reception of calls in cricket frogs.

The populations of *Acris crepitans* we examined (Ryan and Wilczynski 1991), occur along a transect from the Texas-Louisiana border to Lake Balmorhea in west Texas (fig. 11-2). The transect passes through the ranges of two recognized subspecies of cricket frogs (Dessauer and Nevo 1969, Salthe and Nevo 1969), *A. c. crepitans*, which occupies the eastern portion of the range, and *A. c. blanchardi*, which occupies the western portion, as well as the zone of parapatry between them in east Texas. The eastern habitat of *A. c. crepitans* is piny woods characterized by wet, dense forests. The western areas occupied by *A. c. blanchardi* include post-oak savannah, blackland prairies, Edwards Plateau, and Trans Pecos; all these habitats are drier and more open than those in the eastern areas (McMahon et al. 1984). Cricket frogs are also found in an isolated pine forest habitat in Bastrop County, an area of central Texas within the range of *A. c. blanchardi* and surrounded by the drier, open habitat characteristic of this subspecies. Preliminary allozyme analysis suggests that the Bastrop cricket frogs are more closely related to the *A. c. blanchardi* in the grasslands surrounding them than to the *A. c. crepitans* that live in similar forest habitat farther east.

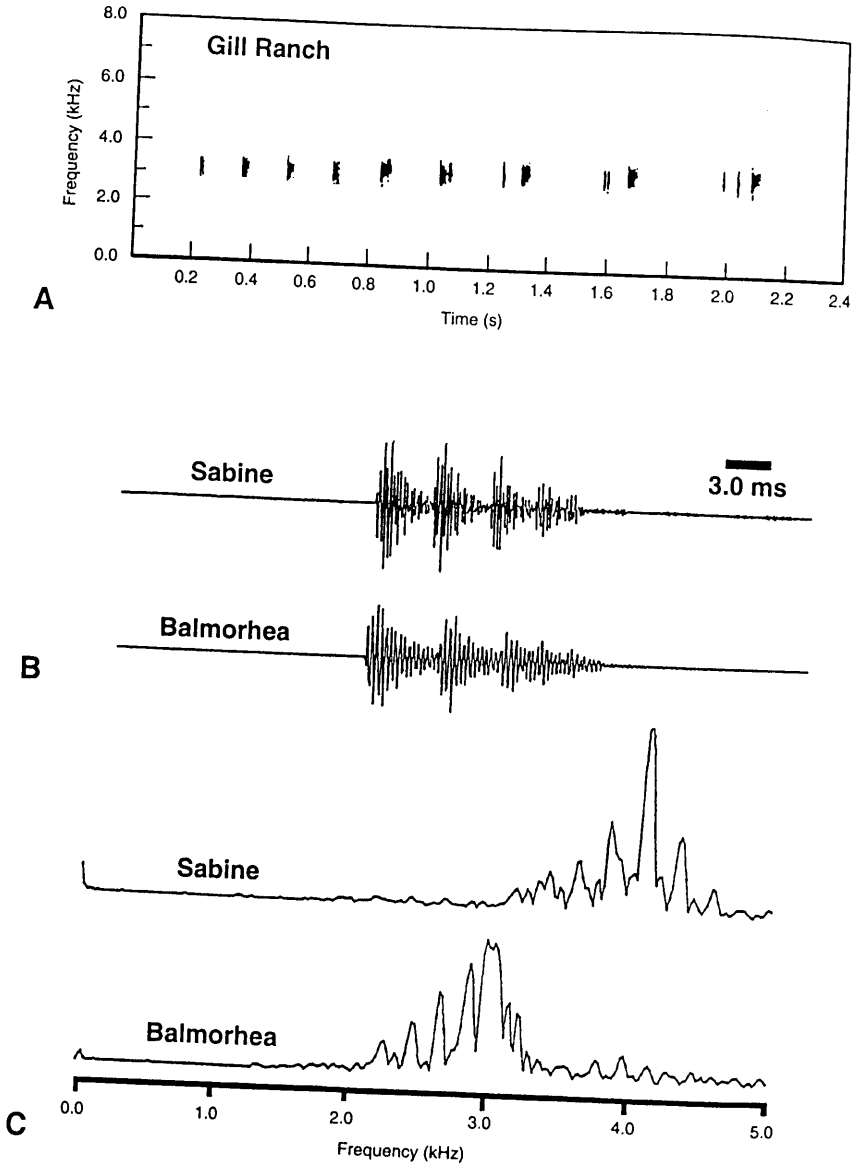


Figure 11-1 (A) Sonogram of a call group from a male cricket frog from the Gill Ranch population at the approximate center of our study transect (from Ryan and Wilczynski 1991). (B, C) Oscillograms and spectrograms of calls from populations on the eastern (Sabine) and western (Balmorhea) ends of our study transect. Note that the western calls and their component pulses are slightly longer (B) and much lower in frequency (C) than the eastern calls.

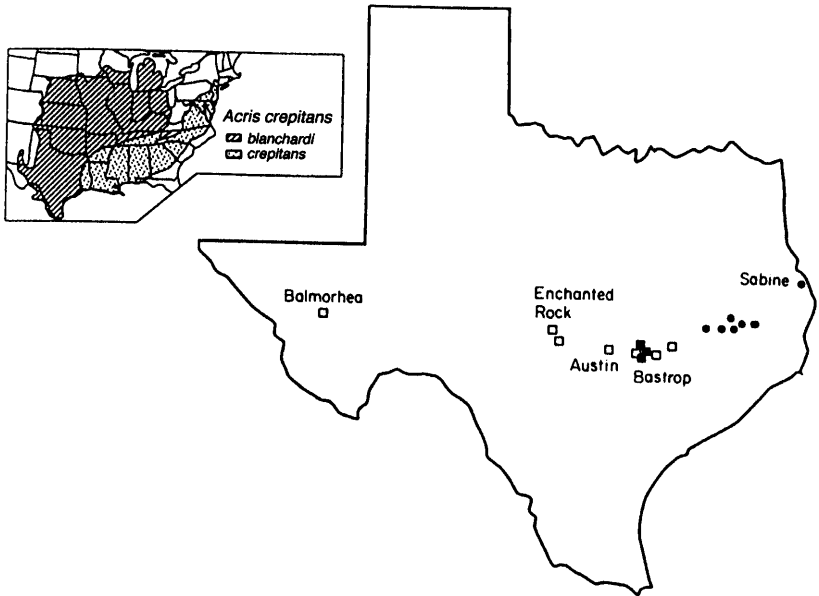


Figure 11-2 Location of cricket frog (*Acris crepitans*) populations studied to assess geographic variation in their communication system. (Circles) Populations of *A. c. crepitans* (all in forest habitats); (open squares) populations of *A. c. blanchardi* from open habitats; (filled squares) populations of *A. c. blanchardi* in forest habitats in the "Lost Pines" area of Bastrop, Texas. Inset at upper left shows the range of the two subspecies of *Acris crepitans*. (From Ryan and Wilczynski 1991.)

Geographic Variation in the Call

Temporal and spectral call characteristics show significant geographic variation among cricket frog populations along this transect (Ryan and Wilczynski 1991). Some temporal characteristics appear to vary randomly, but there is a strong clinal component to much of this variation. The dominant frequency of the call (the frequency with the most energy), call rate, and call group duration most reliably distinguish populations. In general, calls are higher in frequency, shorter, and produced at a faster rate in the eastern part of this range (fig. 11-1). Dominant frequency exhibits the strongest clinal variation of any call character as it descends from east to west.

Call variation is also significantly related to habitat and subspecies (Ryan and Wilczynski 1991). The results of a principal component analysis (PCA) of call variation among populations are shown in figure 11-3. There are two patterns of interest. First, the calls of *A. c. crepitans* tend to be more clumped on the PCA plot than the calls of open-habitat *A. c. blanchardi* populations. Also, the calls of *A. c. blanchardi* from the isolated forest habitats near Bastrop tend to segregate with the calls of *A. c. crepitans* on the PCA plot. However, two of the Bastrop

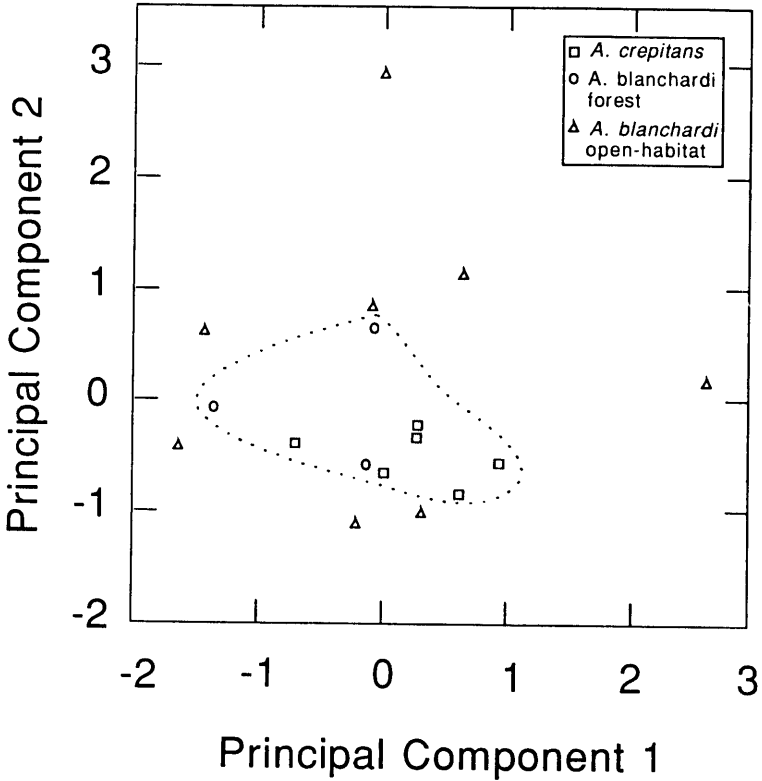


Figure 11-3 Results of a principal component analysis of cricket frog calls. Dotted line encloses populations from forest habitats. Temporal call characters provide the major loading on both components. Principal component 1 is determined mainly by the number of calls per call group, the number of pulses per call in the middle of a call group and at the beginning of a call group, and call group duration. Principal component 2 is determined mainly by the call durations at the end, middle, and beginning of a call group and by the number of pulse groups in calls at the beginning of a call group. Dominant frequency loads more heavily onto principal component 2 than 1, but is less a factor in specifying the components than any of the temporal features listed above. See Ryan and Wilczynski (1991) for a complete description of call characters.

populations are closer to an *A. c. blanchardi* population than to any *A. c. crepitans* population in the PCA-call space; in neither of these cases are the “nearest neighbors” on the PCA plot also the geographical nearest neighbors. The call analysis combined with the preliminary allozyme analysis suggest an evolutionary convergence in calls between *A. c. crepitans* and those of *A. c. blanchardi* that reside in the pine forests of Bastrop. The PCA analysis also shows that variation among populations in open habitats is much greater than variation among populations in the forest habitats.

Geographic Variation in the Auditory System

Across populations, basilar papilla tuning changes in the same general way as does call dominant frequency (fig. 11-4), leading to the maintenance of a rough match between calls and tuning at the population level (Wilczynski and Ryan 1988, Keddy-Hector et al. 1992, Wilczynski et al. 1992), just as has been seen in many frogs at the species level (Zakon and Wilczynski 1988). Complicating this relationship is the fact that basilar papillae of females are tuned to lower frequencies than those of males in all populations in which we sampled both sexes. Furthermore, average female basilar papilla tuning is lower than the average dominant frequency of the male calls in the same population.

In addition to the clinal variation in basilar papilla tuning, the degree of mismatch between female tuning and male calls differs among populations (fig. 11-5). In forest populations, the basilar papillae of males are tuned, on average, higher than the call, whereas those of females are tuned lower. Therefore, the call is pitched between the maximum sensitivities of the two sexes. In grassland populations, the papillae of both sexes are tuned lower than the population's call dominant frequency, and female papillae are tuned lower than those of males. Thus the difference between the dominant frequency of the average male call and the best excitatory frequency of the average female auditory system is much greater in grassland populations than in the forest populations.

Geographic Variation in Mate Choice

Two-choice phonotaxis experiments clearly indicate that females can discriminate call characters (fig. 11-6). When presented with calls that vary only in dominant

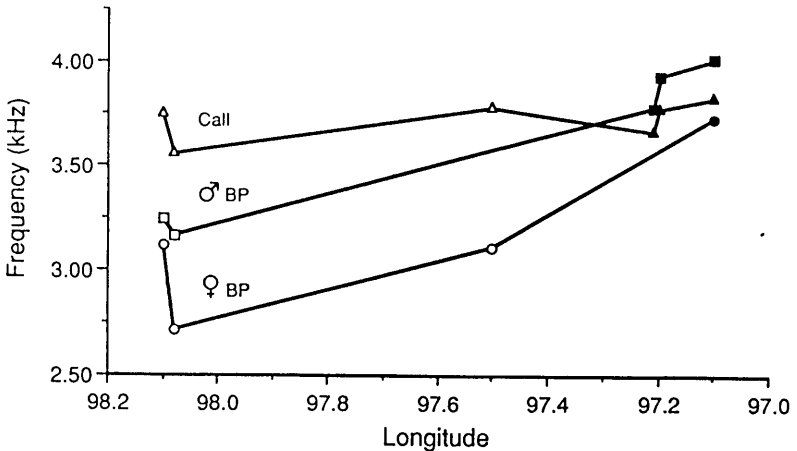


Figure 11-4 Mean advertisement call dominant frequency (triangles) and best frequency of the basilar papilla (BP) in males (squares) and females (circles) in six populations of cricket frogs (not all characters are available in all populations). Open symbols indicate populations from open habitats, filled symbols indicate populations from forest habitats. (From Wilczynski et al. 1992.)

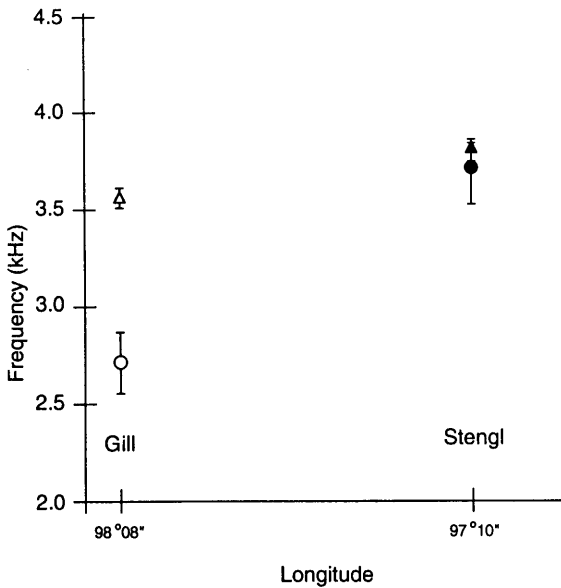


Figure 11-5. Mean (\pm SE) male call dominant frequency (triangles) and mean (\pm SE) female basilar papilla best excitatory frequency (circles) in two populations of cricket frogs, Gill Ranch and Stengl Ranch, from open and forested habitats, respectively. Note the difference in the degree of mismatch between male calls and female tuning in the two populations.

frequency, females in each of three populations prefer low-frequency calls to calls that are at the mean for their population or higher in frequency than that mean (Ryan et al. 1992). This suggests a within-population preference for males with low-frequency calls. These are, on average, calls of the larger males in the population (Wagner 1989a, Keddy-Hector et al. 1992). These preferences are predicted by the basilar papilla tuning in females, which is always lower than the average call dominant frequency in their home population. Additional confirmation comes from examining within-population variation in female tuning and mate choice. As for the calls, basilar papilla tuning is negatively correlated with body size in both sexes (Keddy-Hector et al. 1992). Consequently, larger females prefer lower call dominant frequencies than smaller females (Ryan et al. 1992).

The preference for lower-than-average dominant frequencies has implications for interpopulational mate choice as well. Given a choice between the average calls from their home population and a population with a higher call frequency, females should, and do, prefer calls from their home population (Ryan and Wilczynski 1988). Given a choice between the home call and one from a population with a lower frequency call they should, and do, choose the calls of the foreign population, which the phonotaxis experiments also show (Ryan et al. 1992). Mate

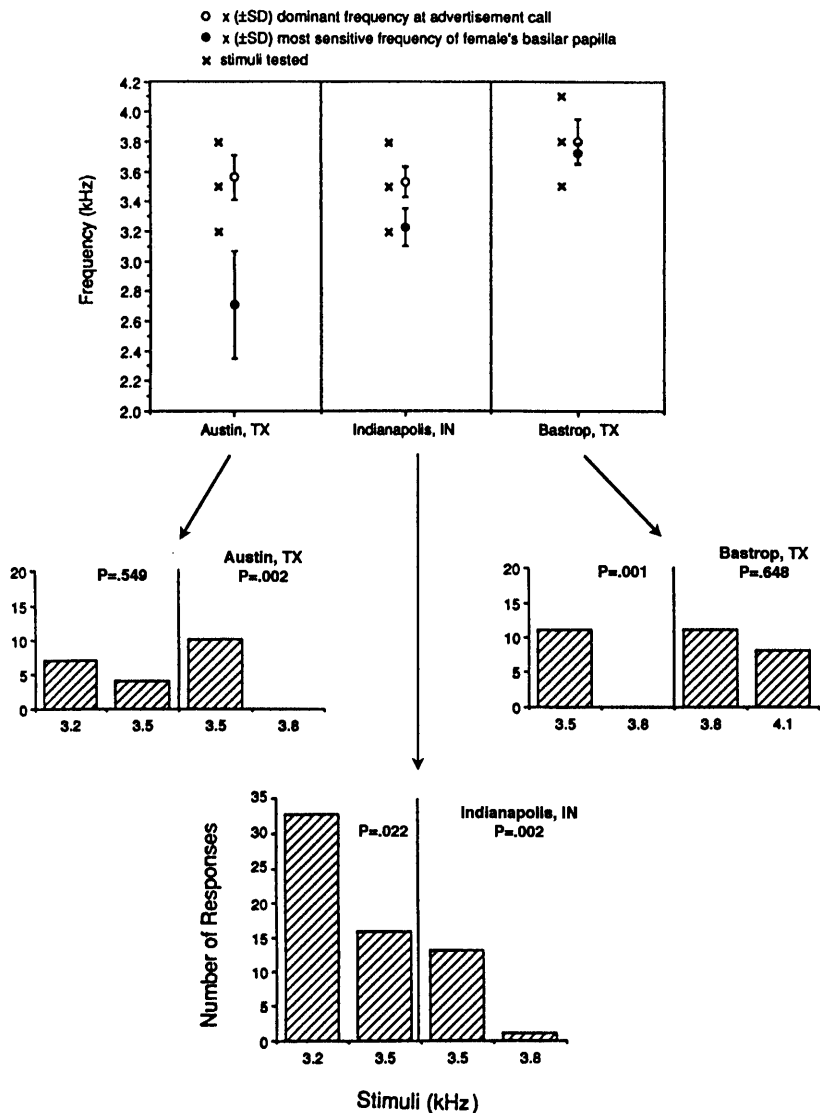


Figure 11-6 Results of choice experiments with females from three populations of cricket frogs. Top panel shows stimuli tested and their relationship to the dominant frequency of male calls and the best excitatory frequency of the basilar papilla of females in the tested population. Lower three panels show the choices made by females presented with calls at the population average versus calls lower than average (left side of graphs) or higher than average (right side of graphs). (From Ryan et al. 1992.)

choice is not based on population affinity per se, but on the relationship of male call dominant frequency and female basilar papilla tuning, causing females to potentially discriminate against foreign calls in some cases and against their own population's call in others. The preference is apparently derived simply from lower frequency calls being a better match with the tuning of the average female's basilar papilla, thereby stimulating her auditory system more (see also Ryan et al. 1990b).

Because female basilar papilla tuning is an important determinant of female mate choice, it is an important predictor of patterns of sexual selection in this species, suggesting that within all populations there is directional sexual selection for lower frequency calls. Furthermore, the mismatch between calls and tuning is greater in grassland populations than in forest populations, suggesting that selection for low-frequency calls may be greater in the more western, grassland populations.

The Evolution of Geographic Variation in Cricket Frogs

Analyzing the patterns of variation in signals and receivers allows an understanding of the interacting and competing forces shaping the evolution of this communication system. Our results, and those of others who have worked with this species (Nevo 1973, Nevo and Capranica 1985, Wagner 1989a,b), have indicated several factors contributing to this variation.

Body-Size Effects on the Communication System

Body size has an influence on both the signal (the call) and the receiver (basilar papilla tuning). Larger animals have lower frequency calls and have basilar papillae tuned to lower frequencies (Wagner 1989a,c, Keddy-Hector et al. 1992). Body-size differences no doubt also contribute to the sex difference in tuning, as females are larger, and have auditory systems tuned to lower frequencies, than males in this species (see also Wilczynski et al. 1984, Wilczynski 1986). Because western populations are on average larger than eastern populations, possibly as an adaptation to resist desiccation in drier western habitats (Nevo 1973), some of the clinal variation in call dominant frequency and basilar papilla tuning could be an indirect effect attributable to this selective influence.

Pleiotropic effects of body size may contribute to population differences, but they are not responsible for all the observed population variation in signal and receiver. Population and sex differences are still apparent when body size is statistically controlled (Ryan and Wilczynski 1988, 1991; Keddy-Hector et al. 1992). Morphological correlates of this can be seen in studies of the cricket frog vocal system. The size of a larynx and its component parts is an important determinant of its resonant properties and hence the frequency characteristics of the vocalizations it produces. Larger larynges are associated with lower call dominant frequencies. Male larynx size is significantly different among populations even after controlling for the effects of body-size differences (McClelland 1994, McClelland et al. 1996).

Selection by Environmental Acoustics

Habitat type (forest or open) is an important predictor of call features, independent of subspecies affiliation (Ryan and Wilczynski 1991). The isolated pine forest populations in the Bastrop area have calls more similar to those of the different subspecies in a similar east Texas habitat. One possible reason is that the calls have diverged in different habitats due to differences in habitat acoustics such that each habitat type, open and forest, contains populations with calls that minimize degradation, excess attenuation, or masking in that habitat.

An analysis of call degradation in open and forest habitats (Ryan et al. 1990a) shows that the forest habitat, as expected (Wiley and Richards 1978, 1982), causes much more call degradation than does the open grassland habitat (fig. 11-7). Furthermore, the calls from east Texas populations native to forest habitats are transmitted much more effectively than the slower, longer calls characterizing populations from the grassland habitat of central and west Texas (fig. 11-7). Somewhat surprisingly, our analysis provides little evidence that the acoustic features of the grassland habitats influence call evolution there. There is no significant difference in the degradation of calls from either habitat in the open grassland sites, and the forest call may even have a slight transmission advantage there.

Forest calls are also higher in frequency than open habitat calls, even though one might expect high frequencies to attenuate faster than low in acoustically cluttered environments. We believe that the higher frequency of the forest call may be an indirect consequence of the much more important selection on temporal features. Morphological studies of the larynx (McClelland 1994, McClelland

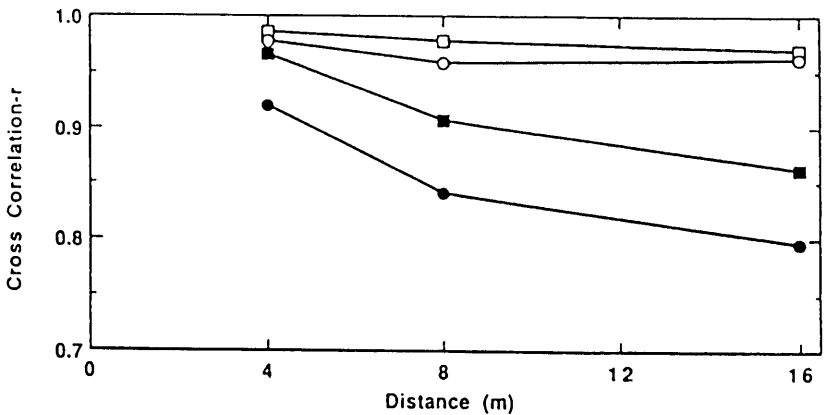


Figure 11-7 Call degradation over distance estimated by cross-correlation coefficients derived from correlating the call as recorded at the indicated distance with the call as originally broadcast. (Squares) Values for *A. c. crepitans* calls from east Texas forest population; (circles) Values for *A. c. blanchardi* calls from open habitat. Open symbols are results of broadcasts in an open habitat, filled symbols are results of broadcasts in a forest habitat. (From Ryan et al. 1990a.)

et al. 1998) indicate that, within a species, the various laryngeal structures are highly intercorrelated in size. These correlation studies also indicate that in larynges of the type found in cricket frogs, faster, shorter calls are predictive of smaller laryngeal muscles. As muscles decrease in size to protect calls from temporal degradation, allometric effects apparently reduce the size of other laryngeal components such as vocal cords and arytenoid cartilages, leading to higher dominant frequencies. Consequently, cricket frogs are forced to suffer a small disadvantage in call transmission in the frequency domain to achieve a larger advantage in call fidelity.

Environmental acoustics may also contribute directly to differences in auditory system characteristics. Signals should attenuate over distance more rapidly in the cluttered forest habitats. One way to achieve better sensitivity to the call is to achieve a better match between frequency peaks in the call (i.e., its dominant frequency) and the peak frequency sensitivity of the receiver (i.e., the best excitatory frequency of the basilar papilla). Indeed, one does observe that average female basilar papilla tuning is closer to average call dominant frequency in forest populations than in open, grassland populations. Other aspects of auditory sensitivity, such as absolute threshold and susceptibility to masking by environmental noise, which might also differ in the two habitat types, have yet to be explored.

Interaction of Social and Environmental Influences

No single factor accounts for the pattern of geographic variation seen in the cricket frog acoustic communication system. Pleiotropic effects of body size on calls and basilar papilla tuning, selection imposed by environmental acoustics, and the patterns of sexual selection based on tuning characteristics of the female basilar papilla interact to generate clinal and habitat-based variation. Moreover, the balance between the different influences may vary among populations.

Selection due to habitat acoustics and sexual selection appear to exert opposing forces on the cricket frog call. In all populations, mate choice selects for low-frequency calls. In forest habitats, however, the demands for preserving call fidelity over distance could provide a selective pressure in the opposite direction for calls that are faster, shorter, and, indirectly, higher in frequency. In these populations, therefore, the effects of sexual selection are mitigated. In open grassland habitats, sexual selection is relatively unopposed by habitat selection, resulting in lower frequency calls and, apparently, in calls that are also slower and longer due to the overall increase in the size of laryngeal components necessary to make such calls. Because forest habitats are more common at the eastern end of the range and dry, grassland habitats are more common at the western end, a clinal trend with shorter, faster, higher frequency calls to the east and longer, slower, lower frequency calls to the west results. Overlying these trends generated by different selection regimes is clinal variation in body size (Nevo and Capranica 1985, Ryan and Wilczynski 1991), which would pleiotropically affect calls and tuning, producing parallel clinal trends.

Migration of individuals between populations remains to be investigated. If populations interact, what might result is a pattern of gene flow from east to west,

and from forest to grassland, driven by female mate choice for low-frequency calls. The net result of all these interacting factors is east–west clinal variation in call dominant frequency and basilar papilla tuning, overlain by habitat variation causing additional nonrandom call variation along the cline.

Regardless of the mix of evolutionary influences, a rough match between calls and basilar papilla tuning exists in each cricket frog population, just as it does in other cases in which geographic variation exists in communication systems. How the match between the signal and the receiver is maintained as a communication system evolves has been a question of considerable debate. In our populations, effects of body size, acting simultaneously on signal and receiver systems, may help maintain the match, but they are not solely responsible for it (Keddy-Hector et al. 1992). Strong genetic linkage between sender and receiver systems (e.g., Hoy et al. 1977, Kyriacou et al. 1992) is also unlikely in this species. The relationship between mean basilar papilla tuning and call dominant frequency varies among populations (Wilczynski et al. 1992), and the allometric relationship of each with body size also varies among populations (Keddy-Hector et al. 1992). This observation is important, as a genetic linkage has been proposed to play an important role in maintaining the congruence between signal and receiver in animal communication dyads (Alexander 1975, Hoy et al. 1977, Doherty and Gerhardt 1983, Boake 1991). The elimination of pleiotropic effects of body size and strong genetic linkage as most likely candidates for producing the relationship between calls and auditory tuning suggests some coevolutionary process underlying the call–tuning relationship.

Intraspecific Geographic Variation in Other Communication Systems

Geographic variation in communication signals and receivers has been documented in several vertebrate and invertebrate groups besides cricket frogs. Most studies of geographic variation in the communication systems of other frog species have examined patterns for evidence of character displacement in the call (Littlejohn 1965, Fouquette 1975, Ralin 1977, Nevo and Capranica 1985, Loftus-Hills and Littlejohn 1992). In addition, Littlejohn (1988; Littlejohn and Watson 1985) has used patterns of geographic variation to document the opposite phenomenon—the generation of stable hybrid zones in areas of sympatry where reproductive isolation breaks down. Both the investigations of reproductive isolation through character displacement and the breakdown of isolation with the subsequent formation of hybrid populations use patterns of geographic variation as a window into the dynamics of speciation (see Littlejohn this volume).

Visual communication systems in fish also show geographic variation. In these systems, attention has focused mainly on variation generated by habitat differences. In guppies (*Poecilia reticulata*), geographic variation in signals is generated mainly by differences in selection pressures among habitats (Endler 1983), although transmission characteristics of a population's habitat may also contribute to signal evolution (Endler and Houde 1995). Females base mate-choice decisions on male color patterns, particularly on the amount of orange coloration (Endler

1983, Houde 1987, 1988; Stoner and Breden 1988, Long and Houde 1989, Houde and Endler 1990, Endler and Houde 1995). Where predation is high, males lack bright color patterns, presumably because predatory fish use vision to find the guppies. Where predators are scarce or lacking, males are brightly colored.

As in frogs, the preferences of female guppies also vary geographically, but the pattern of choice is more complex than that seen in frogs to date. Endler and Houde (1995) report that female guppies generally prefer males from their home populations to alien males, but the male traits on which the preference is based vary among populations. Female preferences maintain a rough match with the expression of three male color traits across populations (amount of orange, amount of black, and degree of color contrast; see also Stoner and Breden 1988, Houde and Endler 1990), but not with many other visual features characteristic of males.

Among the most striking examples of geographic variation in communication systems is the presence of local song dialects in oscine birds. Indeed, the study of intraspecific variation in vocal communication leading to local "dialects" began with an investigation of the song bird *Zonotrichia leucophrys*, the white crowned sparrow (Marler and Tamura 1964; see Baker and Cunningham 1985 for a review of work in this species), although references to geographic variation in bird song do pre-date this work (e.g., Borror 1956, Marler and Isaac 1960, Armstrong 1963). Subsequent investigations have revealed local song dialects in many other passerines, including various sparrows (*Melospiza melodia*, Harris and Lemon 1972; *Zonotrichia capensis*, Nottebohm and Selander 1972; *Melospiza georgiana*, Marler and Pickert 1984) and wrens (*Thryomanes bewickii*, Kroodsma 1974; *Troglodytes troglodytes*, Kroodsma 1981; *Cistothorus palustris*, Kroodsma and Canady 1985), cardinals (*Richmondia cardinalis*, Lemon 1967, 1971), indigo buntings (*Passerina cyanea*, Shiovitz and Thompson 1970, Emlen 1971), cow birds (*Molothrus ater*, King et al. 1980), red-winged blackbirds (*Agelaius phoeniceus*, Searcy 1990), and rufous-sided towhees (*Pipilo erythrophthalmus*, Ewert and Kroodsma 1994).

Each bird species in which local dialects emerge has a species-typical song with discrete components or syllables common to the species. What varies among populations to yield dialects is the preponderance of certain syllables within the populations's song, variations in the sound of certain syllables, or the patterning of the syllables within the song, all within some species-specific limits (fig. 11-8). Most work has concentrated on describing signal variation, but there is now substantial behavioral evidence that population-level song preferences exist. In all cases studied so far, these preferences are for an individual's home dialect over foreign dialects. The ability to discriminate among dialects apparently is present in both sexes in at least some species (King et al. 1980, Baker 1983, Brenowitz 1983, Baker et al. 1987, Balaban 1988, Searcy 1990).

What makes the phenomenon of bird song dialects particularly interesting, and likely different from the situation in frogs and fish, is that many species with dialects learn their songs from conspecifics, and the generation of local dialects and preferences is thought to derive directly from the plasticity of the system that

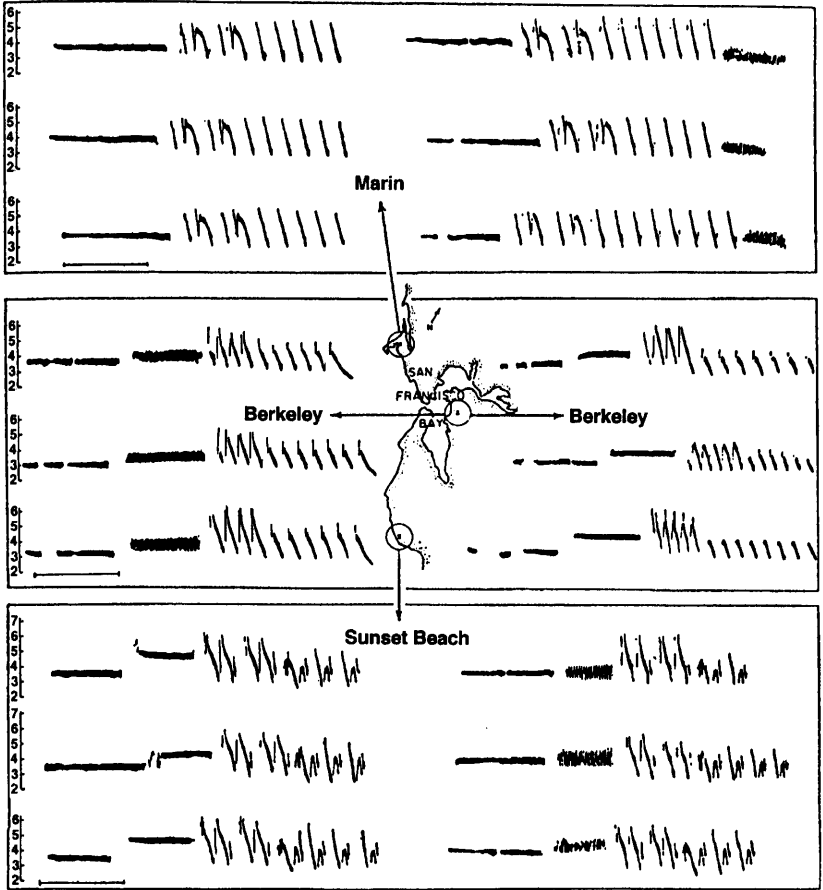


Figure 11-8 Sonograms of songs from six male white-crowned sparrows from each of three locations noted on map in center of figure showing geographic dialects. Vertical scale is in kHz, horizontal scale, bar = 0.5 s. (Reprinted by permission from Marler and Tumara [1964]. Copyright 1964 by the AAAS.)

makes such learning possible (Marler and Tamura 1964, Kroodsma 1974, Baker et al. 1987, Baker and Cunningham 1985).

Geographic variation in bird song systems is not without genetic components, however. The plasticity in song acquisition leading to dialects is constrained by inherent biases in the acquisition process (Kroodsma and Canady 1985, Marler 1990, 1991). For example, Nelson et al. (1995) observed song acquisition in laboratory-reared white-crowned sparrows from sedentary and migratory populations supplied with a variety of tutoring tapes. Although there were no differences

between populations in which song syllables they could learn, birds from migratory populations acquired song at an earlier age in a shorter time and sang more song variations while in their juvenile "plastic song" or acquisition stage. Nelson et al. (1995) suggest that the genetic differences in acquisition strategy are a reflection of the different challenges facing the populations. Migratory populations, faced with greater uncertainty about where individual birds will be during the breeding period, start learning faster and imitate more song types as juveniles, then crystalize one dialect from among them depending on the local dialect where they eventually settle. Sedentary populations, by contrast, have far more certainty about which dialect they will encounter and hence learn later, and with greater accuracy, while imitating fewer syllables.

The greater accuracy with which sedentary populations imitate song may also underlie the observation of Ewert and Kroodsma (1994) that individuals from nonmigratory populations of towhees (*Pipilo erythrophthalmus*) share more songs with immediate neighbors than do individuals from migratory populations of this species. Ewert and Kroodsma (1994) also noted that, as for marsh wrens (Kroodsma and Canady 1985), nonmigratory individuals use a larger number of syllables than migratory individuals after their song has crystalized. The distinction remains in laboratory-reared wrens, suggesting a genetic basis for this difference.

In some bird species, female preference may be less plastic than male song. In cowbirds, regional preferences among females are genetically based, and these preferences channel song learning by the males into regional dialects matching those preferences (King and West 1983, 1987). Geographic variation in bird song is therefore a system that arises from the interaction of cultural evolution and learning and genetic constraints and consequences.

Diversity versus Stability in Communication Systems

The many examples of geographic variation in communication systems provide insight into, and raise additional questions about, the basic nature of animal communication systems. First and foremost among the lessons learned from such examples is that, although there are clearly phylogenetic and mechanistic constraints on both senders and receivers, environmental and social influences can exert strong diversifying effects. Regardless of the pattern of geographic variation, the mere presence of this variation indicates that mate-recognition systems need not be subject to strong stabilizing selection operating at the species level leading to narrow, species-specific characters stable across all populations.

Diversity appears in both sender and receiver portions of the communication dyad. This would almost certainly have to be the case, given the fundamental need of all communication systems to maintain some type of match between the sender's signal and the tuning of the receiver. Nevertheless, both systems are labile. The examples studied in detail to date provide no clear indication that one end of the dyad is more stable or severely constrains the characteristics of the other at the intraspecific level, although the issue of whether senders or receivers are more plastic deserves further attention (Brenowitz 1994).

Furthermore, the case of cricket frogs, in which both signal and receiver characteristics can be quantified, shows that a capacity for change in both parts of the communication dyad can lead to variation in the relationship between them. This variation indicates a looser coupling between the two parts of a species' communication system than has been suspected. In frogs, this has implications for the degree of sexual selection exerted on male calls by female preferences in different populations. It would be significant to determine if the match between signal and receiver varies in other communication systems, as the stability of this relationship at a species level has important mechanistic and evolutionary implications.

As they generate diversity, environmental and social influences can have different effects. West Eberhardt (1983) argued that environmental selection tends to drive traits toward optimization, whereas social, or sexual, selection has no optimal result and is therefore more unpredictable and diversifying (see also Ringo 1977, Lande 1982, Ryan 1990a,b). Indeed, we find some evidence of this. Where the call is under more strenuous environmental selection in the forest habitats, mean male and female basilar papilla tuning tend to lie consistently close to the mean call dominant frequency, whereas among grassland populations the relationship between tuning and the call is more variable (Wilczynski et al. 1992). Moreover, both principal component analysis and discriminant function analysis applied to measures of overall call structure in cricket frogs show that grassland populations are much more diverse and unpredictable than forest populations. Environmental diversity across the range of a species does lead to diversity in that species' communication system via selection due to habitat transmission or masking characteristics, predation differences, or, as may also be the case for cricket frogs, via selection on traits such as body size that pleiotropically affect the system. This diversity is, however, somewhat constrained so that common habitat types lead to similar communication adaptations within and across species.

Social or sexual selection—that is, selection due to the internal dynamics of the communication dyad—also leads to geographic differences within species, but has a more diversifying effect on the system. This is apparent in the more unpredictable patterns of cricket frog calls and tuning in open habitats, where environmental constraints are weak. Bird song dialects, which may be due primarily to social interactions rather than selection due to external forces, may be another example of the relatively unpredictable, highly diversifying nature of this type of change.

One final lesson is a methodological one. Dissecting the factors that influence the evolution of communication systems is aided greatly by examining patterns of geographic variation. All communication systems evolve amid complex social interactions between senders and receivers and a host of external factors such as habitat characteristics and predation pressures that can potentially drive the evolution of communication characters or constrain their expression. The fact that populations do vary in habitat and social interactions and thus in the constellation of potential influences on their behavior, allows one to test hypotheses about how specific factors, or particular patterns of interaction among them, contribute to the evolutionary and mechanistic processes that shape this fundamental component of animal behavior.

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