

# Interspecific Interactions in Anuran Courtship

H. Carl Gerhardt and Joshua J. Schwartz

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|--|--|
| I. Introduction  | IV. Hybridization and Homogamy   |
| II. Acoustic Interference                              | A. Hybrid Zones  |
| A. Temporal Partitioning: Gross Time Scale             | B. Hybridization between Broadly Sympatric Species                             |
| B. Temporal Partitioning: Fine Time Scale              | C. Homogamy and Sexual Selection   |
| C. Spectral Partitioning                               | D. Interspecific Interaction and Homogamy: Reproductive Character Displacement |
| D. Spatial Segregation                                 | V. Acknowledgements  |
| E. Neural Mechanisms that Reduce Acoustic Interference | VI. References   |
| III. Interspecific Aggression                          |  |
| A. Specific Examples                                   |  |
| B. Advantages of Interspecific Aggression              |  |

## I. INTRODUCTION

**T**HERE are three principal forms of reproductive interactions between different species of frogs and toads. First, because males of most species produce intense advertisement calls, the sounds produced by each species may mask the acoustic courtship signals of other species that share the same breeding site. Second, calling males of different species may interact aggressively, producing special vocalizations that are also produced in intraspecific encounters or even engaging in physical contests. Third, matings between individuals of different species may occur. The usual consequence is negative: wasted gametes and a possible loss of the chance for a mating with a conspecific individual. However, under special conditions, mismatings may result in a stable, hybrid zone.

These three forms of interaction are examined from the viewpoint of both mechanisms and evolution. For example, one effect of acoustic interference is the reduction in the auditory system's ability to process and differentiate among conspecific signals. Potential evolutionary responses include divergence in the acoustic properties of vocalizations, spectral and temporal tuning to species-typical signals, and behavioural and ecological changes, ranging from shifts in the timing of calls or call sites to changes in breeding seasons or habitats. However, most of the studies of anurans purporting to have demonstrated such evolutionary adjustments are open to the criticism that the observed patterns have not been tested against appropriate null models. A difficulty of assessing the consequences of interspecific interactions is that evolutionary responses will vary enormously in time and space, and will depend on the evolutionary history of each taxon. This is especially true of conservative features such as basic hearing mechanisms, which are also important for functions other than courtship. Finally, in many communities of breeding anurans, the time period for breeding is exceedingly short and breeding sites are so limited that interspecific interactions, ranging from masking interference to mating mistakes, are inevitable.

## II. ACOUSTIC INTERFERENCE

The complex, multi-species choruses of frogs and toads that are often encountered in tropical, semi-tropical and temperate areas are among the most impressive of biological phenomena. Breeding sites with nine or more species have been observed on several continents (e.g., review by Duellman and Trueb 1986; Aichinger 1987). Most species produce intense vocalizations (e.g., Loftus-Hills and Littlejohn 1971; Gerhardt 1975; Passmore 1981), and there are limits on the degree to which calling males can spatially segregate within a breeding site. Thus, these mixed-species choruses are focal points for interspecific interactions.

Aside from breeding at different times of the year or selecting different, spatially isolated breeding sites, there are three main ways that vocalizing males of one species may reduce masking interference by the calls of other species.

First, males can concentrate their calling in periods when males of other species are silent or less vocally active. Such temporal partitioning may occur at a gross time scale, with males of one species restricting entire bouts of calling to periods of relatively inactivity by other taxa, or at a fine time scale, with individual frogs avoiding acoustic overlap of their calls or notes with those of nearby males of another species.

Second, acoustic interference may be reduced if the spectral properties of the calls differ among interacting species. Obviously, this is a long-term solution, because there are few species in which individuals alter the spectral properties of their calls, and even then the magnitude of frequency change is relatively small (Lopez *et al.* 1988; Wagner 1989). Moreover, the degree of evolutionary change in dominant frequency appears constrained by body size (see below), and species-specific biases in frequency sensitivity have been exaggerated by some authors (see below). At the high sound pressure levels at which most species vocalize (e.g., Gerhardt 1975), the auditory systems of most species in a community will be effectively stimulated by heterospecific signals, even if the calls have distinctively different, species-specific spectral properties.

Third, males of different species may reduce acoustic interference by spatial partitioning within the breeding site. Spatial partitioning will reduce the sound pressure level (SPL) of the interfering vocalizations and the directional hearing properties of the anuran auditory system could augment this reduction if there are species-specific, spectral differences (e.g., Schwartz and Gerhardt 1989). Spatial separation may also reduce the chances that females could accidentally touch or move close to a calling heterospecific male. Because males of most species indiscriminately try to mate with other frogs that move near them, such accidental contacts are probably the major cause of mismatings between broadly sympatric species (e.g., Mecham 1961; Gerhardt *et al.*, in press).

### A. Temporal Partitioning: Gross Time Scale

The most extreme kind of temporal separation possible is seasonal disjunction of breeding seasons. This pattern is known in many sympatric species (e.g., Dixon and Heyer 1968; Pengilley 1971; Heyer 1976; Mac Nally 1979; Hillis 1981), but whether these patterns have been shaped by interspecific interactions is unknown. One simple, preliminary test of such a hypothesis would be to compare the breeding seasons of sympatric and allopatric populations of the same species.

Males of different species could also restrict their calling activity to particular times of a 24-hour period. Males of one species may confine most of their calling to hours when males of another species are relatively quiet (Crump 1974; Bowker and Bowker 1979; Kuramoto 1980; Telford 1982). If chorusing by one species is organized into distinct bouts, with intervening periods of relatively little vocal activity, then males of another species could call between these bouts. Littlejohn and Martin (1969) were the first to show the potential for gross temporal partitioning between two species. Studying a pair of Australian myobatrachids, they found that calling by *Pseudophryne semimarmorata* was inhibited by playbacks of the calls of *Geocrinia victoriana*. These authors provided only anecdotal evidence that such inhibition occurred in nature.

Schwartz and Wells (1983a) conducted a more extensive study of temporal partitioning at a gross time scale in two neotropical treefrogs. The calls of *Hyla ebraccata* have a dominant frequency of 3 kHz, whereas in *H. microcephala* the spectrum of the call is bimodal (energy peaks at 6 kHz and 3 kHz). Males of *H. ebraccata* often call near dense aggregations of *H. microcephala*, which typically produce more intense and often longer, multi-note calls than *H. ebraccata*. Moreover, members of *H. microcephala* choruses typically engage in unison bout singing (Schwartz and Wells 1983a; Schwartz 1991); males call together for an average of about 17 sec., quiet down for a brief period (an average of about 10 sec.), and then call again. Schwartz and Wells (1983a) found that males of *H. ebraccata* in the vicinity of a chorus of *H. microcephala* concentrate their calling during the periods when chorus activity of *H. microcephala* is reduced. Calling in *H. ebraccata* also is inhibited by choruses of another, sympatric species, *H. phlebodes* (Fig. 1), and by playbacks of random noise, especially filtered bands of one-third octave with a spectral peak at 3 kHz (Schwartz and Wells 1983b).

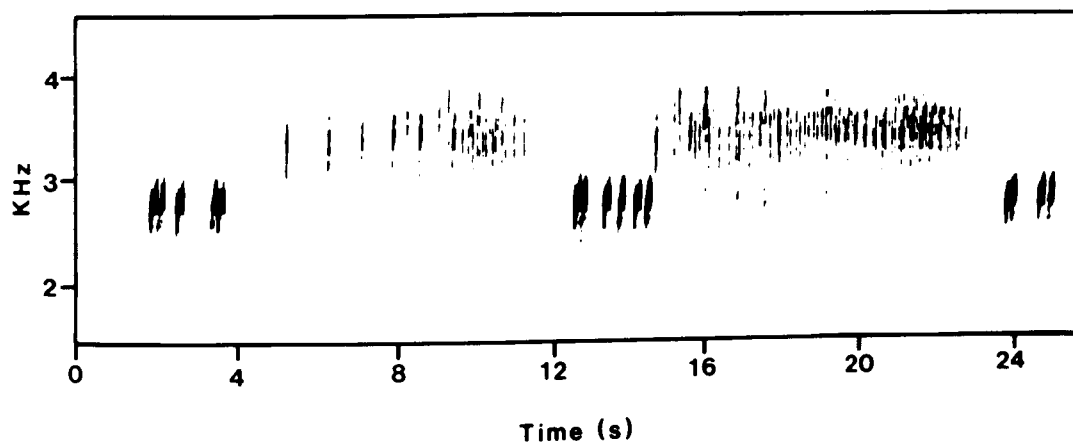


Fig. 1. Sonagram showing a vocal interaction between calling males of *Hyla ebraccata* (2 males; lower frequency calls) and *H. phlebodes* (3 or 4 males; higher frequency calls). Males of *H. ebraccata* called during pauses between bouts of calling by *H. phlebodes*. From Schwartz and Wells 1983b.

The sound of heterospecific choruses appears to mask intraspecific communication in *H. ebraccata* because call complexity and aggressive calling were reduced during the noisy periods of chorusing by *H. microcephala* (Schwartz and Wells 1983a). Moreover, females of *H. ebraccata* discriminate against conspecific calls overlapped by a background chorus of *H. microcephala* (Schwartz and Wells 1983b). Thus, by concentrating their calling in periods of relatively low chorusing activity by *H. microcephala*, males of *H. ebraccata* enhance their ability to attract mates. Discrimination against the stimulus with chorus background noise could have been caused by reducing the detectability of conspecific vocalizations, degradation of species-specific pulse-rate information, or both (Schwartz 1987a).

Studies of other species indicate that, as in *H. microcephala* and *H. ebraccata*, the species that produce longer calls or have longer bouts of calling typically inhibit calling by species with shorter calls or calling bouts (for similar results from insects and birds see Greenfield 1988 and Ficken *et al.* 1974). For example, males of *G. victoriana* produce calls with nearly 100 notes, and playbacks of such calls effectively inhibited calling by males of *P. semimarmorata*, which produce short, single-note calls (Littlejohn and Martin 1969). Mac Nally (1979, 1984) suggested that acoustical interaction between another pair of Australian species, *Ranidella parinsignifera* and *R. signifera* results in spatial displacement of *R. signifera*. Males of *R. parinsignifera* produce longer calls than do males of *R. signifera*, which often stopped calling or even left their calling site when stimulated with playbacks of the calls of *R. parinsignifera* (Mac Nally 1982; Littlejohn *et al.* 1985). Males of *R. parinsignifera* were less likely to be inhibited by playbacks of the calls of *R. signifera*, but males of *R. parinsignifera* sometimes responded with fine-scale shifts in the timing of their calls.

Although *R. signifera* appears to be acoustically subordinate to *R. parinsignifera*, it is acoustically dominant to another congener, *R. riparia*. The sharp clicks of the calls of *R. signifera* have a mean SPL that is 24 dB higher than that of the soft, pulsed calls of *R. riparia*. Moreover, males of *R. signifera* call in continuous choruses and may produce up to 30 calls in rapid succession (intercall intervals of 0.2–0.4 sec.), which overlap spectrally with the more slowly delivered calls (intercall intervals of 15–45 sec.) of *R. riparia*. Within a narrow zone of sympatry in southern Australia, *R. riparia* is limited to swiftly flowing rocky streams (Odendaal and Bull 1982). Elsewhere, *R. riparia* seems to survive and reproduce well in the more heavily vegetated creeks with muddy bottoms that are favoured by *R. signifera*. Odendaal *et al.* (1986) thus proposed that acoustic interference not only may have contributed to the avoidance by *R. riparia* of habitats favoured by *R. signifera* in the area of sympatry, but that this form of interaction may be a factor in the restricted range of distribution of *R. riparia*. There is also evidence from removal experiments that males of the two species may compete for calling sites (Odendaal and Bull 1986).

### B. Temporal Partitioning: Fine Time Scale

There is an extensive literature on the existence and putative proximate mechanisms of fine-scale shifts in call timing between two or more conspecific males (Lemon 1971; Loftus-Hills 1974; Rosen and Lemon 1974; Awbrey 1978; Lemon and Struger 1980; Narins 1982; Ayre *et al.* 1984; Schwartz and Wells 1984b; Schneider *et al.* 1988; Brush and Narins 1989; Moore *et al.* 1989; Schwartz 1991; Walkowiak 1992; Klump and Gerhardt 1992; Ibanez 1991). Some examples of timing shift are quite impressive. For example, males of *Eleutherodactylus coqui* placed their advertisement calls into 750 ms gaps within the broadcast of continuous tones (Zelick and Narins 1982). Males of *H. microcephala* can make note-by-note adjustments to stimuli as brief as 20 ms (Schwartz 1991). Males are also vocally responsive to quiet gaps of 20 ms within longer interrupting stimuli (Schwartz 1993).

Male anurans of some species make timing adjustments to heterospecific calls that are similar to those made to conspecific calls, especially if conspecific and heterospecific signals are similar in structure. Males of *H. ebraccata* show such behaviour when exposed to the calls of *H. microcephala* or *H. phlebodes*, and males of these latter two species also make timing adjustments to heterospecific calls (Schwartz and Wells 1984a, b, 1985). Playbacks of recorded heterospecific calls and synthetic advertisement calls demonstrated that note duration was a particularly important call property in determining whether or not a male of *H. ebraccata* responded; short-latency responses increased sharply and then leveled off as stimulus duration was increased to that typical of the primary note of the conspecific advertisement call (Schwartz and Wells 1984a).

Schwartz and Wells (1984a) experimentally tested the hypothesis that fine-scale timing shifts in response to heterospecific calls can increase a male's chances of attracting a female. Females of *H. ebraccata* were offered a choice between two conspecific 2-note calls: one overlapped the first note of 3-note calls of *H. microcephala* and the other did not. In the non-overlapping stimulus, the primary note of the conspecific call was timed to fall in the interval between the first two notes of the heterospecific call. The relative intensities were adjusted to resemble those of two males calling adjacent to one another (the call of *H. microcephala* was 3 dB greater than that of the call of *H. ebraccata*). Females showed a significant preference for the non-overlapping calls.

### C. Spectral Partitioning

If the auditory system is tuned to frequencies typical of conspecific calls, masking interference between species can, in principle, be diminished if the signals of other species have different spectral properties. Although the effectiveness of such a mechanism has probably been overstated (see below: Neural Mechanisms for Reducing Acoustic Interference), selection to avoid masking interference could cause a divergence in spectral properties of calls, especially in dominant frequency or frequencies.

Demonstrating that such selection has occurred is, however, very problematic, and there are other ways that breeding communities could arise in which each species produces calls with a different dominant frequency. For example, rather than selection for an evolutionary change in the dominant frequency in the calls of one or both pairs of species, species with similar calls may simply avoid breeding at the same kind of site, thus leading to habitat segregation or even a disjunction of ranges of distribution (e.g., as may have occurred in *R. riparia* and *R. signifera*, see above). Furthermore, several studies have found reasonably high correlations between dominant frequency and body size in interspecific comparisons (e.g., Zimmerman 1983; Duellman and Pyles 1983; Ryan 1988; Penna and Veloso 1990). This means that selection on dominant frequency must often be countered or confounded by selection on body size (e.g., Nevo 1973; Littlejohn 1977). Finally, as with speculation about observed patterns of spatial separation of different species within the same breeding site (see next section), most authorities who have dealt with spectral partitioning in anuran communities have based their conclusions on undocumented, historical events (Telford 1982). In fact, no such study has simply compared observed patterns of spectral stratification with patterns that might arise from chance alone.

Many studies have described anuran communities in which the dominant call frequencies of its members are stratified to some extent (Hödl 1977; Duellman 1967, 1978; Straughan and Heyer 1976; Schluter 1979, 1980a, b, c; Drewry and Rand 1983). One of the best examples is the study of eleutherodactylid frogs of Puerto Rico by Drewry and Rand (1983). These authors found that different species in the same assemblages generally use advertisement calls with different dominant frequencies, and spectral overlap among species is low (Fig. 2). Narins and Zelick (1988, p. 522) characterize this pattern as a possible example of a community in which spectral stratification, together with the tuning of the auditory system to frequencies typical of the calls of conspecific males, provides a "private channel" for each species. However, as Littlejohn (1977) pointed out, in many assemblages of synchronously breeding, sympatric species there is extensive overlap in dominant frequency, and there are some counter examples in the Puerto Rican communities (Fig. 2).

To test for patterns of spectral separation in communities of breeding frogs, some workers have subjected measurements of species-specific, call frequencies to univariate or multivariate analyses (e.g., Duellman 1978; Telford 1982). Duellman and Pyles (1983) used multivariate techniques to reveal common patterns in the distributions (by species) of dominant frequency and other call characteristics in 39 species of hylid frogs in three neotropical forest communities in Brazil, Ecuador, and Costa Rica. In general, the calls of closely related allopatric species tended to be more similar than those of closely related sympatric species. Species with similar calls were nearly always in different communities, and a closer inspection of the two exceptions revealed that the species involved either did not breed syntopically (had different breeding habitats) or used different calling perches within a common breeding site.

Duellman and Pyles (1983) also argued that the three communities shared similar overall patterns of acoustic structure, although the biological interpretation of the results of complex statistical procedures such as clustering are always subject to dispute. The divergence in the calls of sympatric hylids is consistent with the hypothesis of an evolutionary response to selection for minimizing mistakes in mate choice. However, three of the seven call variables analyzed — notes per call-group, note-repetition rate, and the number of secondary notes — are not known to be important for species recognition in anurans. Moreover, unlike spectral properties, a detailed contrast of the calling behaviour of pairs of sympatric species would be necessary to demonstrate the potential for reducing masking interference by temporal partitioning.

Rather than partitioning a particular communication channel with other species, at least one species of frog may avoid interference by using a different communication channel entirely. Narins (1990) provides evidence that the white-lipped frog, *Leptodactylus albilabris*, exploits vibrational signals to facilitate communication in an environment with high ambient noise. Males call from the ground along streams and other wetland habitats in Puerto Rico. Background noise levels in these areas are typically high due to the vocal activity of conspecifics, many other species of frogs (Drewry 1970), and acoustically signalling insects.

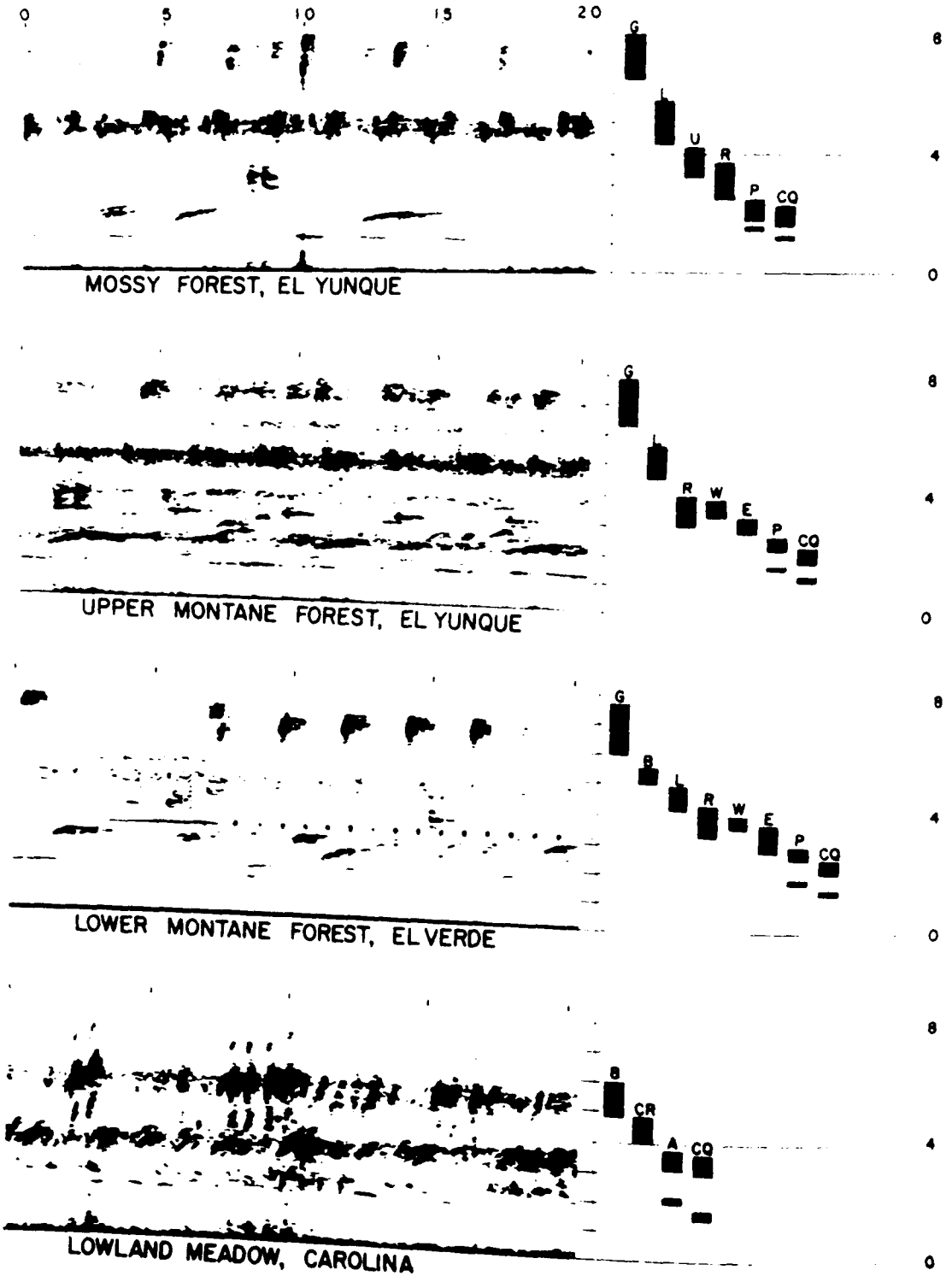


Fig. 2. Sonograms and diagrammatic summaries showing spectral differences in the calls of four assemblages of Puerto Rican species of *Eleutherodactylus* (from Drewry and Rand 1983). The letters refer to the following species of *Eleutherodactylus*: R = richmondi; U = unicolor; K = karlschmidti; CQ = coqui; P = portoricensis; A = antillensis; B = brittoni; CK = cooki; W = wightmanae; H = hedricki; E = eneidae; L = locustus; CR = cochranae; G = gryllus. Notice that although there are definite patterns of spectral differentiation within each community, there is also some spectral overlap, especially in the Mossy Forest and Upper Montane Forest communities.

When a male of *L. albilabris* calls, the impact of the vocal sac on the ground produces a "thump" which travels along the substratum as a Rayleigh wave. The frogs are extremely sensitive to ground vibration and, in fact, recordings from fibres innervating the sacculus of the inner ear demonstrated frogs are most sensitive to the frequency of peak energy in the thump (Lewis and Narins 1985). In the absence of rain, background noise levels in the soil are quite low, and thus the substratum may provide these frogs with an additional channel for communicating with conspecifics that is relatively immune from the airborne noise produced by heterospecifics.

#### D. Spatial Segregation

Anurans calling in multi-species aggregations may exhibit segregation by species at two spatial levels. First, individuals of different species may call in discrete monospecific groups such that most males are well isolated from heterospecifics. Second, members of two different species may call from the same general part of the breeding site, but may differ in their choice of microhabitat (e.g., perch height or vegetation type).

Although males of different species often are observed calling from perches close to one another (Bogert 1960; Hödl 1977; Bowker and Bowker 1979; Mac Nally 1979; Telford 1982; Schwartz and Wells 1984a; Given 1990; Ptacek 1992), some authors have emphasized that segregation of species by calling site is a characteristic of mixed-species choruses (e.g., Littlejohn 1977; Duellman and Trueb 1986). This segregation is believed to reduce the opportunity for acoustic interference (Littlejohn 1977) and to minimize mating mistakes (Mecham 1961; Oldham and Gerhardt 1975; Hödl 1977; Hillis 1981; Etges 1987; Ptacek 1992), thus augmenting any differences in call properties that contribute to species discrimination by females. In fact, call-site segregation should be expected to be especially important in cases where call differences are small (Mecham 1965; Duellman and Pyles 1983). There is also some evidence that acoustic interference generated by one species may drive males of another species away from preferred calling sites (see above).

Only two studies have compared the choices of calling perches by males in areas of allopatry with those in sympatry (Drewry and Rand 1983; Ptacek 1992). Drewry and Rand (1983) reported that two species of Puerto Rican frogs, *Eleutherodactylus locustus* and *E. brittoni*, produced calls with overlapping frequencies. In allopatric areas, males of both species tended to call in similar microhabitats, but they occupied different calling sites in sympatric populations. Ptacek (1992), studying two species of gray treefrogs, found a similar pattern in central Missouri. In syntopic populations males of the diploid gray treefrog, *Hyla chrysoscelis*, were more likely to call at or near ground level, whereas calling males of tetraploid gray treefrog, *H. versicolor*, were more common in elevated perches. A higher proportion of calling males of *H. chrysoscelis* used elevated perches in allopatric populations than in sympatric populations. Males of *H. versicolor* were more likely to call on or near the ground in allopatric populations than in sympatric sites. Ptacek (1992) interpreted these results as an evolutionary response to selection to avoid mismatings, because the two species are genetically incompatible and mismatings were documented in two syntopic localities where the species difference in the elevation of perch sites was not so pronounced as in most other such populations.

In general, however, the reasons for spatial segregation of the calling sites of any given pair of species are unknown. Clearly, they may be the product of selection for reduced interspecific interference, but the differences could also simply be the results of ecological differences or factors that have nothing to do with interspecific interactions. For example, Wells and Schwartz (1982) suggested that males of *Centrolenella fleischmanni* may choose calling sites on the undersides of large leaves to propagate their advertisement calls more effectively. Unfortunately, as in studies of spectral segregation in communities of anurans, there has been no attempt to analyze and compare data on spatial segregation by species, with patterns generated by any kind of null model. Such analyses are neither trivial nor uncontroversial (e.g., Colwell and Winkler 1984; Pimm 1991); nevertheless, we think that they are prerequisites to making real progress in testing hypotheses about the evolution of community-wide patterns.

Another important consideration for studies of microhabitat partitioning by frogs is the pattern of movement of gravid females. Even if groups of males are fairly well separated from heterospecifics, a female may have to pass through loud choruses of heterospecific males before locating a mate (Oldham and Gerhardt 1975; Etges 1987). Experimental studies of the effects of heterospecific choruses on female approaches to conspecific calls would be welcome. A study of the effects of a single source of heterospecific calls is discussed below.

### E. Neural Mechanisms that Reduce Acoustic Interference

Narins and Zelick (1988) reviewed some of the mechanisms by which the auditory system of frogs and toads may extract conspecific signals from background noise generated by other species. First, anurans have auditory neurons with a wide range of thresholds. Such an array of neurons allows the frog to detect changes in sound intensity with time over a wide range of signal and background noise levels. More sensitive neurons can encode intensity changes at low signal and noise levels, and less sensitive neurons can do so at high levels, at which the more sensitive neurons will have reached saturation (i.e., their maximum firing rate). Second, the peripheral auditory system of anurans tends to have enhanced sensitivity to one or more relatively narrow ranges of sound frequencies, some of which correspond to the frequencies emphasized in conspecific calls (reviews by Wilczynski and Capranica 1984; Zakon and Wilczynski 1988). Central auditory mechanisms further sharpen these peripheral biases (e.g., Walkowiak 1980; Narins and Zelick 1988). Third, there are various mechanisms for encoding and processing the stereotyped patterns of amplitude modulation (e.g., pulse duration, pulse rate, call duration) typical of the calls of many species of anurans. Neurons at the peripheral level encode sound pulses by phase locking, and this form of information transfer to the central nervous system may be less vulnerable to degradation by background noise than rate-based coding (Simmons *et al.* 1992). Dunia and Narins (1989) have estimated the temporal-integration time constant in the auditory nerve of *E. coqui* and speculate about its role in explaining the duration sensitivity of males in playback experiments. Many auditory neurons at higher levels have distinctive filtering properties. For example, in the torus semicircularis of the gray treefrog (*H. versicolor*), there are neurons that respond best to stimuli with low pulse rates (low-pass neurons), high pulse rates (high-pass neurons), or to a particular narrow range of pulse rates (band-pass neurons) (Rose *et al.* 1985).

The tuning of the auditory system to species-specific frequencies and pulse rates has been characterized as the "matched filter" hypothesis (Capranica and Moffat 1983; Capranica and Rose 1983; Rose and Capranica 1984). These authors hypothesized that, in addition to facilitating recognition of conspecific calls, the tuning of frogs to species-specific temporal and spectral properties minimizes acoustic interference by vocalizations of other species that differ in these properties. While these mechanisms almost certainly provide some measure of improvement in intraspecific communication in mixed-species choruses, frog vocalizations are typically so intense that heterospecific signals are potent sources of masking interference even if they differ considerably in dominant frequency from conspecific calls (see examples above of interspecific inhibition). Furthermore, heterospecific calls may evoke aggressive responses that typify exchanges between conspecific males at close range, as discussed below. Indeed, Capranica (1992) recently suggested that the extrapolation of frequency selectivity of neurons at near threshold levels (tuning curves) to the much higher levels at which the animals communicate may be quite misleading. Diekamp and Gerhardt (1992) make a similar argument about audiograms based on neurophysiological studies in the midbrain of *Pseudacris crucifer*.

The combination of spectral differences in calls and spatial isolation within choruses theoretically provides a more effective basis for reducing masking interference between different species than do spectral differences alone. That is, to the extent that directional hearing is frequency dependent, individuals should be able to better discriminate between signals of different frequency that arrive at the frog's ears from different directions than if they arrive from the same direction. This phenomenon is called the "cocktail party" effect or "release from masking" in the human psychophysical literature, and Schwartz and Gerhardt (1989) demonstrated its existence in the green treefrog (*H. cinerea*). Gravid female frogs did not reliably detect synthetic advertisement calls from either of two loudspeakers between which they were released when each of the speakers was situated immediately adjacent to loudspeakers that



emitted broadband noise at just below the masked threshold (minimum signal-to-noise ratio at which a tonal signal is detected in background noise; see Ehret and Gerhardt 1980). However, they showed phonotactic responses to these signals at the same signal-to-noise levels when the sources of background noise were spatially separated by 45° or 90° from the signal sources. However, the estimated improvement in detectability with angular separation was only about 3 dB, and the females failed to show their normal preference for a synthetic advertisement call over a synthetic aggressive call even when the noise sources were separated by 90° from the signal sources. In other words, their *detection* of signals in noise was improved slightly by spatial separation, but their *discrimination* of two signals that differed in temporal structure was not.

### III. INTERSPECIFIC AGGRESSION

#### A. Specific Examples

Males of numerous species of anurans with prolonged breeding seasons maintain a degree of inter-male spatial separation within choruses of conspecifics (Whitney and Krebs 1975; Awbrey 1978; Wilczynski and Brenowitz 1988; Wells 1977a). To maintain inter-male spacing, males use call intensity cues (Fellers 1979; Robertson 1984; Brenowitz *et al.* 1984; Brenowitz 1989; Wilczynski and Brenowitz 1988; Gerhardt *et al.* 1989), aggressive calls (Whitney 1980), and even physical contests (Wells 1977b; Littlejohn 1977). Males may defend calling, courtship, and oviposition sites (Wells 1977c; Howard 1978; Wells 1980a, b; Ryan 1980; Greer and Wells 1980; Kluge 1981; Townsend *et al.* 1984; Jacobson 1985; Given 1987; Stewart and Rand 1991), or all-purpose areas containing ecological resources such as food, water, and shelter (Wells 1980a; Crump 1988). Alternatively, males may not be territorial (*sensu* Brown and Orians 1970), but rather merely defend temporary calling sites (Perrill *et al.* 1978; Fellers 1979; Wells and Greer 1981; Ryan 1985).

Among conspecific males, selection may favour aggression because neighbouring males are direct competitors for approaching females, sources of masking interference (Gerhardt and Klump 1988), or both. Selection for interspecific aggression should be weaker because males of different species do not compete for the same females. For example, whereas physical contests between conspecific males of *Rana catesbeiana* and *R. clamitans* are common (e.g., Howard 1978; Wells 1978), interspecific aggression between these two species is unknown. Indeed, reports of fighting between males of different species of frogs are uncommon. Drewry (1970) reported an encounter in which a male of *E. coqui* butted a male of *E. antillensis*. The significance of this particular observation is questionable because at the same time Drewry was broadcasting a recording of the calls of *E. coqui*; these are similar to the calls of *E. antillensis*. Males of *Pseudophryne corroboree* in Australia exhibit interspecific competition for the burrows in which males call and females deposit eggs; males direct "threat calls" at adult males of *Ranidella signifera* and *P. dendyi* (Pengilley 1971). Males and females of *Colostethus inguinalis* in Panama usually defend their territories against encroachment by trespassing heterospecifics (Wells 1980a). The majority of such encounters, which often involved fighting, were between males of *C. inguinalis* and *C. pratti*. During these fights, usually won by the larger *C. inguinalis*, males exchanged encounter calls that were indistinguishable to Wells. These two species typically call near one another and probably are in competition for moist retreat sites during the dry season. Schwartz and Wells (1984a) observed numerous physical encounters between *H. ebraccata* and *H. microcephala*.

The use of specialized vocalizations is common in both intraspecific and interspecific aggression, even if physical contests are not observed. Calls used in aggressive interactions between conspecific males differ in various ways from advertisement calls (Wells 1988). In *Rana virgatipes* and *E. coqui*, males use calls quite similar to their advertisement call but elevate their rates of delivery (Given 1987; Lopez *et al.* 1988). Males of *P. crucifer* produce a tone-like advertisement call and a distinctly pulsed aggressive call (Rosen and Lemon 1974; Schwartz 1989). Males of the two species of gray treefrogs give pulsed advertisement calls with distinctly different pulse rates, but they produce tone-like, slightly frequency modulated, aggressive calls that are very similar in structure (Pierce and Ralin 1972). Males of *H. cinerea* produce aggressive calls by amplitude modulating their advertisement calls and increasing call

rate (Gerhardt 1978; Schwartz, unpubl.). Males of *H. ebraccata*, *H. microcephala* and *H. phlebodes*, as well as three species of sympatric *Ptychadena* from southern Africa, produce amplitude-modulated advertisement and aggressive calls; however, the pulse rate of aggressive calls is higher than that of the advertisement call within each species (Passmore 1977; Schwartz and Wells 1984a).

Although some species produce distinctive long-distance aggressive calls and close-range "encounter calls" (McDiarmid and Adler 1974; Wells 1977a; Littlejohn 1977), males of the three Panamanian treefrogs produce graded aggressive calls in which the duration of the primary note increases as intermale distance decreases (Schwartz and Wells 1984a; Wells 1989). Other species of Central and South American hylids probably behave in similar ways (Cardoso 1981). In fact, there is a growing body of information indicating that graded signaling systems may be fairly common among the Anura (Pengilley 1981; Arak 1983; Littlejohn and Harrison 1985; Backwell 1988; Schwartz 1989; Wagner 1989).

Most demonstrations of interspecific aggression have involved playback experiments (e.g., Gambs and Littlejohn 1979). Mac Nally (1979, 1982) reported that *R. signifera* occasionally responded with aggressive calls to playbacks of the advertisement calls of *R. parinsignifera*, whereas *R. parinsignifera* was less likely to respond in any way to playbacks of the calls of *R. signifera* (Littlejohn *et al.* 1985). Male European water frogs of the *Rana esculenta* complex (*R. lessonae*, *R. ridibunda*, and their hybrid, *R. esculenta*) gave aggressive calls in response to the playback of the aggressive calls of all these phenotypes (Brzoska 1982). Heterospecific advertisement calls also elicited aggressive responses although, in general, the playback level had to be greater than that of heterospecific aggressive calls (Brzoska 1982).

Harrison (1987) studied the vocal behaviour of two species of the *Litoria ewingi* complex, *L. ewingi* and *L. verreauxi*, in a zone of sympatry in southeastern Australia. Males of *L. ewingi* use a wider range of generally more elevated calling sites than do males of *L. verreauxi*, although some spatial overlap between the two species occurs. Males of *L. ewingi* responded to playbacks of conspecific calls with aggressive calls, but when stimulated by playbacks of the advertisement calls of *L. verreauxi*, they either timed their vocalizations to avoid interference or moved away from the speaker. Only a small percentage of males gave aggressive calls. In contrast, males of *L. verreauxi* produced aggressive calls in response to playbacks of both conspecific and heterospecific advertisement calls. Harrison (1987) speculated that the asymmetry in behaviour among the two species may be related to the fact that the advertisement call of *L. ewingi* is more similar to the aggressive call of *L. verreauxi* than is the advertisement call of *L. verreauxi* to the aggressive call of *L. ewingi*. Harrison did not observe natural agonistic encounters between these two species and did not broadcast aggressive calls to males of either species.

Given (1990), as part of an extensive study of the social behaviour of the carpenter frog, *Rana virgatipes*, played back both conspecific and heterospecific advertisement calls to males of *R. virgatipes* and the green frog, *R. clamitans*. These two species of prolonged breeders are intraspecifically territorial and have complex vocal repertoires (Wells 1978; Given 1987). The calls of the two species show considerable spectral overlap and differ mainly in their temporal properties. Males of *R. virgatipes* responded to playbacks of the calls of *R. clamitans* with aggressive calls; however, their agonistic responses did not increase as they normally would in response to conspecific calls. Males of *R. clamitans* appeared to ignore the calls of *R. virgatipes*. Given (1990) speculated that males of *R. clamitans* may simply ignore the calls of *R. virgatipes* because green frogs, which are the larger of the two species, would probably have no trouble defeating a male carpenter frog in a physical encounter.

The most extensive research on interspecific acoustic interactions among male anurans was conducted by Schwartz and Wells (1983a, b, 1984a, b, 1985) on the neotropical hylids *H. ebraccata*, *H. microcephala* and *H. phlebodes*. These species produce pulsed advertisement calls and aggressive calls consisting of a primary note that may be followed by a variable number of secondary notes (Figs 3, 4). Males of *H. ebraccata* responded to the aggressive calls of *H. microcephala* and *H. phlebodes* as they did to conspecific aggressive calls. When exposed to these calls during experimental playbacks or during natural interactions, males responded with a

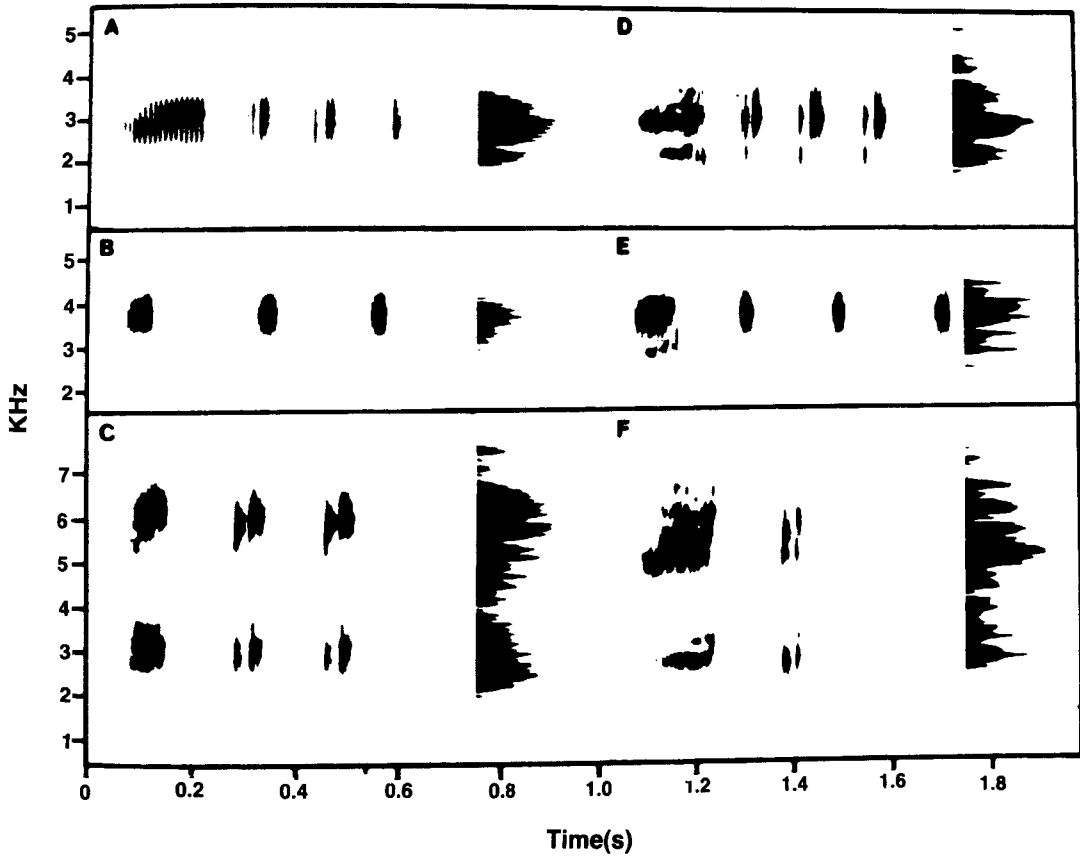


Fig. 3. Sonograms of advertisement calls and amplitude-frequency spectra of the advertisement (A-C) calls and short aggressive calls (D-F) of *Hyla ebraccata* (top), *H. phlebodes* (middle) and *H. microcephala* (bottom). From Schwartz and Wells (1984a).

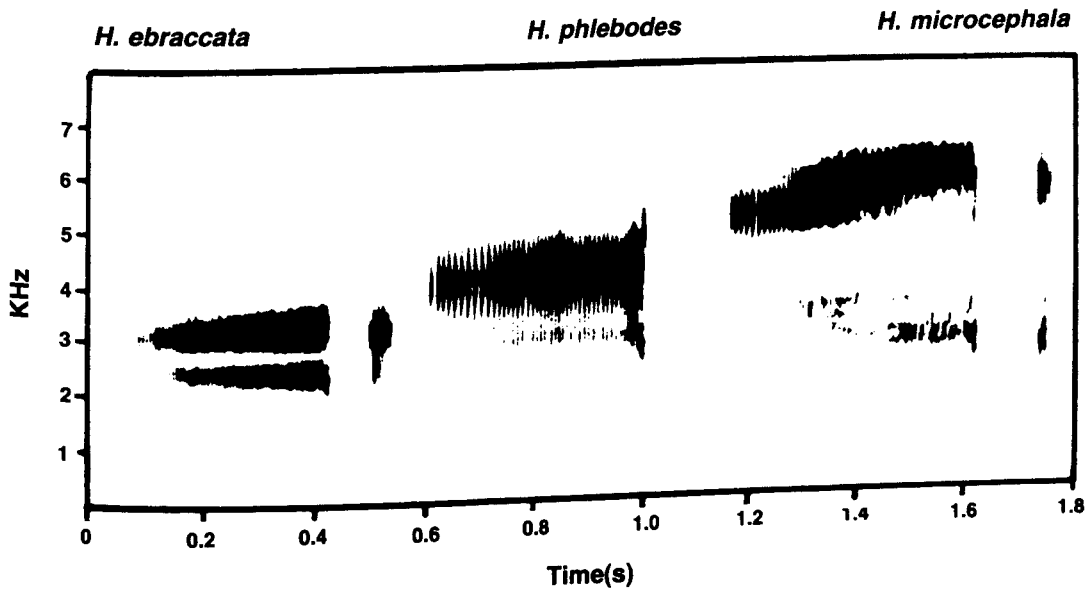


Fig. 4. Sonograms of the long aggressive calls of *Hyla ebraccata*, *H. phlebodes* and *H. microcephala*. From Schwartz and Wells (1984a).

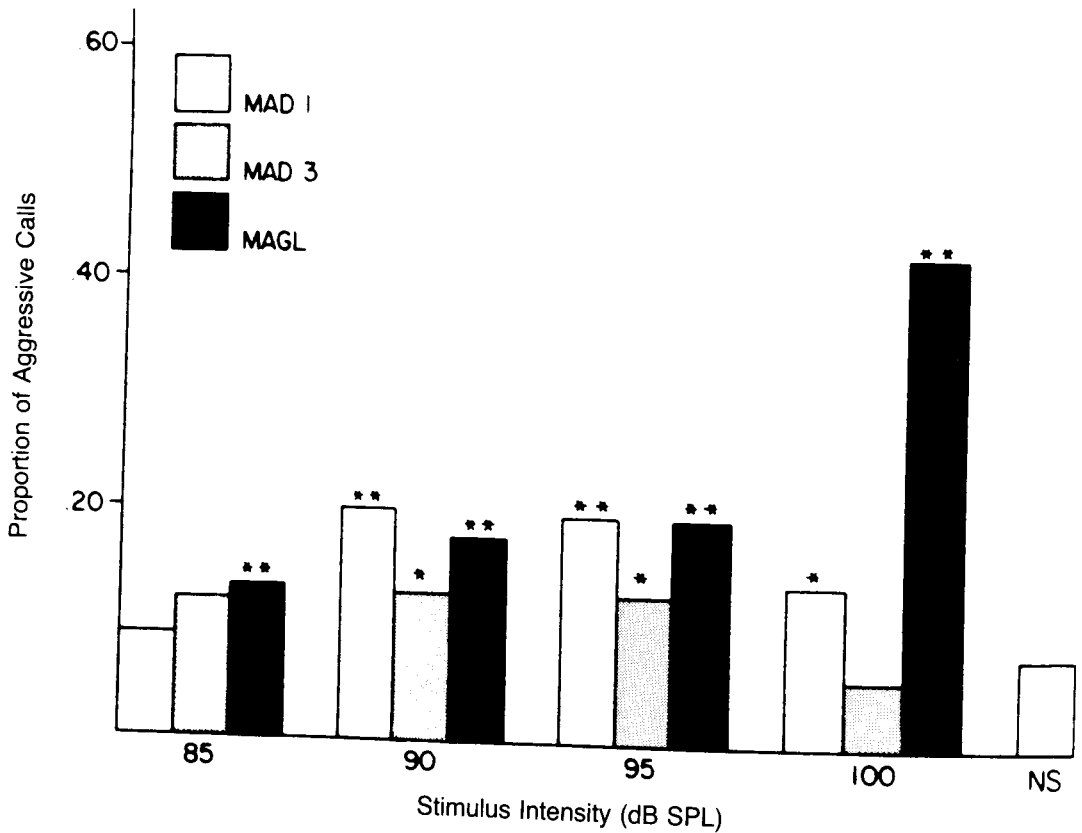


Fig. 5. Summary of aggressive call production by males of *H. ebraccata* in response to playbacks of advertisement calls (MAD 1 = 1-note call; MAD 3 = 3-note call) and long aggressive calls (MAGL) of *H. microcephala*. Asterisks indicate a significant difference compared with the no-stimulus (NS) periods. From Schwartz and Wells (1984a).

high proportion of aggressive calls (Fig. 5). Loud heterospecific advertisement calls also elicit aggressive call responses from *H. ebraccata*, but they are not as effective in doing so as are heterospecific aggressive calls. Males of *H. microcephala* and *H. phlebodes* were less likely than males of *H. ebraccata* to give aggressive vocal responses during playbacks of heterospecific calls, indicating that there may be an asymmetry in the vocal relationships among species pairs. Whether this asymmetry has any meaningful consequences during natural interspecific agonistic encounters is unknown.

In addition to having high pulse rates, the aggressive calls of *H. ebraccata*, *H. microcephala* and *H. phlebodes* are structurally more similar than are their advertisement calls. In particular, aggressive calls overlap in pulse rate whereas the pulse rates of advertisement calls are species-specific (Fig. 6). Playbacks of synthetic calls to males of *H. ebraccata* demonstrated that pulse rate is the most important temporal call feature in eliciting aggressive vocal responses (Wells and Schwartz 1984; see also Schwartz and Wells 1984a). Female choice experiments with *H. ebraccata* and *H. microcephala* showed that pulse rate is also critical to call and species discrimination by females (Schwartz 1986, 1987b; Wells and Bard 1987).

### B. Advantages of Interspecific Aggression

Many researchers have hypothesized that natural selection favours the evolution of interspecific territoriality and aggression if some common resource is contested (e.g., Orians and Willson 1964; Cody 1974; Ebersole 1977; Murray 1981; Ortiz and Jenssen 1982). Furthermore, Cody (1969, 1973, 1974) proposed that selection has caused the convergence of signals used during agonistic encounters. At present one can only speculate about the evolutionary basis of the structural similarities of the aggressive signals of some anuran

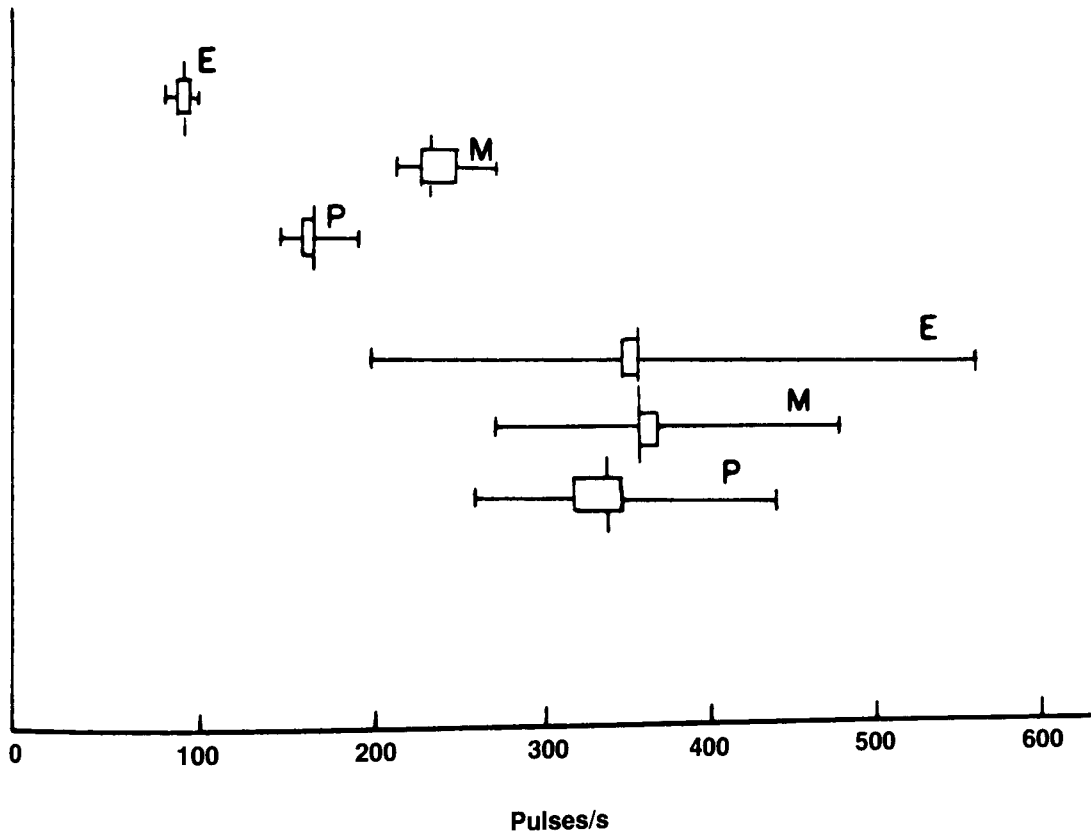


Fig. 6. Graphical summaries of the median values, approximately 95% confidence intervals, and ranges of the pulse rate of the advertisement calls (top left: all pulse-rate means below 300 pulse/s) and aggressive calls (all pulse-rate means between 300 and 400 pulse/s) of *Hyla ebraccata* (E), *H. phlebodes* (P) and *H. microcephala* (M). From Schwartz and Wells (1984a).

species (see Brown 1977), such as those of the Panamanian hylids studied by Schwartz and Wells (1984a). On the one hand, selection to facilitate their interspecific use should be strong because males show considerable spectral overlap among calls, often call in close proximity, and engage in call timing shifts in response to heterospecific vocalizations. Moreover, for males of *H. ebraccata*, acoustic overlap by heterospecific aggressive calls in pulse rate, chance of attracting a mate. The similarity of heterospecific aggressive calls in pulse rate, coupled with the differences in advertisement call pulse rate, suggests that this temporal feature of aggressive calls could have converged over evolutionary time. On the other hand, the similar pulse rate of the aggressive calls may have been the ancestral state in these three closely related species (e.g., Duellman 1970; Cardoso 1981), and selection could have caused the divergence in the pulse rates of their advertisement calls. Among other species using aggressive calls in interspecific encounters, such as gray treefrogs (Pierce and Ralin 1972) and European water frogs (Brzoska 1982), signal similarity is almost certainly attributable to phylogenetic affinity. The species in these two complexes arose through autopolyploidy and hybridization, respectively.

Comparisons of call structure of allopatric and sympatric populations could be used to test these hypotheses. If aggressive and advertisement calls in each species were the same in allopatry, then the phylogenetic affinity of the three species would be the most likely explanation for the similarity among aggressive calls. Reproductive character displacement could then be invoked as an explanation for the divergence of pulse rate in advertisement calls in sympatry. If aggressive calls were more similar in sympatry than in allopatry, then selection, instead of phylogenetic affinity, would be a likely cause of their similarity.

#### IV. HYBRIDIZATION AND HOMOGAMY

The first two parts of this chapter dealt with interactions between species that primarily reduce the efficiency of intraspecific communication through acoustic and behavioural interference. The present section turns to the hypothesis that mating mistakes between species may sometimes constitute a form of selection that shapes the structure of male vocalizations, female phonotactic selectivity, or both. There are two general situations in which hybridization occurs. First, extensive hybridization is typical of pairs of species that have not established broad sympatry; hybridization usually takes place in well-defined, relatively narrow hybrid zones, where backcrossing is also common. Second, occasional hybridization occurs between pairs of broadly sympatric species; backcrossing and introgressive hybridization are rare and usually confined to disturbed environments (e.g., Mecham 1960; Schlefer *et al.* 1986). Here, some examples of both hybrid zones and of hybridization between broadly sympatric species are reviewed. Next, the potential effects of hybridization on the evolution of homogamy and on the establishment of broad sympatry between closely related species are examined. Hybridization occasionally results in speciation in the form of allopolyploidy (review by Tymowska 1991) or in the production and maintenance of hybridogenetic systems (review by Graf and Polls-Pelaz 1989), but these topics are beyond the scope of this chapter.

The selective response of female anurans to conspecific advertisement calls has served for many years as an example of a premating isolating mechanism. However, as pointed out by Paterson (1985) and Littlejohn (1981), the term "isolating mechanism" implies that the structure of advertisement calls and the phonotactic selectivity of the female are characters that evolve in response to selection generated by the usually adverse consequences of hybridization. Paterson (1985) argued that different species rarely mate with each other because they each have a "specific-mate recognition system (SMRS)", which will promote homospecific matings whether or not another species is present. He categorized the older view as the Isolation Species Concept, and the SMRS as central to a Recognition Species Concept (Paterson 1985). However, female frogs sometimes show phonotactic responses to playbacks of the calls of heterospecific males, especially in "no choice" tests, thus indicating that these animals are not categorizing signals as either conspecific or heterospecific (e.g., Backwell and Jennions 1993; Gerhardt 1974c, 1982; Gerhardt *et al.* 1994a). Ryan and Rand (1993) argued that when any signal, whether heterospecific or synthetic, reliably attracts females, then this behaviour should be characterized as "mate recognition", even if the attraction can be viewed as a mistake. When females choose conspecific calls over heterospecific calls in a two-stimulus, playback test, then this is an example of one kind of "mating preference" (Ryan and Rand 1993). Littlejohn (1991) and Gerhardt (1982) emphasized that preferences for conspecific calls simply may be a consequence of intraspecific mate choice (stabilizing sexual selection). The hypothesis that interspecific interactions may sometimes influence the evolution of such patterns of preference or currently constitute a constraint on directional sexual selection is discussed in the last section of this chapter.

Littlejohn (1981, 1993) argued that the term "homogamy" is more appropriate than the term "species recognition". Homogamy is simply defined as positive assortative mating (see Littlejohn 1993, for a historical review). The term has the advantage of applying to a broad range of individuals that share genotypic and phenotypic similarities, regardless of their taxonomic status or which of the several species concepts a researcher may adopt (e.g., Templeton 1989; Endler 1989). As pointed out by Harrison (1990), both the Isolation Species and Recognition Species concepts are difficult to apply in hybrid zones. Indeed, Littlejohn (1993) concluded that homogamy (or possession of a SMRS) alone is not sufficient to be a defining characteristic of a biparental species.

##### A. Hybrid Zones

Hybrid zones have been reviewed by Barton and Hewitt (1985, 1989), Hewitt (1988), Littlejohn and Watson (1985), Littlejohn (1988, 1993), and Harrison (1990). Most hybrid zones, including all of the ones involving anurans that are discussed here, are assumed to be the result of secondary contact between populations or groups of populations that had been previously separated by climatic or geological changes (Harrison 1990). The main factors that

bear on the outcome of interactions between such populations when they re-established contact are: (1) the degree of ecological, behavioural, and genetic compatibility of the previously isolated populations; and (2) the ecology of the zone of contact and adjacent areas. Littlejohn (1993) outlined seven evolutionary scenarios, the probabilities of which depend on various combinations of these two factors. Littlejohn (1993) and Harrison (1990) both emphasized the importance of environmental heterogeneity along and within contact zones. Barton and Hewitt (1989) emphasized the genetic structure of individuals making up the hybrid zone and discounted direct selective effects of the environment. They argued that hybrid zones are maintained principally by the dynamic interactions between selection against unfit hybrids and recombination products and the continual migration of parental types into the zone. Harrison (1990) called for a merging of these ecological and genetical perspectives.

At one extreme of Littlejohn's proposed scenarios, individuals of previously isolated populations may be genetically compatible and hybrids of nearly equal fitness to the parental types in the zone of overlap. Thus, one might expect to find a broad zone of intergradation, the width of which would depend mainly on the time since contact. Any behavioural differentiation that developed during allopatry, such as differences in advertisement calls and selective phonotaxis, would break down in the zone of intergradation. One example that comes close to fitting into this category is the relatively broad hybrid zone between the genetically compatible "northern" and "southern" call races of the *Limnodynastes tasmaniensis* (Littlejohn and Roberts 1975). The zone of intergradation in southeastern Australia is about 215 km long and between 90 and 135 km wide. This zone was mapped by an analysis of two attributes of the advertisement call, note duration and number of notes per call (Fig. 7). These two properties appear to assort independently, thus indicating that backcross individuals and other recombinants are present in the zone. Very few individuals that had calls typical of the "parental" races were found along a well-sampled transect across the zone of integration. However, Littlejohn and Roberts (1975) argued that the width of the zone is too narrow, and the time since the two forms are estimated to have re-established contact is too short, to conclude that unrestricted introgression has occurred. They suggested that the recombination products are fitter than the parental types in the zone.

At the other extreme, individuals of the previously isolated populations may be so well-differentiated ecologically that hybrids would be less fit in any environment. In this case, one would expect the two previously isolated populations to become broadly sympatric if the ecological resources for each are widespread and uniformly distributed (Littlejohn 1993). This outcome would be accelerated if behavioural differences (distinctive advertisement calls and selective phonotaxis) and genetic incompatibility also arise during the period of isolation, in which case the establishment of sympatry would involve little evolutionary interaction. Paterson (1985) contended that broad sympatry cannot be achieved unless divergence has proceeded far enough to insure that there is no evolutionary interaction when the previously isolated systems re-establish contact.

The five other scenarios proposed by Littlejohn (1993) deal with the processes leading to the establishment of broad sympatry by previously isolated populations that have diverged to some intermediate extent relative to the two extremes outlined above. In these, the outcomes of interactions between different taxa are unpredictable. Indeed, one common observation is that the width of hybrid zones, their composition, and, by inference, the degree of direct interaction between "parental" forms often differ along the length of the contact zone. If individuals of the previously isolated populations are incompatible ecologically or genetically (hybrids of lower fitness in the zone of overlap), then there are several potential outcomes of their interaction. If the environment is relatively uniform with respect to the common ecological requirements of the previous isolates, individuals of the competitively superior population are likely to displace those of the other population. If, however, individuals of the two populations are competitively similar in the area of contact, then the result may be a narrow hybrid zone or a parapatric contact. Key (1981) and Barton and Hewitt (1989) termed such an area of contact a "tension zone". Tension zones are characterized by their narrow width, the pre-contact a "tension zone". Tension zones are characterized by their narrow width, the pre-contact a "tension zone". Tension zones are characterized by their narrow width, the pre-contact a "tension zone". Because of their emphasis on the ecological fitness of hybrids in contact zones, Littlejohn and Watson (1985) refer to tension zones as "true hybrid zones".

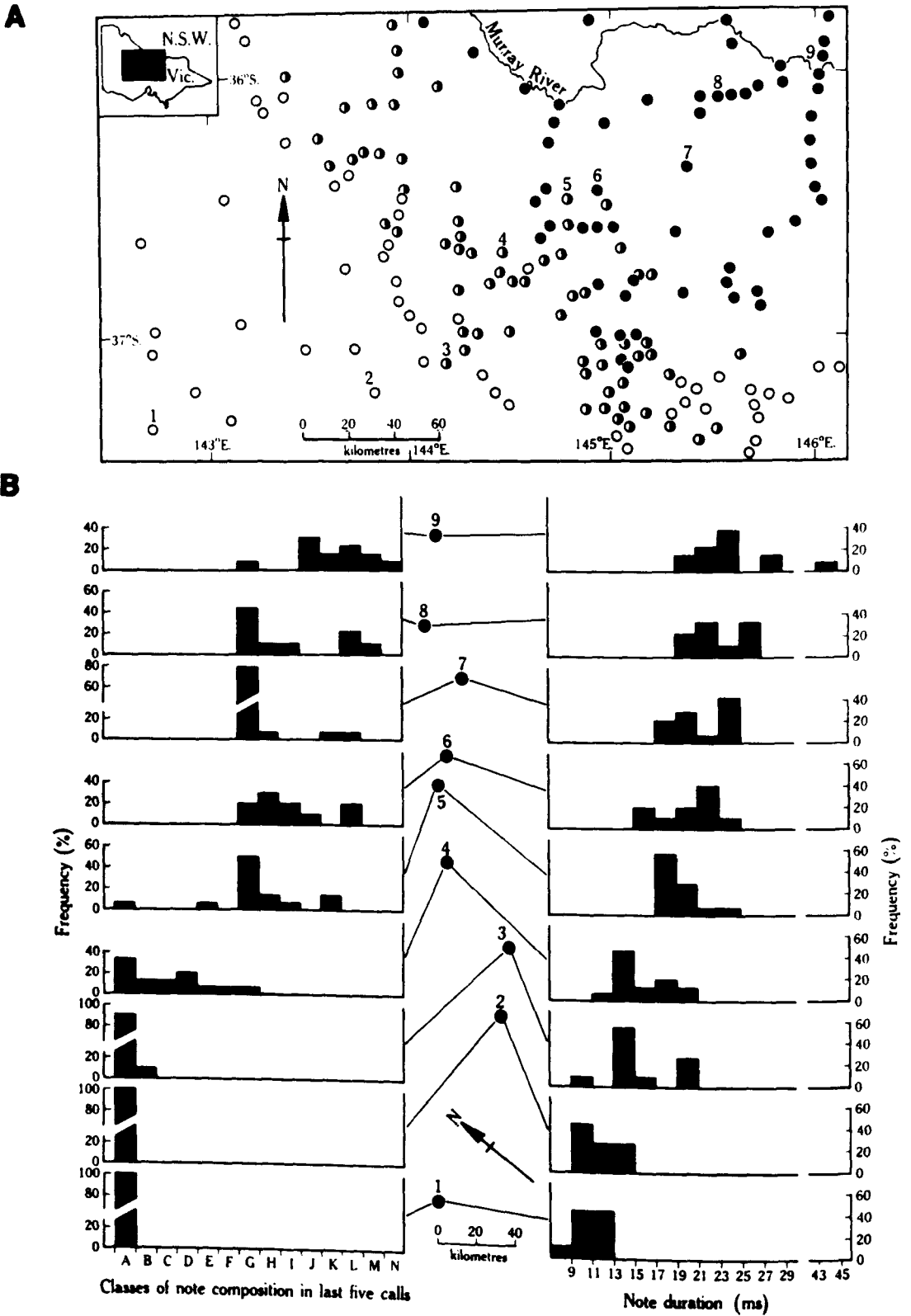


Fig. 7. Histograms showing geographical variation in two properties (notes per call, duration) of the advertisement calls of *Limnodynastes tasmaniensis* in a south-west to north-east transect in southeastern Australia. The transect includes a broad zone of intergradation between northern and southern call races, with pure southern types at localities 1 and 2, and pure northern types at localities 6-9. From Littlejohn and Roberts (1975).



One of the best studied examples of a tension zone in any species is the hybrid zone between *Bombina bombina* and *B. variegata*, which runs for about 1 000 km in eastern Europe (Szymura and Barton 1986; Barton and Hewitt 1989; Sanderson *et al.* 1992). The hybrid zone in southern Poland, which is now situated roughly along an altitudinal transition but does not correspond to any sharp ecotone, is estimated to have originated when the two taxa first came into contact about 8 000 years ago, after having diverged for at least three million years (Barton and Hewitt 1989). There is some genetic incompatibility between the two species that is manifested by higher rates of developmental abnormalities and mortality in individuals from the hybrid zone; individuals of the two taxa also differ in advertisement calls, warning colouration, life history, and preferred habitat (Szymura and Barton 1986). The width of the hybrid zone is about 6 km, as estimated by clinal variation in advertisement calls, morphological characters, enzyme loci, and mitochondrial DNA (Barton and Hewitt 1989; Sanderson *et al.* 1992). The introgression of neutral and especially advantageous genes from one taxon to the other occurs over distances of tens of kilometers (see Barton and Hewitt 1989 for recent estimates).

Sanderson *et al.* (1992) provided a detailed assessment of variation across the hybrid zone in three properties of the advertisement call, the structure of which is estimated to be controlled by three or more genetic loci. Only cycle length (call period) is diagnostic of the two parental forms, and the selection differential is estimated to be only about 6% of the difference in mean cycle length between the two taxa. In most parts of the hybrid zone mating appears to be random, even though mating preferences have been demonstrated in the laboratory and the two species coexist without hybridization in at least one locality (Szymura and Barton 1986). However, there is no evidence that females of either species show selective phonotaxis for conspecific advertisement calls. The weak selection on the advertisement call is also consistent with calculations estimating that 50–300 genes, each with a small effect, contribute to hybrid unfitness in *Bombina* (Barton and Hewitt 1981).

Some parts of stable hybrid zones involving Australian frogs can also be characterized as tension or true hybrid zones. The interaction between *G. laevis* and *G. victoriana* in the northern part of a long (115 km) hybrid zone is an example. Based on variation in advertisement calls, the width of the northern zone is 6–11 km, with most of the transition taking place over less than 2 km. Only recombination products are found in the hybrid zone. The hybrid zone to the south is usually wider and more heterogeneous. Its width, based on advertisement calls, varies from 9–30 km (although most of the transition occurs over about 4 km), and its composition ranges from a hybrid swarm (fewer than 3% parental individuals) at one locality to an overlap with hybridization (20% *G. laevis* and 33% *G. victoriana*) at a locality only 6 km away. As in *Bombina*, presumably neutral enzyme markers show introgression over a much wider area (up to 134 km; Littlejohn 1988). The hybrid zone is near, but does not coincide with, the presumed boundary between the western limit of the original forest cover and open woodland/grassland.

Two species of *Geocrinia*, unlike the two species of *Bombina*, are genetically compatible; even backcrosses with field-collected recombinants resulted in viable and fertile offspring (Littlejohn and Watson 1985). However, Littlejohn *et al.* (1971) report a higher percentage of abnormal embryos in the hybrid zone. Thus, some environmental factors, not present in the laboratory, may have important developmental consequences for hybrid progeny. Females of both species from allopatric areas show selective phonotaxis for conspecific advertisement calls, but they also were attracted by playbacks of the mosaic advertisement call (containing elements of the calls of both parental taxa) of a hybrid male (Littlejohn 1988). The main difference between the two hybrid zones is that strong evidence for selection against hybrids and backcrosses exists for the *Bombina* system (Barton and Hewitt 1989), whereas the approximately ecotonal distribution of the hybrid zone in *Geocrinia* is consistent with the conclusion of Littlejohn and his colleagues that hybrids and recombinants are at an advantage relative to the parental forms in the hybrid zone. However, identifying or defining individuals in hybrid zones as “parental types” and “hybrids” is problematic (Barton and Hewitt 1989; Hewitt 1988) because “parental” individuals of one type may nevertheless possess many genes from the other type unless they are “long-distance” migrants. As Harrison (1990, p. 84) points

out, there has been no direct demonstration of hybrid/recombinant superiority in any hybrid zone. Nevertheless, the importance of spatial variance in the environment is strongly suggested by the coincidence of the *Geocrinia* hybrid zone, and hybrid zones involving other taxa, with ecotones, and by studies of mosaic patterns of hybridization (Harrison 1990).

Some pairs of North American species of frogs and toads also have parapatric distributions and narrow hybrid zones (Green 1983; Hillis 1988). A well-studied example is the interaction between *R. berlandieri* and *R. sphenoccephala* in central Texas (Sage and Selander 1979). Although the advertisement calls are distinctly species-characteristic, hybridization is extensive in some localities (Hillis 1988). Kocher and Sage (1986) reported that very few hybrids survived metamorphosis in a cohort of tadpoles at a site where hybridization occurred, and gene flow between the two species is considered to be minimal (Hillis 1988). The toads *Bufo americanus* and *B. hemiophrys* were studied in a narrow hybrid zone, which is coincident with the ecotone between prairie and forest in southeastern Manitoba (Green 1983). In contrast to the situation in leopard frogs, adult hybrids and backcross products were common, and Green (1983) concluded that this was attributable to hybrid superiority within the hybrid zone.

Sullivan (1986), in reviewing studies of hybridization between the toads *B. microscaphus* and *B. woodhousii* in Arizona, suggested that both recent contact and human disturbance of breeding habitats promote mismatings between individuals of these two taxa. He argued that this situation may fit the "ephemeral zone" hypothesis of Moore (1977), in which the outcome of hybridization will result either in introgression, as in the call races of *Limnodynastes* (Littlejohn and Roberts 1975), or speciation. Alternatively, a stable hybrid zone could result, or one species (e.g., *B. woodhousii*) might displace the other one (*B. microscaphus*).

## B. Hybridization between Broadly Sympatric Species

Natural hybridization between pairs of broadly sympatric species has been documented in most families of frogs and toads. In North America, for example, natural hybrids have been found within the families Bufonidae, Pelobatidae, Hylidae, Microhylidae and Ranidae (Mecham 1961, 1965; Zweifel 1968; Gerhardt 1974a; Green 1984; Gerhardt *et al.* 1985, 1994b; Sattler 1986; Sullivan 1986; Hillis 1988). Many of these hybrids were males that easily were detected by their distinctive advertisement calls among choruses with hundreds of males of the parental species (Gerhardt 1974a). In general, such hybrids are rare in comparison to individuals of the parental species. Mismatings that lead to hybridization between broadly sympatric pairs of species are usually the result of ecological disturbances or unusual weather conditions that bring into contact individuals of two taxa that usually do not breed at the same time and place or that show strong spatial segregation within shared breeding sites (e.g., Blair 1941; Wasserman 1957; Mecham 1960; Gerhardt 1974a; Anderson and Moler 1986). Although selective phonotaxis may be well developed, hybridization between species in the genera *Bufo*, *Scaphiopus* and *Spea* appears to occur somewhat more frequently than in other genera because of the tendency of male toads and spadefoots to stop calling and actively pursue females (e.g., Forester 1973; Wells 1977; Sattler 1985).

There have been few attempts to assess directly the extent of mismating between broadly sympatric species. Jones (1973) used morphological data from Blair (1941) to estimate that among 639 individuals collected near Bloomington, Indiana there were 8.6% hybrids between the toads *Bufo americanus* and *B. woodhousii fowleri*. Morphological criteria were also used to estimate that 9.4% of the mated pairs were heterospecific; these estimates were derived from a separate set of unpublished data that also was collected by Blair (Jones 1973). However, Loftus-Hills (1975) questioned not only the identification of hybrids by morphological criteria alone, but also the data from advertisement calls that Jones (1973) used to support his claim that no hybridization was occurring in the same area thirty years later. Sattler (1985) found at least one hybrid between the spadefoots *Spea* (= *Scaphiopus*; Collins 1990) *bombifrons* and *S. multiplicata* in two-thirds of the 16 sympatric localities sampled in southwestern United States. The average frequency of hybridization was 3.5%; backcrossing to *S. multiplicata* and *S. bombifrons* had frequencies of 1.5% and 0.8% respectively. The observed frequency of F<sub>1</sub> hybrids was similar to previous estimates based on analyses of advertisement calls (Forester 1973) and

morphology (Hughes 1965). Sullivan (1986) provided a survey of qualitative estimates of the frequency of hybridization among various combinations of North American bufonids. Schlefer *et al.* (1986) found that about 11% of the 45 pairs of *H. cinerea* and *H. gratiosa* at disturbed sites near Auburn, Alabama (USA) were mismated. A recent survey of six man-made ponds, where the two species of gray treefrogs, *H. chrysoscelis* and *H. versicolor* bred syntopically in south-central Missouri (USA), revealed that of 176 pairs, five were mismated. The mismated pairs were found among 75 pairs observed at two ponds in Laclede County, Missouri: thus the frequency of mismating in these ponds was about 6.6% (Gerhardt *et al.* 1994b).

The rarity of sexually mature hybrids between the two gray treefrogs is not surprising because of the high degree of genetic incompatibility between these diploid-tetraploid species (Johnson 1959). Because Blair (1941) found that individuals of *B. americanus* and *B. woodhousii fowleri* hybridized in the laboratory and produced fertile offspring, Jones (1973) speculated that selection against hybrids must be ecological in nature. Individuals of *H. cinerea* and *H. gratiosa* also show a high level of genetic compatibility (Mecham 1960, 1965), but some males of *H. cinerea* may not be successful in producing hybrid offspring (Schlefer *et al.* 1986). Schlefer *et al.* (1986) concluded that a combination of ecological (e.g., species differences in the non-breeding habitat that require different degrees of desiccation tolerance) and developmental factors limited the reproductive success of hybrids and backcross products. Better field evidence for hybrid (ecological) unfitness is available from studies of hybrid zones (e.g., Kocher and Sage 1986, see above).

Most females of *H. cinerea* and *H. gratiosa* preferred the calls of conspecific males over those of putative hybrids in two-speaker playback tests (Gerhardt 1974a). Moreover, females of *H. chrysoscelis* and *H. femoralis* chose conspecific calls over those of putative hybrids, and females of *H. chrysoscelis* also discriminated against the calls of putative *H. chrysoscelis* × *H. avivoca* (Gerhardt 1974a). Females of both *H. chrysoscelis* and *H. versicolor* discriminated between synthetic calls with differences in pulse rate that were less than those between conspecific calls and the calls of triploid hybrids (Gerhardt 1982; Gerhardt and Doherty 1988; Gerhardt *et al.* 1994b). Females of *H. andersonii* were less selective than females of *H. cinerea* in situations where the source of heterospecific calls was closer (and hence the calls had a higher SPL at the female's position) than that of conspecific calls (Gerhardt 1974c). Moreover, females of *H. andersonii* preferred the calls of *H. cinerea* to those of *H. gratiosa* in two-speaker playback experiments. This led Gerhardt (1974c) to predict that hybridization between *H. andersonii* and *H. cinerea* was likely to occur in areas where their usual segregation by breeding habitat was not maintained. Anderson and Moler (1986) not only found a natural hybrid between these two species near the site of a mixed-species chorus, but they also found a hybrid between *H. andersonii* and *H. femoralis*, a member of another species group.

Schlefer *et al.* (1986) argued that the relatively stable population of hybrids, backcrosses and parental individuals of *H. cinerea* and *H. gratiosa* that has persisted near Auburn for 20 years is maintained as a dynamic equilibrium. Relatively unfit hybrids are continually replaced as individuals of the parental species migrate into the disturbed habitat and mismate. The majority of individuals involved in mismatings with the other species or hybrids or backcrosses were females of *H. gratiosa* (Schlefer *et al.* 1986; Lamb and Avise 1987). These data support the speculation that females of *H. gratiosa* must often be intercepted on their way to conspecific males, which call from floating positions in the pond, by males of *H. cinerea* that typically call from the margins of the pond (Mecham 1960, 1961). Probably the mowed grass margins of the ponds facilitated accidental contacts because males of *H. cinerea* would be forced to call from the ground, whereas in ponds with normal vegetation (trees, bushes and cattails) a large proportion of males call from elevated perches. In addition, Lamb and Avise (1987) suggested that mismatings of this combination are more likely because non-calling, satellite males, which intercept females as they move to calling males, are common in *H. cinerea* (Perrill *et al.* 1978).

Despite the obvious disadvantages of being clasped by heterospecific males, there is little evidence that treefrogs recognize and avoid the calls of heterospecific males. Some females of five species of North American hylids responded phonotactically to playbacks of the calls of other, closely related, sympatric species if conspecific calls were unavailable (Gerhardt 1982;

Gerhardt and Doherty 1988). Moreover, females of *H. versicolor*, *H. chrysoscelis* and *H. gratiosa* were as likely to move to a speaker that emitted a combination of a conspecific and a heterospecific call as they were to move to a speaker that broadcasted the same conspecific call alone (Gerhardt *et al.* 1994a). Females of *H. versicolor* did not deviate from a more or less straight-line approach to a distant speaker that emitted conspecific calls even though this path took them very close to a nearby, intervening speaker through which the calls of *H. chrysoscelis* were played back. These results suggest that selective phonotaxis may sometimes be simply a result of a greater quantity of acoustic stimulation by conspecific calls than by heterospecific calls of generally similar acoustic structure. Thus, it is unnecessary to invoke special mechanisms different from those used in intraspecific mate choice. Perhaps the high degree of phonotactic selectivity in natural breeding sites, where there may also be some degree of spatial segregation by species, make accidental contacts and hybridization so uncommon that there has been little opportunity for selection for avoidance behaviour.

### C. Homogamy and Sexual Selection

The preference functions of female anurans for some properties of advertisement calls constitute stabilizing (sexual) selection in that females prefer values of call properties that are very close to the mean value in the population and discriminate against values at one or both ends of the range of variation (Gerhardt 1974b, 1982, 1991). In these cases, homogamy is most parsimoniously viewed as a consequence of intraspecific mate choice because the value of the property in the most similar heterospecific signals will nearly always differ more from the mean value than the value in the least attractive (extreme) conspecific calls (Fig. 8). One hypothesis for the existence of stabilizing preference functions is that directional selection is constrained in one or both directions by the possibility of mating mistakes with males of other

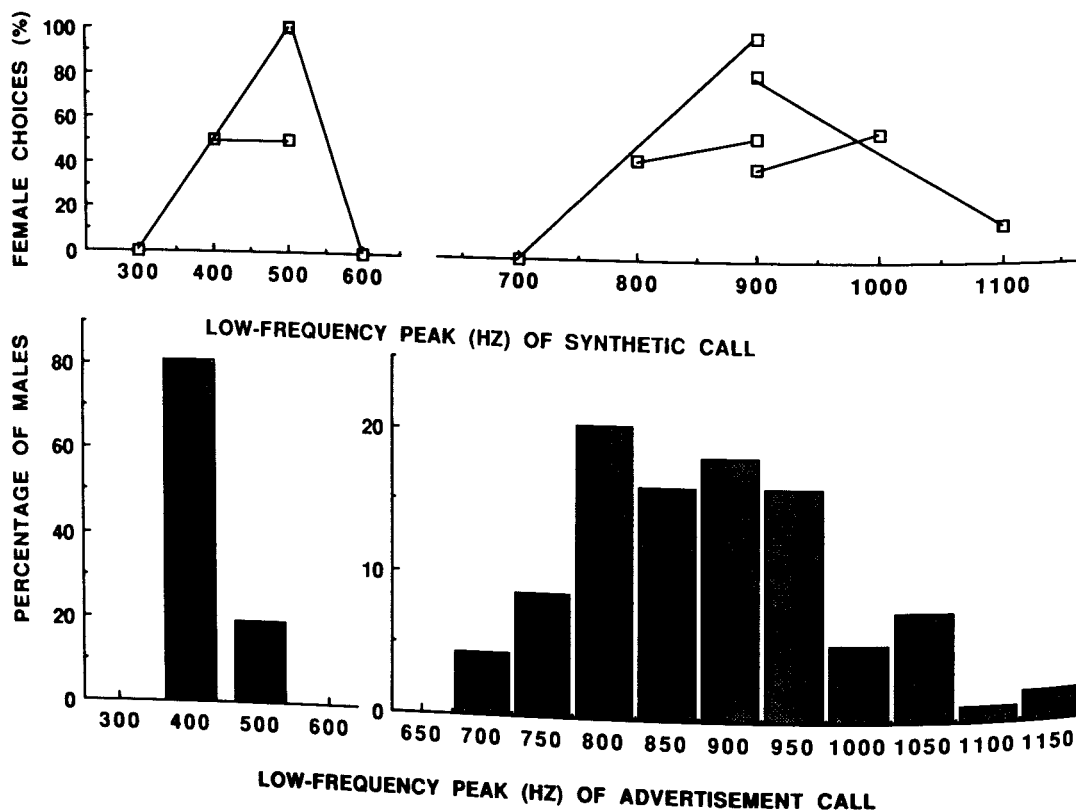


Fig. 8. Diagram showing the distributions of the low-frequency spectral peaks in the advertisement calls of *H. cinerea* and *H. gratiosa*. As indicated by the preference functions (right = *H. cinerea*; left = *H. gratiosa*), females prefer low-frequency spectral peaks that are at or near the mean values in the populations from which they were collected.

synchronously breeding species that result in offspring with reduced fitness (Gerhardt 1982). This perspective was recently misrepresented by Ryan and Rand (1993), who cited Gerhardt's (1982) paper as "... suggesting that if there is species recognition there cannot be sexual selection (Ryan and Rand 1993, p. 647)." In fact, as stated above, Gerhardt's (1982) position was that species recognition is best viewed as a consequence of the intraspecific selectivity of females, including stabilizing selection, for certain call properties, and that other properties of the same calls might mediate directional selection (see below).

Another, proximate explanation for preference functions, stabilizing or otherwise, is that they arise from conservative, pre-existing sensory biases, whose evolutionary origin and causation are unknown (e.g., Ryan *et al.* 1990). For example, females of the barking treefrog (*Hyla gratiosa*) prefer synthetic calls with low-frequency spectral peaks at frequencies close to the species-typical mean to alternative stimuli with spectral peaks of lower frequency (Fig. 8). Yet there are no sympatric species of treefrogs with similar calls that have spectral peaks that are lower than those of *H. gratiosa* (Gerhardt 1982). A more direct test of the idea that patterns of female preference are sometimes affected by interactions between species is to compare the phonotactic selectivity of females from allopatric areas with those of females from areas where another species with similar calls breeds synchronously in the same breeding sites (see next section).

In many species, some properties of advertisement calls are stereotyped and under stabilizing female choice, whereas other properties are highly variable and are often subject to highly directional female preferences (Gerhardt 1991; see Passmore *et al.* 1992 for evidence of directional selection based on a dynamic call property, call-repetition rate). When the values of variable properties overlap broadly among sympatric species, the stabilizing preferences for static properties that do not overlap usually dominate the directional preferences for variable properties in determining the overall attractiveness of the signal (Gerhardt 1991). Rather than having some properties of the same signal subject to stabilizing selection and other properties, to directional selection, some species of frogs produce two types of note. One type is necessary and sufficient to elicit phonotaxis, whereas the other type may increase the attractiveness of the call to the female. The best-studied example is the "chuck" note that is added to the "whine" note of the túngara frog *Physalaemus pustulosus* (Ryan 1985). The "chuck" note is often added in response to vocalization by other, nearby conspecific males, and it may have a negative impact on the direct fitness of the male because predatory bats, as well as females, find calls with chucks to be more attractive than calls consisting of whines alone (Ryan 1985; Sullivan *et al.* 1995).

#### D. Interspecific Interaction and Homogamy: Reproductive Character Displacement

Female mate choice and interspecific interactions, both behavioural and ecological, are forces that potentially play important roles in the evolution of acoustic communication in both allopatry and sympatry (e.g., Littlejohn 1977; but see Paterson 1985, for a contrary view). This is not to deny the possibility that broad sympatry may be commonly or even usually achieved through non-interactive processes. Moreover, there is no question that selective pressures other than those associated with interspecific interactions as well as other evolutionary forces (mutation, drift) affect population-level changes in courtship behaviour within sympatric and allopatric populations (e.g., see Ryan and Wilczynski 1991, for examples from frogs, and Maksymovitch and Verrell, in press, for examples from salamanders). The traditional approach to provide evidence for interspecific effects has been to compare the calls and behaviour of individuals from areas of sympatry with those of individuals from areas of allopatry.

The term "reproductive character displacement" is used here to refer to both the predicted geographical pattern (accentuation of differences in courtship behaviour in sympatry compared to allopatry) and the natural and sexual selection that may lead to such patterns. Loftus-Hills and Littlejohn (1992) and Howard (1993) argued that the term be applied only to the geographic pattern, and that the term "reinforcement" be used to label the selective processes. Butlin (1987) recommended that both terms be used to describe

patterns and selective processes, but he restricted "reproductive character displacement" to pairs of species that are completely genetically incompatible. Because of the practical difficulties often encountered in assessing genetic incompatibility, Butlin's definition seems too restrictive. The term "reinforcement" has the disadvantage of being historically linked with a generally outdated term, "isolating mechanisms". Reinforcement is also a common term in the psychological and behavioural literature, where it describes any entirely different phenomenon. However, both terms are in widespread usage, and thus it is important for future studies to make explicit which definitions apply.

Three of the best examples of geographical patterns consistent with reproductive character displacement involve the advertisement calls of frogs: *Litoria ewingi* and *L. verreauxi* in south-eastern Australia (Littlejohn 1965; Littlejohn and Loftus-Hills 1968); *Pseudacris nigrita* and *P. triseriata feriarum* in the southeastern USA (Fouquette 1975); and *Gastrophryne carolinensis* and *G. oliveacea* in the south-central USA (Loftus-Hills and Littlejohn 1992). In each of these species-pairs, differences in at least one property of the advertisement calls were greater in sympatric areas than they were in allopatric areas. In the study of *Pseudacris*, advertisement calls were sampled from a wide enough range of allopatric populations to demonstrate that the shift in pulse rate in one of the taxa (*P. triseriata*) in sympatry was not merely the continuation of a cline established in allopatry (Fouquette 1975). Sampling of allopatric populations of *G. carolinensis* was more limited, but consistent with the same conclusion (Loftus-Hills and Littlejohn 1992).

Littlejohn and Loftus-Hills (1968) showed that the differences in advertisement calls presumably generated by reproductive character displacement are biologically significant. In playback experiments, females of *L. ewingi* and *L. verreauxi* from sympatry preferred conspecific calls. However, females of *L. ewingi* did not prefer conspecific calls from sympatry to those of *L. verreauxi* from remote allopatry, presumably because they are so similar in pulse rate. Females of *L. verreauxi* from sympatry preferred the calls of local males to those of remote allopatric males of the same species. The last result supports the hypothesis that the "sound environment" can bring about evolutionary changes in courtship signals that potentially affect speciation (i.e., within *L. verreauxi*; Littlejohn and Loftus-Hills 1968). Although no preference tests are available, the displaced attributes (dominant frequency in *Gastrophryne* and pulse rate in *Pseudacris*) are of known importance in selective phonotaxis in anurans (Gerhardt 1988). Additional studies of these species-pairs are needed to document in more detail geographic patterns in male calls, to assess female selectivity in sympatry and allopatry (see below), and to learn about the nature and magnitude of selection against mismatching and any hybrids that may be produced.

Despite many examples of partial overlap of the ranges of closely related species of frogs and other animals, examples of reproductive character displacement in male signals are rare (e.g., Butlin 1987; Ewing 1989; but see Howard 1993, for a different viewpoint). There are several theoretical reasons why this should be so, especially if the interacting taxa produce even partially fertile offspring (reviews by Littlejohn 1981; Butlin 1987; Harrison 1992). Reproductive character displacement may also be difficult to detect if it occurs relatively rapidly (Littlejohn 1981; Butlin 1987). However, Waage (1979) suggested that reproductive character displacement may have gone undetected because researchers have tended to focus exclusively on geographical variation in male signals. If the signals of the interacting taxa diverge sufficiently in allopatry to be perceptually distinctive to females, then selection simply may favour those females that use existing differences in the signals to mate assortatively. There would then be no logical necessity for the signals of the two taxa to diverge further in sympatry. One appeal of this hypothesis is that females generally have more to lose by a mating mistake with another species than do males, and hence selection on their phonotactic behaviour should be stronger than that on male signals.

Gerhardt (1994) recently tested Waage's hypothesis by comparing the phonotactic selectivity of females of the diploid gray treefrog (*H. chrysocelis*) from sympatric (with the genetically incompatible tetraploid *H. versicolor*) localities with that of females from remote allopatric populations (Fig. 9). Males of the two species produce advertisement calls that have

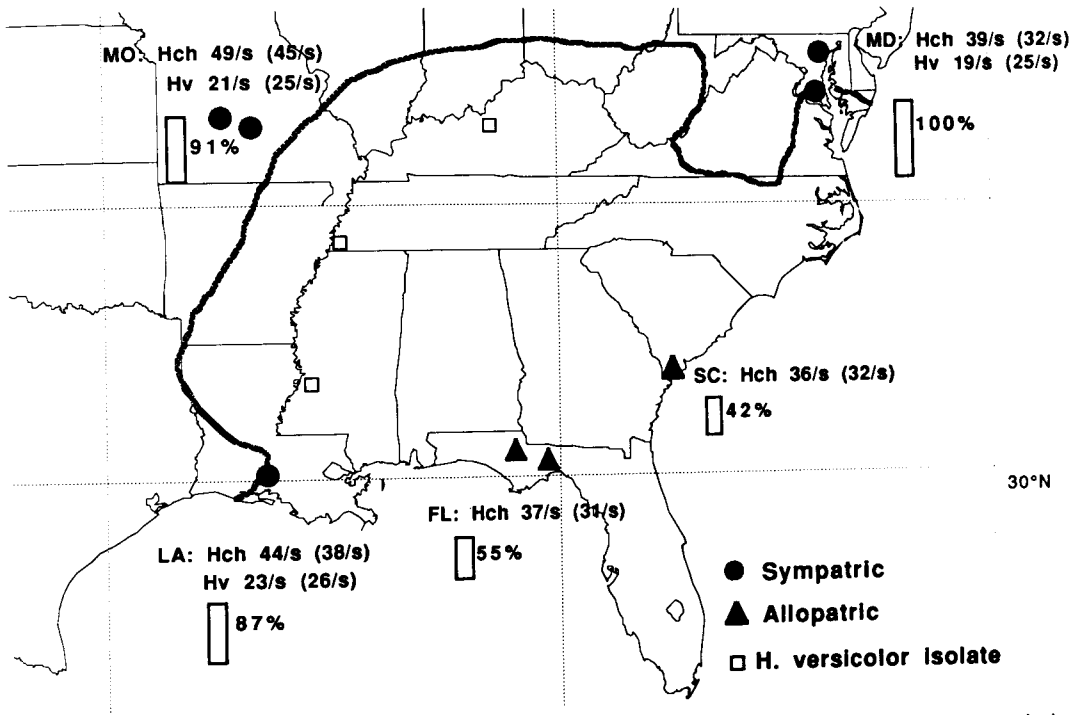


Fig. 9. Map showing localities from which females of *H. chrysoscelis* were collected for testing in two-stimulus playback experiments. Solid circles = sympatric localities (syntopic with *H. versicolor* or within 50 km of populations of *H. versicolor*); Triangles = remote allopatric populations; Open squares = isolated populations of *H. versicolor* along the Mississippi River drainage, within the general area (to the east and south of the solid line) of the southeastern USA where only *H. chrysoscelis* occurs. The mean pulse rate (corrected to 20°C) for *H. chrysoscelis* (Hch) and for *H. versicolor* (Hv), if present, is shown for each area. The numbers in parentheses show the minimum, temperature-corrected pulse rate for *H. chrysoscelis* and the maximum corrected pulse rate for *H. versicolor*. These are conservative estimates of the typical minimum difference in pulse rate that females are expected to encounter in sympatric areas. The bars show the percentages of females of *H. chrysoscelis* that chose the short synthetic call with a pulse rate typical of a local conspecific male rather than a long synthetic call with a pulse rate that was 30% lower. See Figure 10 and the text for more details. Modified from Gerhardt (1994).

about the same dominant frequency; the mean, temperature-adjusted (20°C) pulse rate of the calls of *H. chrysoscelis* is about twice that of the calls of *H. versicolor* (Gerhardt 1994). Females of *H. chrysoscelis* were offered a choice between a synthetic call with a pulse rate typical of a local conspecific male and an alternative with a pulse rate that was 30% lower. A difference in pulse rate of 30% has been found between the calls of males of the two species in the same pond on the same night. The signal with the lower pulse rate had a call duration that was three times that of the signal with the conspecific pulse rate (Fig. 10). Females of both *H. chrysoscelis* and *H. versicolor* (Klump and Gerhardt 1987; Gerhardt 1994) strongly prefer long to short calls if pulse rate is held constant at conspecific values. Thus, the females faced the dilemma of choosing between a relatively unattractive (short) call with the conspecific pulse rate and a relatively attractive (long) call with a pulse rate that fell within the range of variation typical of a genetically incompatible male of another species. As shown in Figure 10, 87 to 100% of the females from sympatric and nearby localities chose the short call with the appropriate pulse rate, whereas only about 50% of the females from remote allopatric populations did so. Thus, it can be hypothesized that in sympatric areas, the risk of mating with a genetically incompatible male has selected against confounding a preference based on pulse rate by a difference in call duration. Obviously no such selection exists in remote allopatry, and so the choice of the long call would have no adverse consequences on fitness. Data from studies of species isolation in salamanders may provide a parallel example. Although there is evidence for allopatric divergence in mate recognition systems, the proportions of interspecific pairings that led to insemination was uniformly low among combinations of different species from sympatric populations, whereas heterospecific pairings resulted in proportions of 14%–36% in about one-third of the combinations of different species from allopatric populations (Table 3 in Maksymovitch and Verrell, in press).

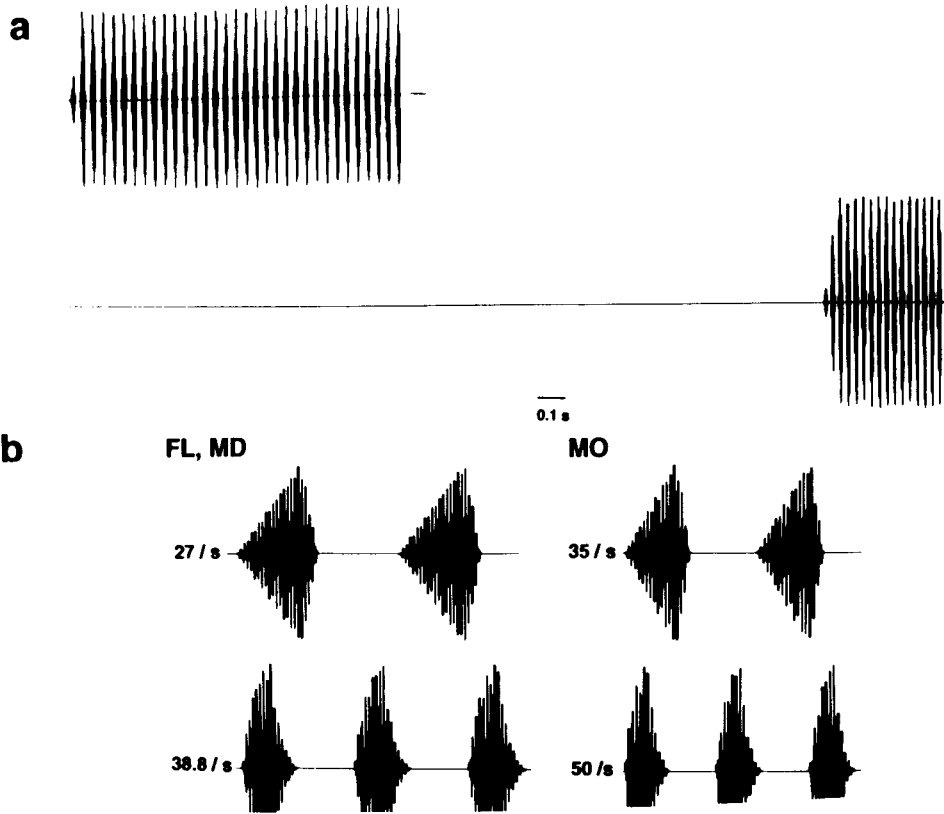


Fig. 10. Oscillograms of some of the synthetic sounds used in female choice experiments with *H. chrysocelis*. (a) Gross temporal properties of long (top trace) and short (bottom trace) synthetic calls. There were equal intervals of silence between the ends of one stimulus and the beginning of the alternative stimulus. (b) The fine-temporal structures of long (top traces) and short (bottom traces) synthetic calls were based on the advertisement calls of *H. versicolor* and *H. chrysocelis*, respectively. The pair of oscillograms to the left show alternative stimuli (27 p/s, top trace versus 38 p/s, bottom trace) that were presented to all females from Maryland (MD) and all except four females from Florida (FL). Other frogs from Florida and the frogs from South Carolina (SC) were given a choice between long calls with a pulse rate of 25 p/s and short calls with a pulse rate of 36 p/s. One female from Florida was tested two times with each of these pairs of stimuli. The pair of oscillograms to the right show alternative stimuli (35 p/s, top trace versus 50 p/s, bottom trace) that were presented to all females from Missouri. Frogs from Louisiana were given a choice between calls with pulse rates of 31 p/s and 44 p/s. Modified from Gerhardt 1994.

As in nearly all studies of reproductive character displacement, females from more populations need to be tested to obtain a more complete assessment of geographical variation in female preferences. These data are also necessary to rule out the possibility that differences in the preferences of females from sympatric and allopatric areas are merely continuations of trends established in allopatry. Moreover, these studies are likely to uncover geographical differences within the large areas where only one species of gray treefrog occur. It is important to emphasize again that interspecific interactions are only one of many selective forces that can shape courtship signals and behaviour, and that when such interactions do occur, their importance relative to other evolutionary forces will vary in time and space.

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