CALLING SITES USED BY MALE GRAY TREEFROGS, *HYLA VERSICOLOR* AND *HYLA CHRYSOSCELIS*, IN SYMPATRY AND ALLOPATRY IN MISSOURI

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ABSTRACT: Results of this study show strong evidence for segregation of calling sites by two species of gray treefrogs in sympatric choruses. A greater proportion (61.3%) of males of *H. chrysoscelis* called from sites that were ≤50 cm above the ground, whereas 68.7% of the males of *H. versicolor* occupied calling sites at elevations >50 cm. There was a weaker trend for males of *H. chrysoscelis* to call from sites closer to the edge of the pond than males of *H. versicolor*.

In ponds in allopatry, males of both species frequently called from sites that were avoided in sympatry. That is, males of *H. chrysoscelis* more often called from elevated sites (73.7%) and males of *H. versicolor* called from the ground or from sites ≤50 cm (59.6%). These within-species differences between allopatry and sympatry could not be explained by differences in distribution of vegetation between the two pond types.

Thus, the presence or absence of heterospecifics influences calling sites used by male gray treefrogs of both species. These observations may provide evidence for character displacement in calling site preference in sympatry and character release in allopatric choruses.

Key words: *Hyla chrysoscelis*; *Hyla versicolor*; Gray treefrogs; Call sites; Interspecific interactions

CHARACTER displacement is defined as the divergence in a character between closely related species in areas of sympatry (Brown and Wilson, 1956; Lack, 1947). Reproductive character displacement results in the accentuation of isolating mechanisms in the area of sympatry (White, 1978). Butlin (1989) emphasized that unlike reinforcement (Blair, 1955, 1974), reproductive character displacement acts on the mate recognition systems of already existing species. He defined reinforcement as a process that completes the speciation of incipient taxa (Butlin, 1989). Grant (1972) defined character displacement as the presence of a character state in sym-

patry that is shaped by natural selection in the form of competition with a closely related species. A different character state exists or is absent in allopatry, where selection is relaxed or absent because the competitive species is absent. Grant defined the change or absence of the character state in allopatric populations as character release.

Reproductive character displacement has been the subject of controversy. Many authors (e.g., Butlin, 1987; Grant, 1972; Littlejohn, 1981; Paterson, 1985) have pointed out that there are few well documented cases. Moreover, these authors have suggested that differences observed in sympatric populations that have been attributed to character displacement may be merely the result of clinal variation or are accidental by-products of divergence caused by other factors. Organisms whose

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mate-recognition systems involve acoustic communication have provided the best examples of reproductive character displacement. In several species of insects and frogs, acoustical signals of one species may interfere with those of another, and these coexisting species may adjust their songs in a fashion that reduces signal interference (Otte, 1979, 1989; Schwartz and Wells, 1983, 1984). Reproductive character displacement has been suggested for several species of anurans (Blair, 1955, 1958, 1974; Fouquette, 1975; Littlejohn, 1960, 1965), Hawaiian crickets (Otte, 1989), and *Drosophila* (Markow, 1981). In the anuran examples, researchers have invoked reproductive character displacement to explain divergence in species-specific properties of the advertisement calls in sympatric populations when compared to allopatric populations. Within large, multispecies communities, synchronously calling species usually have distinctive acoustic signals differing from other species in the community in frequency and/or pulse rate (Duellman and Trueb, 1986). Although differences in the mating calls of anurans are usually the most important premating isolating mechanism, other ecological factors such as time and place of breeding may also provide examples of character displacement (Blair, 1974).

Interactions between species may cause spatial adjustments in sympatry as well. The role of interspecific interactions in influencing spatial and behavioral organization between sympatric species has been documented for many vertebrate taxa (e.g., birds: Orians and Horn, 1969; rodents: Brown, 1971; caudate amphibians: Highton, 1970; Jaeger, 1974). Studies of multispecies anuran communities comprising nine species in Florida (Bogert, 1960), 10 hylid species in Costa Rica (Duellman, 1967), and seven species in Victoria, Australia (Littlejohn, 1977) have revealed that spatial and acoustic partitioning exists in any given community at a particular time. In all cases, species with the most similar calls exhibited the greatest spatial differences. Three studies have quantitatively examined the effects of both acoustic and non-acoustic behaviors on coexistence of

anuran congeners: *Ranidella signifera* and *R. parinsignifera* in Australia (Littlejohn et al., 1985; Mac Nally, 1979, 1984), *Hyla ebraccata, H. microcephala,* and *H. phlebodes* in Panama (Schwartz and Wells, 1984), and *Rana clamitans* and *R. virgatipes* in New Jersey (Given, 1990).

My study also examines interspecific interactions that affect calling sites in two species of gray treefrogs, *Hyla chrysoscelis* and *H. versicolor*. Both species are widespread in Missouri, occurring in allopatry in certain parts of the state and in a broad region of sympatry in south-central Missouri. Within areas of sympatry, mixed-species choruses are found in most available breeding habitats. The two species are morphologically indistinguishable but can be readily identified by the distinctive advertisement calls of the males. Heterospecific matings result in sterile triploids with decreased viability (Johnson, 1959, 1963). Thus selection favors reproductive traits that enhance conspecific matings. Although differences in advertisement calls are known to act as strong premating isolating barriers in sympatric choruses (Gerhardt and Doherty, 1988), three mismated pairs (out of 142 sympatric pairs examined) have been observed in Missouri (Gerhardt, Ptacek, Barnett, and Torke, unpublished data).

The purpose of my study was to examine the possibility that call site segregation is another factor that reduces mating mistakes in sympatric choruses. Evidence for differential use of available calling habitat within sympatry would suggest that females might use spatial cues as well as acoustic cues to discriminate against heterospecifics. The hypothesis of character displacement in calling sites would be supported by two observations. First, species differences in the use of available calling habitat should occur in sympatric choruses. Second, there should be a difference between the call sites of allopatric and sympatric males of the same species. If males in allopatry show a distinct preference for heterospecific sympatric call sites, this would provide evidence of character release and further support the hypothesis of character displacement in sympatry.

MATERIALS AND METHODS

Male gray treefrogs of both species form breeding choruses from late April to mid-July in Missouri. I collected data on male call site positions in 10 sympatric ponds and in five allopatric ponds for each species during the peak of the breeding seasons (May–June) of 1987–1989. There was broad overlap in the times during the breeding season when I made these measurements both in allopatric and sympatric ponds and between years. I measured one sympatric pond twice (in 1987 and in 1989) and treated the data as independent measurements. Measurements were taken only on nights when air temperatures were between 18 and 24 C in ponds where I had observed chorusing activity for at least 1 wk. This insured that no data were collected early or late in the breeding season. Seasonal effects are known to influence calling site distribution (personal observation), and by sampling during this time, temperatures on a given night were within the temperature range at which females breed (Gerhardt and Doherty, 1988).

I chose ponds with trees or shrubs on at least two sides so that elevated perches were available as calling sites. The distance from the water's edge to trees or shrubs was 1–3 m, so that ground calling stations and elevated calling sites were both available near the water's edge. In late May and early June 1991, I sampled vegetation along 20-m transects (the same transects from which call site data had been collected) in eight of the sympatric ponds and four each of the allopatric ponds for each species. I recorded height of the nearest vegetation from 10 randomly selected points along the transect line and used the line intercept technique (Cox, 1985:64–67) along the transect to estimate density and percent canopy coverage of vegetation.

Chorus density was at least 10 calling males within a 100-m² plot, thus insuring that calling males could hear their nearest neighbors. Male gray treefrogs produce calls of approximately 78 dB SPL at 4 m (extrapolated from values at 1 m given in Gerhardt, 1975), which is well above auditory threshold (in dB SPL) at advertise-ment call frequencies (Lombard and Straughan, 1974). Nearest neighbor distances were seldom >4 m at densities of 10 males/100 m².

I waited 1 h after males began calling before taking measurements to allow each male to establish a calling site. I then sampled as many non-overlapping 100-m² plots (20 m in length parallel to the water's edge × 5 m perpendicular to the water's edge) as possible within a night until chorusing activity ceased, and I pooled the data for all plots within a pond. Male gray treefrogs exhibit little call site fidelity from night to night and sometimes change calling positions within a night (Fellers, 1979; Ritke et al., 1990). However, most males remained at the same or a nearby calling station throughout the 3–4 h calling period unless they were disturbed (personal observation). I located all calling males within a plot and marked their positions with colored tape before making any measurements. During marking of the call site, males usually did not leave the site or at least remained close enough to their original positions so that they could be relocated after I had marked all call sites. I then recorded cloacal temperature, snout–vent length (SVL in mm), and species of the calling male, air temperature at the call site, distance to the ground, distance to water, distance to nearest neighbor, and species of nearest neighbor. I measured distance to water for elevated males diagonally from the call site to the water's edge and converted this measurement to horizontal distance by using the Pythagorean theorem.

Differences in distributions for height of vegetation between sympatry and the two allopatric pond types, and differences in distributions of call sites within sympatry, and between sympatry and allopatry for each species, were tested for significance with 2 × 2 contingency tables using proportions (Zar, 1984). A Chi-square analysis was used to test if either species formed conspecific or heterospecific aggregations in sympatry (only males whose nearest neighbor was within 4 m were used in this analysis, and I calculated expected values based upon the percentage of males
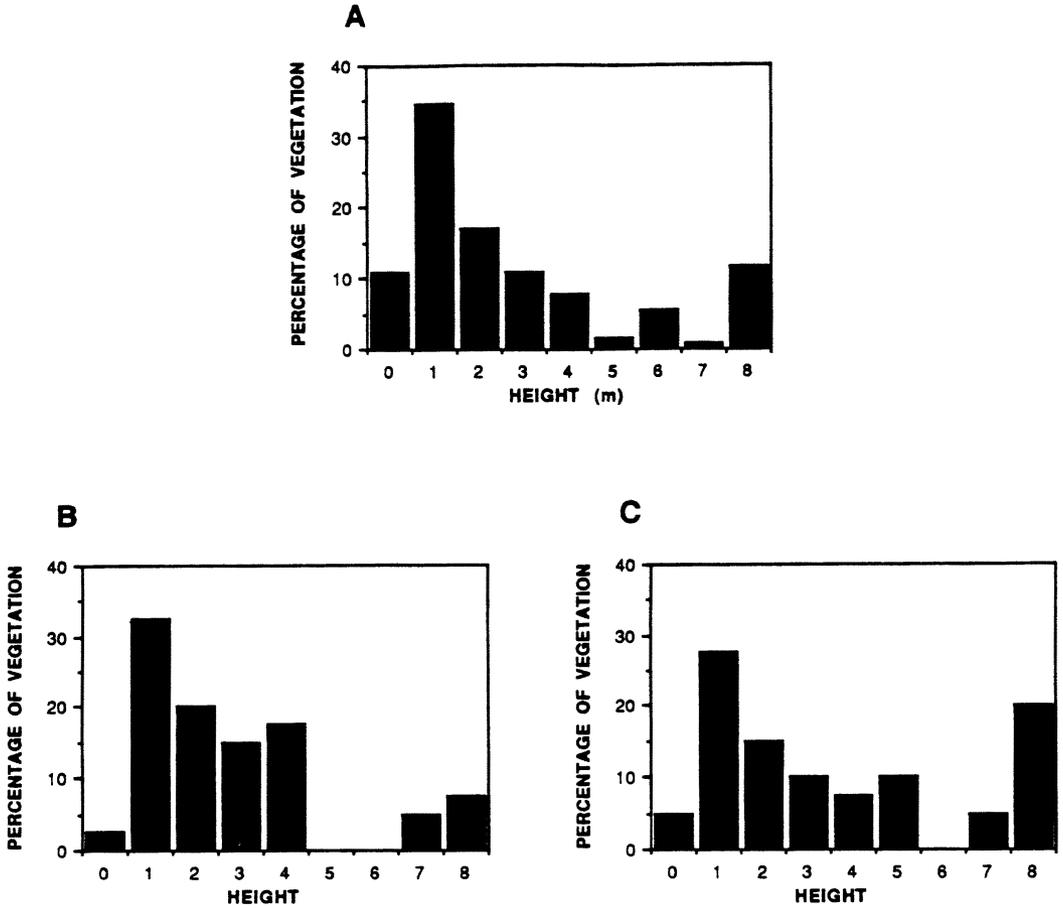
A

B

C

FIG. 1.—Distribution of vegetation height in the three pond types: (A) sympatry, (B) *H. chrysoscelis* in allopatry, and (C) *H. versicolor* in allopatry.

of each species within sympatric choruses). All tests of significance were at the $P < 0.01$ level.

RESULTS

Little difference in vegetation was detected among ponds for the three population types: sympatry, *H. chrysoscelis* in allopatry, and *H. versicolor* in allopatry (Fig. 1). No statistically significant differences were detected between the proportions of vegetation ≤ 4 m and >4 m in comparisons of sympatric ponds with allopatric ponds for *H. chrysoscelis* ($Z = 0.371$, $P < 0.10$) or allopatric ponds for *H. versicolor* ($Z = 1.87$, $P < 0.10$). Thus, the availability of elevated calling sites was similar among the three pond types. Al-

lopatric ponds with *H. versicolor* had a greater percentage of trees taller than 4 m than did the other two pond types, but this was not statistically significant ($P < 0.10$). Results of density and percent coverage along the transect lines are shown in Table 1. Mean density and percent coverage were

TABLE 1.—Vegetation characteristics of sympatric and allopatric ponds.

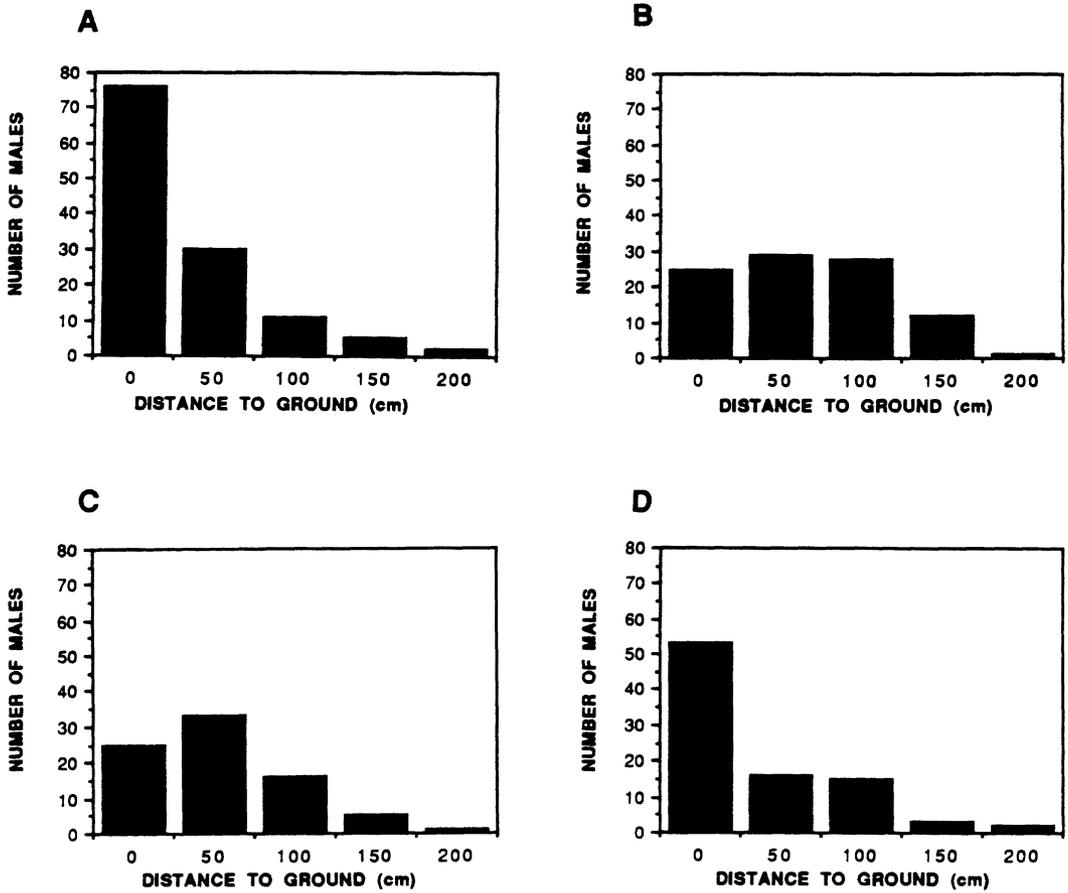|	Density $\bar{x}$ (1 SE)	% coverage $\bar{x}$ (1 SE)
Hyla chrysoscelis:		
allopatric ponds	0.95 (0.54)	154.9 (18.65)
Hyla versicolor:		
allopatric ponds	1.95 (1.7)	192.0 (32.1)
Sympatric ponds	0.96 (0.21)	148.03 (12.2)

A

B

C

D

FIG. 2.—Distributions of distance to ground for (A) *H. chrysoscelis* in sympatry, (B) *H. versicolor* in sympatry, (C) *H. chrysoscelis* in allopatry, and (D) *H. versicolor* in allopatry.

nearly identical for sympatric ponds and allopatric ponds for *H. chrysoscelis*; allopatric ponds with *H. versicolor* again had higher density and percent canopy cover.

I measured 388 calling sites: there were 124 males of *H. chrysoscelis* in sympatry, 95 males of *H. chrysoscelis* in allopatry, 80 males of *H. versicolor* in sympatry, and 89 males of *H. versicolor* in allopatry. There were no differences between species in either mean clocal or air temperature at the calling site. Both cloacal and ambient air temperatures exhibited a range of 4° for any night, 18–21 C in May and 21–24 C in June. Ground temperatures were usually 1–2° warmer than those of elevated calling sites.

Differences in distributions of distance to ground and distance to water were de-tected. Distributions of distance to ground for the two species in the three pond types are shown in Fig. 2. A significantly greater proportion ($Z = 4.21$, $P < 0.01$) of males of *H. chrysoscelis* called from sites ≤50 cm than did males of *H. versicolor* in sympatry. The proportion of sympatric males of *H. chrysoscelis* calling from sites ≤50 cm was significantly greater ($Z = 5.14$, $P < 0.01$) than that of males of *H. chrysoscelis* in allopatric ponds. In allopatric ponds, a significantly greater proportion ($Z = 3.68$, $P < 0.01$) of males of *H. versicolor* called from sites ≤50 cm than did males of *H. versicolor* in sympatry. In other words, calling males of *H. chrysoscelis* showed a stronger tendency to occupy elevated sites in allopatry than in sympatry, while males of *H. versicolor* in allopatry
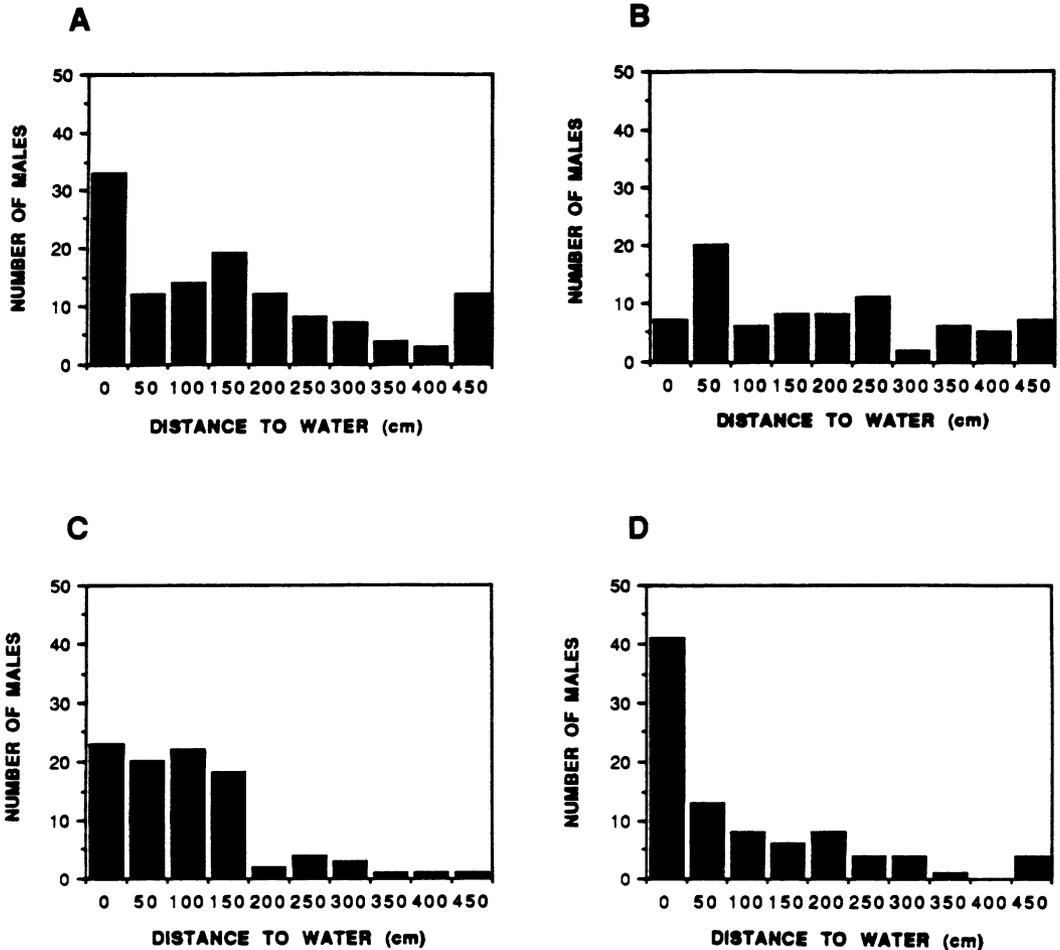
FIG. 3.—Distributions of distance to water for (A) *H. chrysoscelis* in sympatry, (B) *H. versicolor* in sympatry, (C) *H. chrysoscelis* in allopatry, and (D) *H. versicolor* in allopatry.

showed a strong preference for ground calling sites. In sympatry, males of *H. chrysoscelis* tended to call on or near the ground, and males of *H. versicolor* called from more elevated positions.

Distributions of distance to water for the two species in the three pond types are shown in Fig. 3. No statistically significant differences in the proportions of males in the two categories (≤100 cm and >100 cm) were detected by contingency table analyses for the two species in sympatry ($Z = 0.379$, $P < 0.10$), or for males of *H. chrysoscelis* in sympatry and allopatry ($Z = 1.33$, $P < 0.10$). A significantly greater proportion ($Z = 3.50$, $P < 0.01$) of males

of *H. versicolor* in allopatry called from sites ≤100 cm than did sympatric males.

There were no differences in distributions of distance to nearest neighbor. The expected values used in Chi-square analyses to test for conspecific or heterospecific aggregations were calculated based upon a ratio of 61% males of *H. chrysoscelis* and 39% males of *H. versicolor* in sympatric choruses. For *H. versicolor*, 24 nearest neighbors were conspecific and 38 nearest neighbors were heterospecific, and there was no evidence for either conspecific or heterospecific aggregations ($\chi^2 = 0.134$, $P < 0.50$). Males of *H. chrysoscelis* had 61 nearest neighbors that were conspecific and

37 nearest neighbors that were hetero-specific, and these were not significantly different from expected ($\chi^2 = 0.06$, $P < 0.75$).

DISCUSSION

This study provides evidence for partitioning of available calling habitat by species of gray treefrogs occurring in sympatry in Missouri. The most important difference between the two species was height of the call site. Males of *H. chrysoscelis* were more often found calling on or near the ground while males of *H. versicolor* called from elevated perches. The study does not address how differences in location of call sites may reflect differences in male mating success, but it provides evidence that females have the potential to use spatial as well as acoustic cues in locating conspecific mates.

Partitioning of available calling habitat has been reported for other sympatric hylids: *H. cinerea* and *H. squirella* (Goin and Goin, 1953); *H. avivoca* and *H. cinerea* (Secor, 1988); *H. gratiosa* and *H. cinerea* (Oldham and Gerhardt, 1975; Schlefer et al., 1986). In ponds in Alabama where shoreline vegetation had been removed, forcing *H. cinerea* to call from the ground, hybridization between the two species was observed (Lamb and Avise, 1986; Schlefer et al., 1986). Subdividing calling habitat by height may be important in preventing mismatings in gray treefrogs as well. In Missouri, males of the two species can be observed calling from adjacent sites in ponds with little shoreline vegetation (personal observation). The three mismated pairs that have been observed in the last 3 yr in Missouri were collected in ponds where males of both species called frequently from the ground (Gerhardt, Ptacek, Barnett, and Torke, unpublished data).

Three studies have addressed interspecific interactions in both utilization of call sites and division of acoustic space. Mac Nally (1979) found no differentiation of calling sites between two species of *Ranidella*, but that males of *R. parinsignifera* appeared to displace their congeners from preferred calling stations. Subdivision in

this species appears to operate through temporal differences in the calling seasons. Given (1990) found little evidence for microhabitat separation in two species of *Rana*, but he did report that males of *R. clamitans* occurred in vegetation immediately adjacent to the water's edge whereas males of *R. virgatipes* were located approximately 0.1–0.5 m away from the water's edge. Schwartz and Wells (1983, 1984) reported that three species of *Hyla* in Panama called from similar microhabitats in close proximity and adjusted the timing of their calls, resulting in subdivision of acoustic space by heterospecifics. Males of *H. chrysoscelis* and *H. versicolor* have also been observed to call antiphonally in response to heterospecific calls in sympatric choruses (Klump and Gerhardt, in press).

Both conspecific and heterospecific aggregations of calling males have been observed in mixed species choruses of frogs. Given (1990) found that males of *Rana virgatipes* positioned themselves closer to conspecifics than to heterospecifics within mixed-species aggregations. In sympatric populations of *Ranidella signifera* and *R. parinsignifera*, nearest neighbor distances between heterospecific males were less than between conspecific males (Mac Nally, 1979, 1984). Little evidence for conspecific or heterospecific aggregations was found in this study. Many ponds in Missouri in areas of sympatry tend to have more males of *H. chrysoscelis* than males of *H. versicolor*. The ratio of males of *H. chrysoscelis* to males of *H. versicolor* from sympatric ponds included in this study was 61% to 39%.

Johnson (1966) first suggested a subdivision of calling habitat within sympatric choruses of gray treefrogs. During his field work in sympatric ponds in Texas, he noted that males of *H. versicolor* were calling from higher positions than males of *H. chrysoscelis*. Johnson (1966) did not, however, provide quantitative measurements. My quantitative results agree with Johnson's assessment (Fig. 2A,B). By contrast, Ralin's (1968) study in sympatric ponds in Texas found that more males of *H. ver-*

sicolor called from ground sites than did males of *H. chrysoscelis*; however, males of *H. versicolor* called at greater distances from the water's edge than did males of *H. chrysoscelis*. Ralin found that *H. chrysoscelis* ate more arboreal prey items than *H. versicolor*, and he speculated that this may have influenced their choice of call sites.

Ralin (1968) did not describe the vegetational characteristics of the ponds that he studied. Differences in microhabitats within ponds can influence a male's call site position. The vegetational characteristics of sympatric ponds chosen for this study provided both ground and elevated calling sites in close proximity to water, where egg deposition occurs. Males calling in different habitats or different geographic localities may subdivide calling sites differently than those observed in populations from Missouri. Differences of microhabitats within the ponds studied by Ralin could have favored a different division of call sites than in Missouri.

The most striking result of this study was the contrast observed in call sites in allopatric and sympatric choruses of both species. In allopatry, *H. chrysoscelis* more often used elevated calling sites. In three of the five ponds measured, no males used ground sites. In all sympatric choruses, a greater proportion of males of *H. chrysoscelis* called from sites ≤50 cm from the ground. The opposite trend was observed in *H. versicolor*. Almost half of the males of *H. versicolor* used ground calling sites in allopatry, whereas only 16 of 80 males of *H. versicolor* used ground calling sites in sympatry. Thus, there again appeared to be a difference in preferences for call sites. This was clearly not the result of differences in availability of elevated perches between sympatry and allopatry. Indeed allopatric ponds for *H. versicolor* had a greater percentage of trees >4 m, higher density, and higher percent canopy cover than sympatric ponds (Fig. 1, Table 1), yet more males of *H. versicolor* called from the ground. Differences observed in distributions of call sites between allopatry and sympatry are more likely due to the influence of heterospecifics in sympatry.

Males of *H. versicolor* in allopatry called significantly closer to the water's edge than in sympatry. This is probably attributable to increased use of ground calling sites. In most allopatric and sympatric ponds, trees or shrubs that provided elevated perches were further from the water's edge. Thus males that occupied ground calling sites were more likely to be closer to the water than elevated males.

The differences observed in the two species of gray treefrogs between sympatry and allopatry in location of calling sites fit the pattern expected if reproductive character displacement were acting on both species. Partitioning of the calling habitat within sympatry may enhance reproductive isolation between the species of gray treefrogs in two ways. First, by partitioning the available calling habitat, females of the two species can use spatial as well as acoustic cues to locate conspecific mates. There is no evidence suggesting that female gray treefrogs use spatial cues in locating conspecific mates, but behavioral tests have thus far concentrated only on acoustic differences between the two species. Second, differences in heights of call sites could enhance differences in pulse rates between males of the two species. Ground calling sites were usually 1–2° warmer than elevated sites. This should result in increased pulse rates of male *H. chrysoscelis* calling from the ground and decreased pulse rates of male *H. versicolor* calling in the vegetation, thus accentuating species-specific differences.

Stronger evidence for character displacement could be obtained from further studies that address the question of the adaptive significance of subdivision of calling sites by sympatric males. As previously stated, no evidence exists for differential mating success by males at different locations of calling sites. Differential mating success as a result of subdivision of calling habitat would show that natural selection is operating on this behavior for sympatric males of the two species.

Before reproductive character displacement could be fully supported, many more populations, both sympatric and allopatric, should be examined. Populations of

both species from remote allopatry should be measured to see if similar call site characteristics exist. Finally, clinal variation in call site distribution cannot be completely discounted until more populations are examined.

Character release was observed for both species in allopatry. This trend towards movement by allopatric males into the preferred calling station of heterospecific males in sympatry is most evident for males of *H. versicolor*. Because of the recent origin of *H. versicolor* from *H. chrysoscelis* (Ralin and Selander, 1979; Romano et al., 1987; Ptacek, 1991), *H. versicolor* evolved in sympatry and may have been forced to use calling sites that were not already occupied by *H. chrysoscelis*. Males of *H. chrysoscelis* showed a significant trend towards calling from elevated perches in allopatry, but the range of heights used were much greater than for males of *H. versicolor* in allopatry. Differences in heights of calling sites in sympatry exist, and the occurrence of males of the two species in allopatry in the call sites preferred by heterospecific males in sympatry suggest character release when heterospecifics are absent.

LITERATURE CITED

BLAIR, W. F. 1955. Mating call and stage of speciation in the *Microhyla olivacea-M. carolinensis* complex. Evolution 9:469–480.

——. 1958. Mating call in the speciation of anuran amphibians. Am. Nat. 92:27–51.

——. 1974. Character displacement in frogs. Am. Zool. 14:305–311.

BOGERT, C. M. 1960. The influence of sound on the behavior of amphibians and reptiles. Pp. 137–320. *In* W. E. Lanyon and W. N. Tavolga (Eds.), Animal Sounds and Communication. American Institute of Biological Science, Publication 7, Washington, D.C.

BROWN, J. H. 1971. Mechanisms of competitive exclusion between two species of chipmunks. Ecology 52:305–311.

BROWN, W. L., AND E. O. WILSON. 1956. Character displacement. Sys. Zool. 5:49–64.

BUTLIN, R. K. 1987. Species, speciation and reinforcement. Am. Nat. 130:461–464.

——. 1989. Reinforcement of premating isolation. Pp. 158–179. *In* D. Otte and J. A. Endler (Eds.), Speciation and Its Consequences. Sinauer, Sunderland, Massachusetts.

COX, G. W. 1985. Laboratory Manual of General Ecology, 5th ed. Wm. C. Brown, Dubuque, Iowa.

DUELLMAN, W. E. 1967. Courtship isolating mechanisms in Costa Rican hylid frogs. Herpetologica 23:169–183.

DUELLMAN, W. E., AND L. TRUEB. 1986. Biology of Amphibians. McGraw-Hill, New York.

FELLERS, G. M. 1979. Aggression, territoriality, and mating behaviours in North American treefrogs. Anim. Behav. 27:107–119.

FOUQUETTE, M. J. 1975. Speciation in chorus frogs. I. Reproductive character displacement in the *Pseudacris nigrita* complex. Syst. Zool. 24:16–23.

GERHARDT, H. C. 1975. Sound pressure levels and radiation patterns of the vocalizations of some North American frogs and toads. J. Comp. Physiol. 102:1–12.

GERHARDT, H. C., AND J. A. DOHERTY. 1988. Advertisement call recognition in the gray treefrog, *H. versicolor*: Evolutionary and neurobiological implications. J. Comp. Physiol. 62:261–278.

GIVEN, M. F. 1990. Spatial distribution and vocal interaction in *Rana clamitans* and *R. virgatipes*. J. Herpetol. 24:377–382.

GOIN, C. J., AND O. B. GOIN. 1953. Temporal variation in a small community of reptiles and amphibians. Ecology 34:406–408.

GRANT, P. R. 1972. Convergent and divergent character displacement. Biol. J. Linn. Soc. 4:39–68.

HIGHTON, R. 1970. Evolutionary interactions between species of North American salamanders of the genus *Plethodon*. Part 1. Genetic and ecological relationships of *Plethodon jordani* and *P. glutinosis* in the southern Appalachian Mountains. Evol. Biol. 4:211–256.

JAEGER, R. G. 1974. Interference or exploitation? A second look at competition between salamanders. J. Herpetol. 8:191–194.

JOHNSON, C. 1959. Genetic incompatibility in the call races of *H. versicolor* Le Conte in Texas. Copeia 1959:327–335.

——. 1963. Additional evidence of sterility between call-types in the *H. versicolor* complex. Copeia 1963:139–143.

——. 1966. Species recognition in the *H. versicolor* complex. Texas J. Sci. 18:361–364.

KLUMP, G. M., AND H. C. GERHARDT. 1991. Mechanisms and function of call-timing in male-male interactions in frogs. In press. *In* P. MacGregor (Ed.), Playback and Studies of Animal Communication: Problems and Prospects. Plenum Press, New York.

LACK, D. 1947. Darwin's Finches. Cambridge University Press, Cambridge.

LAMB, T., AND J. C. AVISE. 1986. Directional introgression of mitochondrial DNA in a hybrid pop-

ulation of tree frogs: The influence of mating behavior. Proc. Natl. Acad. Sci. USA 83:2526–2530.

LITTLEJOHN, M. J. 1960. Call discrimination and potential reproductive isolation in *Pseuacris triseriata* females from Oklahoma. Copeia 1960:370–371.

———. 1965. Premating isolation in the *Hyla ewingi* complex (Anura: Hylidae). Evolution 19: 234–243.

———. 1977. Long range acoustic communication in anurans: An integrated and evolutionary approach. Pp. 263–294. *In* D. H. Taylor and S. I. Guttman (Eds.), The Reproductive Biology of Amphibians. Plenum Press, New York.

———. 1981. Reproductive isolation: A critical review. Pp. 298–334. *In* Evolution and Speciation. Cambridge University Press, Cambridge.

LITTLEJOHN, M. J., P. A. HARRISON, AND R. C. MAC NALLY. 1985. Interspecific acoustic interactions in sympatric populations of *Ranidella signifera* and *R. parinsignifera* (Anura: Leptodactylidae). Anim. Behav. 21:781–787.

LOMBARD, R. E., AND I. R. STRAUGHAN. 1974. Functional aspects of anuran middle ear structures. J. Exp. Biol. 61:57–71.

MACNALLY, R. C. 1979. Social organization and interspecific interactions in two sympatric species of *Ranidella* (Anura). Oecologia 42:293–306.

———. 1984. Chorus dynamics of two sympatric species of *Ranidella* (Anura): Within-year and between-year variability in organization and their determination. Z. Tierpsychol. 65:134–151.

MARKOW, T. A. 1981. Courtship behavior and control of reproductive isolation between *Drosophila mojavensis* and *Drosophila arizonensis*. Evolution 35:1022–1026.

OLDHAM, R. S., AND H. C. GERHARDT. 1975. Behavioral isolation of the treefrogs *Hyla cinerea* and *Hyla gratiosa*. Copeia 1975:223–231.

ORIANS, G. H., AND H. S. HORN. 1969. Overlap in foods and foraging of four species of blackbirds in the potholes of central Washington. Ecology 50: 930–938.

OTTE, D. 1979. Chorusing in *Syrbula*. Cooperation, interference competition or concealment? Entomol. News 90:159–165.

———. 1989. Speciation in Hawaiian crickets. Pp. 482–526. *In* D. Otte and J. A. Endler (Eds.), Speciation and Its Consequences. Sinauer, Sunderland, Massachusetts.

PATERSON, H. E. H. 1985. The recognition concept of species. Pp. 21–29. *In* E. Vrba (Ed.), Species and Speciation. Transvaal Museum Monograph 4, Pretoria, South Africa.

PTACEK, M. B. 1991. Evolutionary Dynamics and Speciation by Polyploidy in Gray Treefrogs. Ph.D. Dissertation, University of Missouri, Columbia, Missouri.

RALIN, D. B. 1968. Ecological and reproductive differentiation in the cryptic species of the *H. versicolor* complex (Hylidae). Southwest. Nat. 13:283–300.

RALIN, D. B., AND R. K. SELANDER. 1979. Evolutionary genetics of diploid-tetraploid species of treefrogs of the genus *Hyla*. Evolution 33:595–603.

RITKE, M. E., J. G. BABB, AND M. K. RITKE. 1990. Life history of the gray treefrog (*H. chrysoscelis*) in western Tennessee. J. Herpetol. 24:135–141.

ROMANO, M. A., D. B. RALIN, S. I. GUTTMAN, AND J. H. SKILLINGS. 1987. Parallel electromorph variation in the diploid-tetraploid gray treefrog complex, *Hyla chrysoscelis* and *Hyla versicolor*. Am. Nat. 130:864–878.

SCHLEFER, E. K., M. A. ROMANO, S. I. GUTTMAN, AND S. B. RUTH. 1986. Effects of twenty years of hybridization in a disturbed habitat on *Hyla cinerea* and *Hyla gratiosa*. J. Herpetol. 20:210–222.

SCHWARTZ, J. J., AND K. D. WELLS. 1983. An experimental study of acoustic interference between two species of neotropical treefrogs. Anim. Behav. 31:181–190.

SCHWARTZ, J. J., AND K. D. WELLS. 1984. Interspecific acoustic interactions of the neotropical treefrog *Hyla ebraccata*. Behav. Ecol. Sociobiol. 14: 211–224.

SECOR, S. M. 1988. Perch sites of calling male bird-voiced treefrogs, *Hyla avivoca*, in Oklahoma. Proc. Oklahoma Acad. Sci. 68:71–73.

WHITE, M. D. J. 1978. Modes of Speciation. W. H. Freeman, San Francisco.

ZAR, J. H. 1984. Biostatistical Analysis. Prentice-Hall, Englewood Cliffs, New Jersey.