

Call Site Choice in Male Anurans

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Variations in male call site location within and among 12 species of anurans from the Coastal Plain of South Carolina were measured to elucidate the extent of call site choice between species as an extension of acoustic premating isolation behavior. Of 41 microhabitat, meteorological, and vegetational measurements made at the point of capture of calling males, 38 were found to differ among species. A subset of 22 variables was found to significantly discriminate between species, notably height of the call site above water, local precipitation, water temperature, and seasonal activity. Correlations among call site variables identified microhabitat, habitat, and seasonal sets of variables using principal components analysis. Based on these call site variables, *Hyla femoralis* and *H. chrysoscelis* shared similar calling locations, as did *Acris gryllus* and *Rana clamitans*, *A. crepitans* and *H. crucifer*, and to a lesser degree *H. squirella* and *Gastrophryne carolinensis*. Other species studied, including *H. gratiosa*, *H. cinerea*, *H. avivoca*, and *Bufo terrestris* varied significantly from the other species in some aspect of call site choice. Most species were found in multispecies choruses. More closely related species were ecologically dissimilar at calling sites, with the exception of *H. femoralis* and *H. chrysoscelis*, suggesting male call site choice is a further phylogenetic extension to acoustic premating isolating behavior for many anuran species.

PREMATING isolation among many groups of closely related anurans has evolved through the differentiation of male mating calls (Blair, 1959; Mecham, 1965; Littlejohn et al., 1971; Gerhardt, 1982). Yet, breeding assemblages of frogs and toads, sometimes containing several species, occasionally produce interspecific hybrids between closely related species (Blair, 1958; Pyburn, 1960; Mecham, 1960a; Gerhardt et al., 1980). In treefrogs (Hylidae), the rare occurrences of interspecific hybrids, caused by females that approach or are confronted by males of the wrong species and mate with them, suggest that breeding communally results in a reproductive "cost" to individuals that sometimes mate with other species (Littlejohn et al., 1971). These viable hybrids are discriminated against during breeding by females of either parental species (Gerhardt, 1974), but not always other hybrids (Mecham, 1960a; Doherty and Gerhardt, 1984; Schlefer et al., 1986).

Choices of different places and times of breeding made by males are thought to enhance premating isolation between species (Blair, 1974). Such behavioral attributes help minimize losses in reproductive effort, thus reinforcing premating isolation (Mayr, 1963; Gerhardt, 1974). Mecham (1960a) demonstrated that removal of arboreal calling sites of *Hyla*

cinerea caused introgressive hybridization with *H. gratiosa*, which calls from the water surface. He detected both parental species, their F_1 hybrids, and the F_2 backcrosses to both parental species in this altered habitat. Gerhardt et al. (1980) discovered F_1 hybrids between these same two species in roadside ditches cleared of standing vegetation. Clearly, premating isolation is dependent upon male calling behavior in both acoustic and spatial qualities. Unfortunately, little is known of the circumstances causing interspecific hybridization in undisturbed natural environments, or the frequency with which it occurs (Gerhardt, 1974; Gerhardt et al., 1980; Schlefer et al., 1986).

Closer inspection of spatial and temporal differences of the call sites of communally breeding anurans in both disturbed and undisturbed habitats will help to detail the contribution of male call site differentiation to premating isolation, and hence interspecific gene flow. Specifically, is call site differentiation between closely related species, e.g., *H. cinerea* and *H. gratiosa*, a general rule in anuran species assemblages? Therefore, this study was designed to: 1) assess the degree of call site similarity among males within and between 12 species of anurans common to the Coastal Plain in South Carolina across a diverse array of habitats; 2) identify

major environmental gradients along which calling male frogs and toads distributed themselves; and 3) assess the contribution of male call site variation to premating isolation. These call site data were then used to generate testable hypotheses about relationships between species coexistence and the evolution of anuran premating isolation barriers.

MATERIALS AND METHODS

Calling male frogs and toads were captured by hand after dusk during the spring and summer of 1977 and 1978 within the boundaries of the 77,720 ha Savannah River Plant (SRP) in South Carolina. The SRP contains a wide diversity of wetlands including abandoned farm ponds, vernal and river hardwood swamps, Carolina bays (Reid, 1961), large cooling impoundments, numerous drainage areas, and other temporary aquatic habitats (Langley and Marter, unpubl.). Frogs and toads are active throughout most of the year in these habitats (Gibbons and Patterson, 1978).

Individual calling males were collected from within active choruses, and all species present within a chorus were usually sampled to determine patterns of co-occurrence. Calling positions were then marked, and six environmental measurements were immediately recorded (Appendix 1). Within a week of capture, 32 microhabitat, vegetational, and distance measurements were recorded at or near each point of capture. Also, three water quality measurements of possible importance to tadpoles were recorded for each call site (Appendix 1). While the justifications for variable selection may be slightly subjective, here the 41 environmental variables were chosen for the following reasons: 1) each variable furnished a partial characterization of the environment at the capture location (Green, 1971) which was either known or suspected to influence the distribution of breeding male anurans (Wright and Wright, 1949; Marshall and Buell, 1955; Conant, 1975); and 2) each variable was easily measured using nondestructive sampling methods (Dueser and Shugart, 1978).

Differences among species for each environmental variable were analyzed with one-way analyses of variance (ANOVAs), multiple comparisons tests from these ANOVAs (Scheffé, 1959), discriminant function analyses, and principal components analyses (Rohlf et al., 1974). Discriminant function analysis allowed objec-

tive separation between species with a reduced set of ecologically relevant variables (Levins, 1968). Principal components analysis was used to identify correlated groups of call site variables.

RESULTS

Thirteen species of frogs and toads ($N = 291$) were captured at 21 sites on the SRP (Fig. 1) during 2 yr characterized by droughts, as shown by comparison with previous meteorological records (Langley and Marter, unpubl.). Identification of all *H. chrysoscelis* was verified by means of starch gel electrophoresis (Etges, 1979); no tetraploid *H. versicolor* were found (Ralin and Selander, 1979).

A simple measure of species co-occurrence, the number of other species present at the time of capture, illustrated patterns in chorus composition (Fig. 2). These data include all observations of other species present within choruses for each species, thus portraying the entire array of observed co-occurring species across many habitats and nights of calling. Most species occurred together at breeding sites, yet some were found calling with few other species, i.e., *H. crucifer*, *A. gryllus*, and *H. gratiosa* (Fig. 2). On average, most males were found calling in choruses comprising 4–5 species (number other species calling [NOSC], Appendix 2).

Analyses of variance revealed significant differences among species in call site location for 38/41 of the variables measured (Appendix 2). The largest F values indicated large differences among the 12 species for air temperature, water temperature, water quality (temperature, hardness, pH), time of breeding, and height of call sites above the ground.

Pairwise multiple comparisons (Scheffé, 1959) between all species for the variables call site height, breeding period during the season, and local precipitation were calculated to show some of the species differences underlying the ANOVAs (Table 1). Height of call sites above water (VPAW) and breeding period through the season (TFFM) were among the strongest discriminators (Table 2) and differences in local precipitation (LPRP) indicated the degree to which reproductive activity depended on rainfall. All hylids except *H. gratiosa* and *H. crucifer* called from similar heights above water level.

Seasonal differences in breeding activity between species were more pronounced than were differences in call site height (VPAW, Table

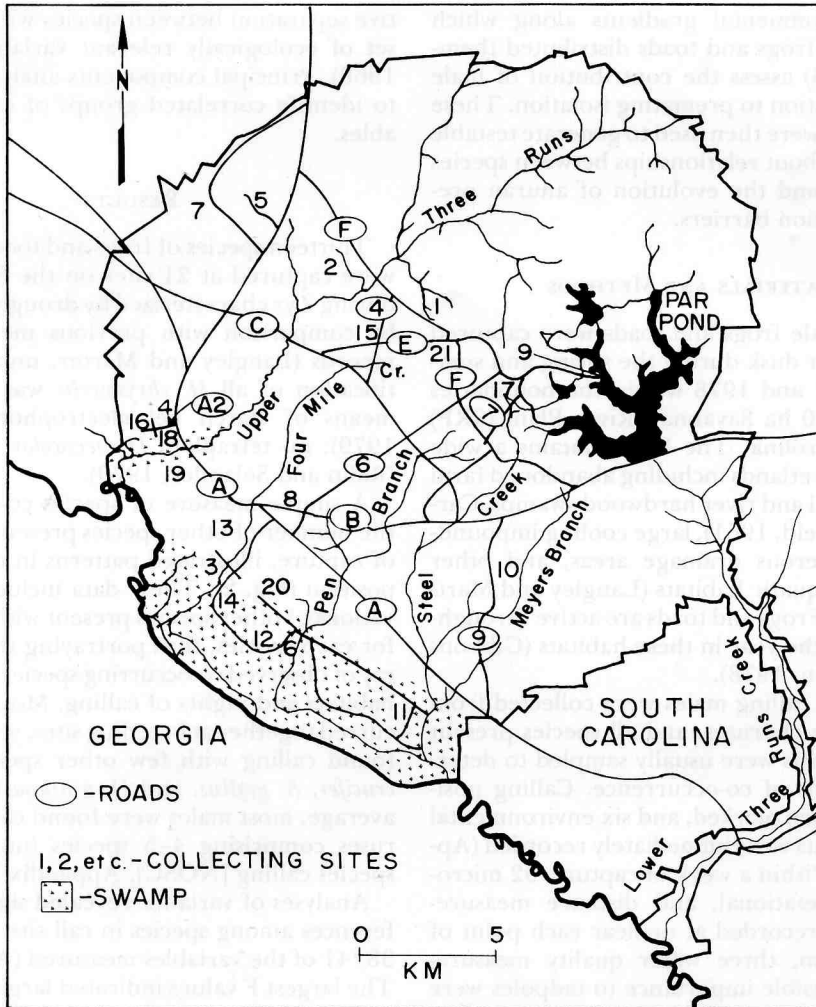


Fig. 1. Location of collecting sites where species were sampled on the Savannah River Plant site during 1977 and 1978. Species abbreviations are the first letter of the genus and the first and second letter of the species as listed in the footnote to Table 1. Collecting locations and (species) are as follows: 1) Dick's Pond—(Ac, Ag, Hc, Rc); 2) Fire Pond—(Ag, Hc, Rc); 3) Double Ponds—(Ac, Hcr); 4) Brinkley Road Bay—(Ag, Hc, Hf, Hg, Hch); 5) Steed Pond—(Hc, Gc, Hch, Bt); 6) Pen Branch Marsh—(Hc, Hs); 7) Lost Lake (bay)—(Hc, Gc, Hs, Hg, Hch); 8) Artesian Well B—(Hc); 9) Par Pond (boat dock)—(Hc); 10) Pond Nine—(Hc, Hf, Hg, Hch); 11) R. R. track drainage near Steel Creek—(Hc, Hg, Hch); 12) Hogbarn Swamp drainage—(Hc, Hs, Hc, Ha); 13) Asphalt Pond (bay)—(Hs, Hf, Bt); 14) Hogbarn Road drainage ditch—(Hs, Hf, Hch); 15) E-4 intersection drainage—(Hs); 16) Brinkley Road Artesian Well—(Hf); 17) H-7 intersection drainage—(Hf); 18) Brinkley Road Swamp—(Hg, Hch, Hcr); 19) Bulldog Bay—(Hch); 20) Risher Road Marsh (vernal)—(Hch, Hcr, Bt); 21) and E-F intersection drainage (vernal)—(Hch, Hcr, Bt).

1B). Breeding activity during rainy periods did not correspond to seasonal variation (Table 1C). Dry weather callers were usually associated with more permanent habitats such as farm ponds, lakes, and river swamps, e.g., *Acris crepitans* and *A. gryllus*, *Rana clamitans*, *H. avivoca*, and *H. cinerea*. The presence of *Bufo terrestris* was asso-

ciated with spring rains, while summer precipitation was found to be a good indicator for the presence of *Gastrophryne carolinensis* and *H. squirella*.

The largest consistent differences among species from the 22 variable set produced by the discriminant function analysis were height

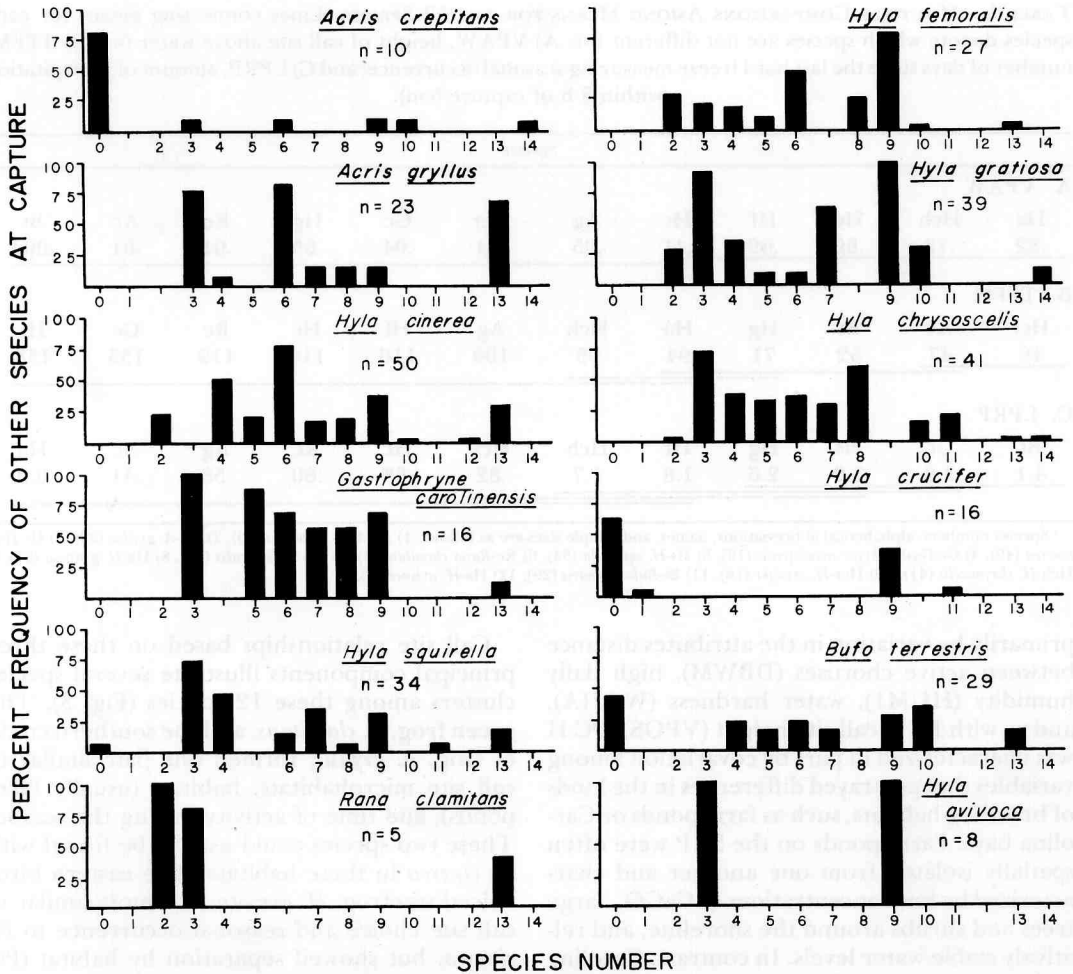


Fig. 2. Percent frequency of occurrence of all other anuran species present at the time of capture of each individual for the 12 species studied. Data were collected from all captures in choruses across all collecting sites. Species are numbered as in Table 1 except for 13 and 14, which are *Rana catesbeiana* and *Bufo quercicus*, respectively. Zeros refer to captures in single species choruses. Sample sizes refer to all captures made, some of which were not included in the statistical analysis.

of call sites above water level (VPAW), low daily temperature (LDTM), water temperature (LWTP), and the number of days from the last freeze (TFFM; Table 2). The latter three variables were highly correlated with season, and hence were correlated with each other. Height of call sites was correlated with low daily temperature ($r = 0.22$; $P < 0.01$) with water temperature ($r = 0.17$; $P < 0.01$), but not with time of breeding ($r = 0.13$; $P > 0.05$).

The first three principal components accounted for 73% of the total variance among the 22 best discriminating variables (Table 2). High daily temperature (HDTM), the distance

to the nearest sapling (DNWS), and the stem density 1 m above the ground (NSOM) were highly correlated with PC I. The pattern of variable loadings of PC I represented a complex gradient of correlated meteorological and vegetational attributes along which the species were distributed from cool, open evergreen sites where species were found calling close to the ground to warmer, heavily vegetated, hardwood sites where species were found calling from high in the vegetation. Seasonal differences in breeding activity were also correlated with PC I.

Principal component II was characterized

TABLE 1. MULTIPLE COMPARISONS AMONG MEANS FOR THE 12 SPECIES. Lines connecting means for each species denote which species are not different for: A) VPAW, height of call site above water (m); B) TFFM, number of days since the last hard freeze measuring seasonal occurrence; and C) LPRP, amount of precipitation within 8 h of capture (cm).

Species*											
A. VPAW											
Ha	Hch	Hc	Hf	Hs	Ag	Hcr	Gc	Hg	Rc	Ac	Bt
.82	.72	.69	.69	.41	.05	.04	.04	.03	.01	.01	.004
B. TFFM											
Hcr	Ac	Bt	Hg	Ha	Hch	Ag	Hf	Hc	Rc	Gc	Hs
10	47	52	71	94	95	109	116	116	119	133	138
C. LPRP											
Bt	Gc	Hs	Hg	Hf	Hch	Hcr	Hc	Rc	Ag	Ac	Ha
4.1	3.8	3.0	2.6	1.8	1.7	.82	.63	.60	.58	.41	0.0

* Species numbers, alphabetical abbreviations, names, and sample sizes are as follows: 1) Ac-*Acris crepitans* (10), 2) Ag-*A. gryllus* (23), 3) Hc-*Hyla cinerea* (49), 4) Gc-*Gastrophryne carolinensis* (19), 5) Hs-*H. squirella* (34), 6) Rc-*Rana clamitans* (5), 7) Hf-*H. femoralis* (27), 8) Hg-*H. gratiosa* (37), 9) Hch-*H. chrysoscelis* (41), 10) Hcr-*H. crucifer* (16), 11) Bt-*Bufo terrestris* (29), 12) Ha-*H. avivoca* (8).

primarily by variation in the attributes distance between active choruses (DBWM), high daily humidity (HUM1), water hardness (WAHA), and as with PC I, call site height (VPOS). PC II was characterized in part by covariation among variables that portrayed differences in the kinds of breeding habitats, such as farm ponds or Carolina bays. Farm ponds on the SRP were often spatially isolated from one another and characterized by low concentrations of CaCO₃, large trees and shrubs around the shoreline, and relatively stable water levels. In contrast, Carolina bays and vernal ponds tended to be spatially aggregated (Fig. 1), fluctuated in water level throughout the year, and sometimes dried up completely. High loadings on PC I and PC II by VPAW, NSTM, WAHA, and LWTP describe the similarity of call sites across most habitat types, and suggest that males prefer particular call sites within suitable breeding habitats, whether a Carolina bay or vernal pond.

The pattern of variable loadings on PC III was due to increased covariation in stem densities (DNWP), water alkalinity (WAAL), local precipitation (LPRP), calling activity early or late during the night (TFSS), low daily humidity (HUM2), seasonal differences in calling activity (TFFM), and low daily temperature (LDTM). No obvious ecological interpretation of PC III seems apparent except for seasonal activity variation, even though there is little overlap in variation with the first two principal components (Table 2).

Call site relationships based on these three principal components illustrate several species clusters among these 12 species (Fig. 3). The green frog, *R. clamitans*, and the southern cricket frog, *A. gryllus*, formed one pair similar in call site microhabitats, habitats (usually farm ponds), and time of activity during the season. These two species could usually be found with *H. cinerea* in these habitats. The eastern bird-voiced treefrog, *H. avivoca*, was most similar in call site choice and seasonal occurrence to *H. cinerea*, but showed separation by habitat (PC II) as it was the only species found exclusively calling in river swamp choruses (Gibbons and Patterson, 1978).

Hyla chrysoscelis and *H. femoralis* formed the closest associated species pair due to similarities in seasonal activity and arboreal call sites (Fig. 3, Table 1). Since both of these species called from the ground in habitats lacking such sites, they showed similarity with the *A. gryllus*-*R. clamitans* pair. *Hyla squirella* was a relatively late season caller (PC III), and along with *G. carolinensis*, was found calling from shallow water, frequently during periods of heavy precipitation, early in the summer. Later in summer, *H. squirella* was found calling from arboreal sites in high bushy shrubs or small trees near shorelines.

Individuals of *H. cinerea* and *H. gratiosa* were always found to be separated by height of the call sites (VPAW, PC I); *H. gratiosa* called from the surface of the water, usually close to the

TABLE 2. THE 22 BEST DISCRIMINATING ENVIRONMENTAL VARIABLES AND THEIR CORRELATION (r) WITH THE DISCRIMINANT FUNCTION FOR THE 12 ANURAN SPECIES AND THE LOADINGS ON THE FIRST THREE PRINCIPAL COMPONENTS. The absolute value of the correlation indicates the power of the variable in the overall discrimination between species. Detailed descriptions of the variables are given in Appendix 1.

Variable*	Correlation (r)	Loadings on principal components		
		I	II	III
VP AW	.750	-.668	-.647	.194
LDTM	-.594	-.612	.368	.648
LWTP	-.573	-.704	.410	.507
TFFM	-.552	-.548	.222	.702
HDTM	-.445	-.881	.295	.258
WAHA	.430	-.497	-.629	-.053
HUM2	.402	.593	-.058	.668
TFSS	-.388	.202	.036	.511
LPRP	-.385	.643	-.038	.724
PCEV	.384	.607	-.215	-.141
DNWS	.382	.786	-.028	.400
WAAL	-.377	-.277	.412	.506
HUM1	.374	.328	-.835	.311
DNWT	-.360	.709	.081	.129
NSTM	.331	-.591	-.588	-.072
DBWM	-.328	-.186	.944	.026
NSOM	.323	-.720	-.423	.147
DEPW	-.319	-.375	.486	.041
DNWP	-.317	.651	-.063	.670
VPOS	.302	-.659	-.654	.217
PRCP	.220	.589	-.137	.368
PCHD	-.203	-.667	.286	.307
Eigenvalue		7.81	4.37	3.81
Percent of total variance		35.51	19.85	17.32
Total variance explained		72.67		

* See Appendix 1 for variable definitions.

shoreline (DFSH, Appendix 2; Oldam and Gerhardt, 1975). This suggests that over all breeding sites on the SRP, natural disturbance by man has not changed call site choice in these two species (Mecham, 1960a; Gerhardt et al., 1980). However, one exception, a presumed hybrid between these two species, was found in a vernal hardwood swamp chorus comprising *H. cinerea* and *H. gratiosa* (site 18, Fig. 1). This large green treefrog was heard producing an irregular rasping call high in a woody shrub, a presumed 'release' call which serves to space males around the breeding site as the individuals arrive at the site early in the evening (Gerhardt, 1978). This

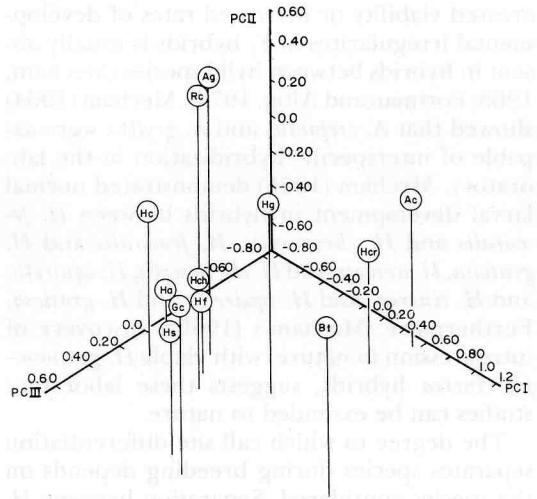


Fig. 3. Relative positions of the 12 anuran species shown by a three dimensional plot of the first three principal components representing microhabitat, interhabitat, and temporal gradients, respectively. Species abbreviations are given in Table 1.

individual resembled *H. gratiosa* in the green phase and possessed yellow lateral stripes characteristic of *H. cinerea*, characteristics denoting a hybrid between these two species (Fortman and Altig, 1974). It was found calling almost 1 m above the water, uncharacteristic for *H. gratiosa* during breeding (Neill, 1952). Proof of a hybrid origin was inconclusive as determined by subsequent electrophoretic analyses (Etges, 1979).

DISCUSSION

Accurate estimates of the rates of interspecific hybridization, and hence interspecific gene flow, remain unavailable for these species. Among closely related species, such as *H. gratiosa* and *H. cinerea*, no genetic evidence of interspecific hybridization was found (Etges, 1979). The few instances of natural interspecific hybridization events between *H. gratiosa* and *H. cinerea* (Smith and List, 1955; Mecham, 1960b; Gerhardt, 1974; Gerhardt et al., 1980; Schlefer et al., 1986), *H. femoralis* and *H. chrysoscelis* (Pyburn, 1960; Mecham, 1965; Gerhardt, 1974), *H. chrysoscelis* and *H. avivoca* (Mecham, 1960b; Gerhardt, 1974; R. H. Mount pers. comm.), and *A. crepitans* and *A. gryllus* (Neill, 1954) suggest that interspecific hybrids are rare, but recurring in unaltered habitats.

Postmating isolation acting through de-

creased viability or increased rates of developmental irregularities in F_1 hybrids is usually absent in hybrids between hylid species (Mecham, 1965; Fortman and Altig, 1974). Mecham (1964) showed that *A. crepitans* and *A. gryllus* were capable of interspecific hybridization in the laboratory. Mecham (1965) demonstrated normal larval development in hybrids between *H. femoralis* and *H. chrysoscelis*, *H. femoralis* and *H. gratiosa*, *H. avivoca* and *H. chrysoscelis*, *H. squirella* and *H. cinerea*, and *H. squirella* and *H. gratiosa*. Furthermore, Mecham's (1960a) discovery of introgression in nature, with viable *H. gratiosa*-*H. cinerea* hybrids, suggests these laboratory studies can be extended to nature.

The degree to which call site differentiation separates species during breeding depends on the species considered. Separation between *H. cinerea* and *H. gratiosa* depends on the presence of arboreal call sites for *H. cinerea* (Mecham, 1960a). Both *H. chrysoscelis* and *H. femoralis* typically use arboreal call sites, but do not require them (Fig. 2, Appendix 2). These two species were often found calling together. Separation by habitat is probably most apparent in *H. avivoca*, as this species seems restricted to river swamps in which *H. chrysoscelis* infrequently occurs (Neill, 1948; Gibbons and Patterson, 1978; and pers. obs.). Across a variety of habitats, the results from this study suggest that *H. chrysoscelis* and *H. femoralis* should be more prone to accidental mismatings than the other two species pairs due to ecological proximity. In undisturbed habitats, *H. cinerea* and *H. gratiosa* should rarely hybridize because of their consistent differences in call site height. Hybridization between *H. avivoca* and *H. chrysoscelis* can be expected around the borders of river swamps (Gerhardt, 1974). Both *Acris* species show potential for interspecific hybridization due to similarity in call sites (Neill, 1954), even though they were not found calling together during this study. There are unfortunately few quantitative data with which to determine the relative frequency of these events.

Both the *A. gryllus*-*R. clamitans* and *H. squirella*-*G. carolinensis* species pairs showed broad overlap in call sites (Fig. 2). Presumably, none of these species are interfertile because of body size and phylogenetic differences (Mecham, 1965). Early spring callers, *H. crucifer* and *A. crepitans*, also call from similar locations but were not found together during this study. Winter calling assemblages on the SRP are frequently characterized by the presence of *H. crucifer* and

species of chorus frogs, *Pseudacris ornata*, *P. triseriata* and *P. nigrita* (Gibbons and Patterson, 1978). The latter two species are interfertile, can cross with *H. crucifer* and produce viable offspring, and exhibit some call site differentiation (Mecham, 1965).

Consistent choice of call sites by males should act to minimize interspecific matings with potential mates in order to further precluding isolation. As females move towards multispecies choruses at the onset of breeding activity, they may pass through areas inhabited by congeneric males (Garton and Brandon, 1975; Oldham and Gerhardt, 1975). Presumably, interspecific hybridization may occur during such times (Lamb and Avise, 1986). However, if the attraction to conspecific males calling from sites removed from other species minimizes time spent by females moving through patches of other species, then differences in call sites should facilitate precluding isolation. Once females reach conspecific male call sites, loss of reproductive fitness due to interspecific hybridization should be minimized.

These results and observations suggest that genetic similarity between species may be inversely correlated with a measure of overall ecological similarity in call sites: such a general rule in breeding assemblages of closely related species lacking postmating isolation barriers is testable. Using electrophoretic markers for 19 loci, Etges (1979) demonstrated a weak, but significant positive correlation between genetic similarity and a multivariate measure of ecological dissimilarity between the 12 species considered here. An exception to this trend is the close genetic and ecological affinity of *H. femoralis* and *H. chrysoscelis* because they readily hybridize and show few call site differences (Fig. 3). Acoustic differences in mating calls of *H. femoralis* and *H. chrysoscelis* (Blair, 1958) may be large enough that female discrimination is ensured in spite of call site similarity (Doherty and Gerhardt, 1983, 1984). Extension of precluding isolation through call site differentiation should be considered on a species pair basis.

Significant differences in call site characteristics between particular hylid frog species imply that the evolution of precluding isolation barriers includes more than female call discrimination alone (Blair, 1974; Gerhardt, 1974). Within-species interactions, such as competition for preferred call sites (Fellers, 1979), may also determine call site choice. However, the consistent choice of particular call sites by some

species, e.g., *H. cinerea* and *H. gratiosa*, indicates that these behaviors are important to premating isolation because when preferred call sites are removed, acoustic premating barriers are insufficient to prevent hybridization (Mecham, 1960a; Gerhardt et al., 1980). Evidence from species undergoing reproductive isolation (Littlejohn et al., 1971) or recently diverged (Fouquette, 1975) suggests that mating call differences arise before calling site differences. Once evolved, call site choice may be plastic, dependent upon the presence of nearby oviposition sites and vegetation structure, but indicative of overall ecological similarity between species for sites of copulation, egg-laying, and subsequent growth and survival of tadpoles. Adult anurans show different ecological preferences during nonbreeding periods than during active breeding (Wright and Wright, 1949; Duellman and Schwartz, 1958) but habitat choice may be similar because adults remain at breeding sites for more than a single night (Garton and Brandon, 1975; Wells, 1977). Thus, among many anuran species, evolutionary divergence has been accompanied by not only the evolution of acoustical premating barriers and lack of postmating isolating barriers, but also a complex set of breeding site choice behaviors which serve to reinforce premating isolation.

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APPENDIX 1. DESCRIPTIONS OF ENVIRONMENTAL VARIABLES AND ABBREVIATED CODES USED TO DESCRIBE ANURAN ENVIRONMENTS. All measurements were taken at or from the point of capture of each individual or obtained from the closest Savannah River Plant meteorological station.

Code	Variable measured	Method of measurement
PRCP	daily precipitation (cm)	data from SRP weather stations
LPRP*	local precipitation (cm) within 8 h of capture	rain gauge on site
HUM1	high daily humidity	data from SRP weather stations
HUM2	low daily humidity	data from SRP weather stations
MDTM	mean daily temperature (C)	data from SRP weather stations
HDTM	high daily temperature (C)	data from SRP weather stations
LDTM	low daily temperature (C)	data from SRP weather stations
LTMP*	local air temperature at capture (C)	Weston dial thermometer
LWTP*	local water temperature at capture (C)	Weston dial thermometer
DBWM	distance to nearest other anuran breeding aggregation (m)	steel tape measure or topographic map (1:48,000, Geological Survey, Washington, D.C.)
DSNB	distance to the second nearest other anuran breeding aggregation (m)	steel tape measure or topographic map (1:48,000, Geological Survey, Washington, D.C.)
DSTB	distance to the third nearest other anuran breeding aggregation (m)	steel tape measure or topographic map (1:48,000, Geological Survey, Washington, D.C.)
ADSD	average distance to nearest other anuran breeding aggregations (m)	average of DBWM, DSNB, DSTB
DTPC	point density of trees (≥ 7.5 cm diameter at breast height-DBH) within 16 m	point-quarter method (Cottam and Curtis, 1956)
PCHD	percent hardwood trees	percentage hardwoods of trees measured for DTPC
PCEV	percent evergreen trees	percentage evergreens of trees measured for DTPC
ADPC	average distance of trees from point of capture (m)	steel tape measure
PSAC	percent surface area within 1 m ² quadrat covered by vegetation	visual estimate in 1 m ² quadrat centered on point of capture
DEPW	depth of water (cm)	steel tape measure and staff
WAHA	water hardness (ppm CaCO ₃)	EDTA titration (Anonymous, 1960)
WAAL	water alkalinity (ppm CaCO ₃)	acid titration (Anonymous, 1960)
PHOO	water pH	portable pH meter
DFV	distance to nearest floating vegetation (m)	steel tape measure
DFSH	distance to nearest shoreline (m)	steel tape measure
DFRV	distance to nearest rooted herbaceous vegetation	steel tape measure
DNAB	ground density of vegetation	total count live stems in 1 m ² quadrat centered on capture point
DNWP	distance to nearest woody seedling <1 m high	steel tape measure
DNWS	distance to nearest woody sapling or stem ≥ 1 m high and <7.5 cm DBH	steel tape measure
DNWT	distance to nearest tree or stem ≥ 1 m high and ≥ 7.5 cm DBH	steel tape measure
VPOS	vertical height above the ground (m)	steel tape measure
VPAW	vertical height above the water (m)	steel tape measure
DBWP	DBH of nearest woody plant	steel tape measure
DOLC	diameter of stem or substrate on which individual was captured (cm)	steel tape measure
NSTM	number of stems 2 m above ground in 1 m ² area	stems touched in 1 m ² circle centered on capture point by axial sweep (James and Shugart, 1971)
NSOM	number of stems 1 m above ground in 1 m ² area	stems touched in 1 m ² circle centered on capture point by axial sweep (James and Shugart, 1971)
NSHM	number of stems 0.5 m above ground in 1 m ² area	stems touched in 1 m ² circle centered on capture point by axial sweep (James and Shugart, 1971)
DDWS	density of dead woody stems	total count in 1 m ² quadrat centered on capture point
DFLG	density of fallen logs or stems	total count in 1 m ² quadrat centered on capture point
TFFM*	date of capture used to calculate the number of days from the last recorded freeze (below 0 C)	calendar and data from SRP weather station
TFSS*	time of capture used to calculate the minutes from sunset when captured	difference obtained from recorded time of capture and time of dusk (National Almanac Office, 1965)
NOSC*	number of other species calling	count number of vocally active species at the capture location

* Measurements taken immediately after capture.

APPENDIX 2. ANALYSIS OF VARIANCE RESULTS FOR OVERALL SPECIES* DIFFERENCES AND THE MEANS AND STANDARD DEVIATIONS (IN PARENTHESES) FOR THE 41 ENVIRONMENTAL MEASUREMENTS DESCRIBED IN APPENDIX 1. All F ratios have 11 degrees of freedom (df) for species effects and the degrees of freedom for error are indicated. Probability levels * $P \leq .05$, ** $P \leq .01$, *** $P < .0005$, n.s. = not significant at the .05 level.

Variable	Species					
	1	2	3	4	5	6
Daily precipitation—cm	.25 (.787)	.63 (.771)	.12 (.560)	.84 (.981)	1.7 (1.28)	.64 (.917)
Local precipitation—cm	.41 (1.30)	.58 (.723)	.63 (1.32)	3.8 (.258)	3.0 (1.61)	.60 (.869)
High daily humidity	95.0 (4.74)	84.0 (11.2)	93.2 (4.35)	98.0 (0.0)	98.0 (.696)	86.4 (11.0)
Low daily humidity	29.4 (11.1)	37.5 (5.21)	39.4 (9.22)	66.4 (13.4)	58.8 (17.7)	40.4 (4.88)
Mean daily temperature—C	17.2 (4.87)	28.8 (2.87)	27.9 (2.26)	24.6 (.861)	26.0 (1.97)	28.7 (2.91)
High daily temperature—C	26.1 (3.92)	34.6 (3.62)	33.8 (3.18)	29.2 (1.73)	31.1 (3.46)	34.2 (4.37)
Low daily temperature—C	8.3 (6.22)	23.0 (2.43)	22.0 (1.92)	20.0 (0.0)	21.0 (.871)	23.2 (1.64)
Local air temperature—C	12.3 (4.64)	23.5 (1.73)	28.3 (23.4)	22.9 (1.45)	23.6 (1.70)	24.0 (1.41)
Local water temperature—C	19.8 (5.12)	27.0 (2.04)	28.0 (2.57)	25.8 (2.49)	25.0 (1.57)	26.8 (1.30)
Distance to nearest chorus— km	2.0 (.85)	3.7 (1.49)	1.8 (1.57)	2.3 (0.0)	1.8 (.64)	4.6 (.08)
Distance to second nearest chorus—km	3.0 (.85)	4.3 (1.83)	3.1 (2.03)	5.9 (0.0)	3.9 (2.25)	5.0 (.48)
Distance to third nearest chorus—km	4.0 (1.70)	7.1 (2.89)	4.2 (2.78)	6.9 (0.0)	5.3 (2.05)	8.1 (1.13)
Average distance to closest anuran chorus—km	3.0 (1.13)	5.0 (2.06)	3.0 (2.05)	5.0 (0.0)	3.7 (1.61)	5.8 (.587)
Point density of trees	.08 (.095)	.89 (1.29)	34.2 (138.1)	.07 (.019)	7.3 (15.3)	1.5 (.580)
Percent hardwood trees	60.0 (12.9)	88.6 (20.0)	94.9 (16.9)	96.9 (8.84)	82.4 (34.6)	100.0 (0.0)
Percent evergreen trees	40.0 (12.9)	11.4 (20.0)	5.1 (16.9)	3.1 (8.84)	17.6 (34.6)	0.0 (0.0)
Average distance to closest trees—m	13.3 (3.04)	5.6 (2.68)	5.4 (4.15)	12.5 (1.84)	8.0 (5.75)	2.7 (.523)
Percent vegetation cover	44.7 (25.7)	77.9 (24.3)	70.3 (34.9)	16.3 (34.61)	474.0 (8574.0)	60.0 (11.5)
Depth of water—cm	.18 (.193)	.44 (.552)	.31 (.307)	.04 (.04)	.02 (.036)	.16 (.167)
Water hardness	8.4 (2.58)	8.3 (6.17)	24.6 (16.4)	7.0 (3.82)	18.4 (20.9)	6.5 (4.04)
Water alkalinity	6.3 (2.46)	7.1 (6.24)	32.5 (24.0)	73.4 (7.27)	52.8 (29.2)	4.5 (.577)
Water pH	5.6 (.488)	6.3 (.572)	6.5 (.757)	8.2 (.455)	7.2 (1.35)	6.3 (.364)
Distance to floating vegeta- tion—m	1.3 (3.24)	3.1 (5.87)	3.0 (5.58)	13.9 (3.78)	10.8 (6.55)	.26 (.421)
Distance to shoreline—m	1.2 (1.58)	4.9 (8.42)	5.6 (6.79)	.78 (3.22)	2.3 (4.53)	1.9 (2.01)
Distance to herbs—m	.16 (.196)	.47 (.686)	.30 (.639)	.49 (.690)	1.5 (2.40)	.61 (.733)

APPENDIX 2. EXTENDED.

Species						F	P	df
7	8	9	10	11	12			
.66 (.606)	.17 (.656)	.45 (.758)	1.5 (1.13)	2.0 (.864)	0.0 (0.0)	17.08	***	276
1.8 (1.66)	2.6 (2.56)	1.7 (2.17)	.82 (1.00)	4.1 (1.26)	0.0 (0.0)	14.44	***	278
95.0 (4.61)	90.3 (5.31)	95.1 (4.01)	94.1 (8.50)	97.9 (4.88)	98.0 (0.0)	13.58	***	276
40.7 (7.77)	40.0 (11.6)	46.9 (12.9)	54.7 (24.2)	62.6 (13.1)	32.0 (0.0)	16.60	***	276
26.6 (1.89)	23.0 (4.05)	24.6 (3.78)	17.6 (1.43)	19.6 (2.82)	25.3 (0.0)	36.51	***	276
32.7 (1.90)	29.1 (4.34)	30.3 (4.14)	23.7 (3.76)	24.0 (2.66)	32.8 (0.0)	26.26	***	276
20.6 (1.96)	16.8 (3.88)	19.0 (3.69)	11.5 (1.61)	15.2 (3.28)	17.8 (0.0)	42.45	***	276
22.5 (1.90)	21.0 (3.00)	21.9 (3.95)	15.2 (1.92)	16.5 (3.06)	22.8 (1.22)	4.18	***	278
24.8 (2.80)	24.8 (4.06)	24.2 (3.02)	16.9 (1.20)	19.7 (2.33)	24.1 (.954)	31.40	***	278
1.0 (.89)	2.1 (2.29)	1.3 (1.10)	.86 (.43)	1.0 (.45)	.53 (0.0)	10.77	***	278
1.6 (1.25)	3.1 (2.77)	3.0 (2.19)	1.3 (.59)	2.7 (1.12)	.58 (0.0)	8.21	***	278
2.5 (1.59)	5.6 (11.1)	3.7 (2.50)	1.8 (.981)	3.3 (1.48)	1.1 (0.0)	3.29	***	278
1.7 (1.14)	3.0 (2.63)	2.7 (1.86)	1.3 (.654)	2.3 (.772)	7.4 (0.0)	10.25	***	278
27.5 (42.9)	1.5 (6.33)	14.0 (45.2)	3.7 (3.19)	.31 (.767)	6.9 (5.38)	1.04	n.s.	262
63.0 (35.6)	100.0 (0.0)	96.0 (13.8)	68.9 (47.6)	53.5 (46.6)	100.0 (0.0)	8.66	***	262
36.4 (33.9)	0.0 (0.0)	4.1 (13.8)	31.1 (25.0)	46.6 (46.6)	0.0 (0.0)	9.17	***	262
3.4 (3.95)	8.2 (4.30)	5.3 (5.08)	3.2 (3.94)	12.9 (4.11)	1.5 (.549)	14.47	***	262
58.7 (41.7)	38.1 (28.9)	69.7 (37.3)	6.5 (24.9)	43.5 (32.9)	94.4 (10.5)	0.63	n.s.	262
.07 (.117)	.36 (.190)	.08 (.123)	.10 (.091)	.11 (.104)	.02 (.046)	9.30	***	262
11.7 (4.34)	15.0 (8.32)	17.3 (13.7)	16.5 (8.12)	12.1 (3.18)	78.3 (31.7)	19.48	***	259
7.7 (4.55)	17.8 (22.34)	26.7 (31.7)	15.4 (9.16)	6.4 (2.40)	75.5 (25.3)	20.74	***	259
5.5 (.541)	6.1 (.698)	6.0 (.610)	5.5 (.322)	5.0 (.414)	6.9 (.158)	22.42	***	259
15.2 (0.0)	5.9 (7.25)	9.4 (6.78)	12.5 (5.85)	8.5 (6.90)	6.4 (7.34)	12.76	***	262
.74 (5.82)	11.4 (9.74)	.30 (5.73)	1.3 (3.50)	1.8 (3.43)	-1.0 (1.33)	7.80	***	262
1.1 (1.55)	.28 (.659)	3.2 (5.52)	5.3 (6.96)	1.0 (2.02)	4.1 (6.91)	5.21	***	262

APPENDIX 2. CONTINUED.

Variable	Species					
	1	2	3	4	5	6
Vegetation density	115.3 (85.5)	114.8 (243.7)	152.5 (154.6)	115.6 (239.2)	110.3 (129.8)	155.8 (177.6)
Distance to seedling—m	.72 (.577)	1.0 (1.31)	1.2 (2.24)	5.7 (4.48)	3.8 (4.85)	1.2 (1.11)
Distance to sapling—m	7.0 (3.75)	2.0 (1.70)	2.6 (3.05)	9.4 (3.70)	6.0 (6.20)	1.3 (.848)
Distance to tree—m	11.7 (4.44)	5.9 (4.91)	8.4 (6.31)	8.5 (5.13)	7.9 (5.13)	1.6 (.616)
Height above ground—m	0.0 (0.0)	.0009 (.0043)	.69 (.359)	.06 (.106)	.40 (.530)	0.0 (0.0)
Height above water—m	.008 (.012)	.05 (.072)	.69 (.411)	.04 (.111)	.41 (.584)	.01 (.025)
Diameter of nearest plant—m	.006 (.006)	.008 (.014)	.02 (.031)	.01 (.016)	.02 (.029)	.06 (.037)
Diameter of perch—m	.005 (.007)	.0001 (.00064)	.02 (.030)	.001 (.0039)	.01 (.030)	0.0 (0.0)
Number of stems 2 m high	.50 (1.58)	2.1 (5.04)	4.1 (8.96)	0.0 (0.0)	1.2 (2.97)	2.5 (4.36)
Number of stems 1 m high	.20 (.633)	1.8 (3.76)	29.5 (41.9)	0.0 (0.0)	10.9 (17.2)	7.6 (8.34)
Number of stems .5 m high	3.8 (3.71)	7.9 (9.30)	71.7 (106.4)	10.5 (29.3)	24.7 (34.5)	23.3 (33.9)
Density dead woody stems	5.8 (4.19)	2.1 (6.82)	8.0 (16.9)	.25 (.463)	1.2 (2.98)	1.8 (.957)
Density fallen logs	63.0 (71.4)	2.4 (4.19)	6.1 (20.3)	1.4 (2.56)	7.8 (1.50)	1.0 (1.41)
Days from last ^b freeze	46.9 (22.4)	109.3 (1.43)	115.9 (24.06)	133.2 (1.033)	138.2 (11.40)	119.0 (7.62)
Minutes from sunset	191.8 (51.9)	119.8 (47.81)	98.7 (35.19)	92.1 (40.43)	151.9 (57.21)	139.4 (49.3)
Number other species calling	.40 (.967)	2.6 (1.03)	3.0 (1.33)	4.4 (2.07)	2.3 (1.20)	2.4 (.894)

^a Species identifications are given in Table 1.

^b The last hard freeze occurred on 23 March for 1977 and 18 March for 1978.

APPENDIX 2. EXTENDED. (Continued).

Species						F	P	df
7	8	9	10	11	12			
161.7 (191.9)	204.8 (270.6)	102.2 (141.2)	25.9 (62.9)	97.6 (124.1)	43.8 (38.8)	1.63	**	261
2.1 (4.00)	3.1 (3.87)	1.3 (1.40)	.44 (.378)	8.0 (6.96)	1.1 (.888)	9.22	***	262
2.0 (3.52)	5.3 (4.81)	2.9 (4.23)	.76 (.653)	11.2 (5.23)	.45 (.274)	14.06	***	261
3.9 (3.97)	10.8 (4.05)	4.7 (5.25)	3.4 (4.74)	14.4 (2.12)	1.7 (1.29)	13.10	***	262
.64 (.468)	.03 (.152)	.65 (.498)	.02 (.03)	.0007 (.004)	.77 (.234)	19.93	***	262
.69 (.498)	.03 (.152)	.72 (.553)	.04 (.043)	.004 (.020)	.82 (.273)	17.41	***	262
.04 (.053)	.03 (.127)	.05 (.092)	.01 (.018)	.04 (.059)	.05 (.079)	1.15	n.s.	262
.07 (.248)	.002 (.009)	.06 (.083)	.04 (.097)	.004 (.008)	.02 (.020)	1.82	*	262
16.7 (20.7)	0.0 (0.0)	5.1 (9.76)	2.4 (3.63)	.17 (.658)	14.0 (16.9)	7.48	***	262
20.6 (20.9)	5.5 (15.0)	12.8 (14.1)	3.9 (5.50)	1.1 (3.81)	18.0 (13.6)	5.50	***	262
21.6 (16.3)	23.6 (59.5)	22.3 (25.3)	8.3 (6.31)	8.5 (24.9)	22.8 (13.2)	4.20	***	262
2.1 (3.89)	13.9 (25.7)	2.9 (5.54)	1.1 (2.13)	16.3 (40.3)	3.3 (3.24)	2.28	***	262
4.8 (9.31)	30.9 (90.5)	16.3 (17.7)	27.6 (14.3)	18.5 (27.5)	35.6 (23.3)	3.46	***	262
115.9 (34.7)	70.9 (28.5)	94.8 (38.9)	10.3 (6.23)	51.6 (32.5)	94.0 (0.0)	42.40	***	278
134.3 (35.2)	119.2 (41.2)	124.7 (52.4)	136.4 (44.3)	183.1 (37.2)	89.4 (19.6)	10.30	***	277
2.4 (1.40)	3.8 (1.31)	3.2 (1.74)	.50 (.633)	2.6 (2.24)	2.0 (0.0)	9.95	***	277