Calling Site Choice by Hyla Chrysoscelis: Effect of Predators, Competitors, and Oviposition Sites

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CALLING SITE CHOICE BY *HYLA CHRYSOSCELIS*: EFFECT OF PREDATORS, COMPETITORS, AND OVIPOSITION SITES[1]

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Abstract. We examined the effect of predators, competitors, and conspecifics on the choice of calling sites by male gray treefrogs, *Hyla chrysoscelis*, and the correlations between choice of calling sites by males and choice of oviposition sites by females. The experiment was conducted in an array of wading pools and utilized a replicated block design for variance analysis. Pools were open to natural colonization by male and female treefrogs. The treatments consisted of controls containing no predators or competitors, four treatments containing one species of predator (either *Ambystoma maculatum* larvae, *Enneacanthus chaetodon* adults, *Notophthalmus viridescens* adults, or *Tramea carolina* larvae), and two treatments containing one species of competitor (either *Rana catesbeiana* or *Hyla chrysoscelis*). Male and female treefrogs avoided pools containing conspecific tadpoles and pools containing adult black-banded sunfish, *Enneacanthus chaetodon*. Females also avoided pools containing larval spotted salamanders, *Ambystoma maculatum*. Correspondence between calling sites and oviposition sites was examined in response to treatment, block (consisting of a location and a time), and location. Correspondence between male choices and female choices was weak. Number and location of calling males showed no significant correlation with the number and location of eggs along any of the axes of choice.

Both males and females chose sites based on the species present, and both showed preferences in regard to location and time. The differences between male and female choices indicate that the potential choices have different values to each sex, or that different criteria are used to rank potential choices. Anuran reproductive behavior is not a simple consequence of the direct interactions between males and females, but is a result of complex interactions between the behavior of the two sexes and the environment in which their behavior is embedded.

Key words: anuran; breeding behavior; calling site; competitors; habitat selection; Hyla chrysoscelis; *male–female interactions; oviposition site; predators; reproduction; temporary ponds; tree frogs.*

INTRODUCTION

The evolution of mating systems and the potential conflict between the selective pressures on males and females of a species has generated much interest since Darwin's (1859, 1871) original presentation of the concepts of natural and sexual selection. More recently, the relationship between sexual selection and natural selection has been the focus of both theoretical and empirical work designed to determine the relationship between mating systems and the environment in which they evolve (e.g., Tinkle 1965, Cade 1975, Emlen and Oring 1977, Howard 1979, Wade 1979, Downhower and Brown 1980, Endler 1980, Lennington 1980, Kluge 1981, Rand and Ryan 1981, Clutton-Brock et al. 1982, McCauley 1983, Arnold and Wade 1984*a, b,* Houck et al. 1985, Howard and Kluge 1985, Fincke 1986, Townsend 1989).

In general, theory has suggested that male reproductive success is best served by maximizing the num-

ber of mates, whereas female reproductive success is maximized by optimizing such factors as clutch size, egg size, mate quality, and offspring environment (Halliday 1978, 1983). Though this statement is obviously an oversimplification, it illustrates the view that the selective pressures on males and females generated within the mating system are highly dependent in both their evolutionary and ecological manifestations on the environmental context in which breeding takes place (Vehrencamp and Bradbury 1984). Thus, mating systems are the net result of selection within the context of breeding (sexual selection) and natural selection (Arnold and Wade 1984*a, b,* Horn and Rubenstein 1984).

Animals face numerous choices regarding the timing, location, and duration of breeding activities. For anuran amphibians, how these choices are made has been shown to impact areas ranging from sexual selection (Fellers 1979*a, b,* Godwin and Roble 1983, Howard and Kluge 1985) to the ecological structure of communities (Woodward 1983, Wilbur and Alford 1985, Resetarits and Wilbur 1989) and provides a framework in which to address the relationship between the mating system and the ecological background against which it is set.

Typical breeding systems in anurans consist of males establishing choruses at potential breeding sites and

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females subsequently moving to these sites to either select a male or be "selected" by males as they enter the chorus (Wells 1977a). Most studies have focused on alternative mating strategies in males, male–male competition, and the mechanisms of mate selection by females within these choruses (e.g., Wells 1977b, Howard 1978a, b, Wilbur et al. 1978, Fellers 1979a, b, Arak 1983, Godwin and Roble 1983, Forester and Czarnowsky 1985, Ryan 1985). Little work has dealt directly with the relationship between choice of calling site by males and choice of oviposition site by females or the environmental factors influencing these choices. The degree of correspondence between choices made by males and by females is important for understanding anuran breeding systems. Do males and females share the same criteria for their choices of calling and oviposition sites? Males presumably choose a calling site in order to maximize their likelihood of obtaining a mate. In choosing an oviposition site females are choosing an environment for their offspring (Resetarits and Wilbur 1989; see also Woodward 1987). Is female activity a direct response to male activity, or do female frogs respond to multiple environmental cues in choosing an oviposition site? Do males chose their calling sites in response to the preferences of females for oviposition?

Offspring performance (survival, growth rate, size at metamorphosis, and time to metamorphosis) in many anurans is highly dependent upon the species present in a pond (Morin 1983, Wilbur and Alford 1985, Wilbur 1987); therefore the species present in a pond was used as an assay of oviposition site preferences, calling-site preferences, and their interrelationships in the gray treefrog, *Hyla chrysoscelis*. Our study took a statistical, rather than a direct observational, approach to addressing the interaction between male calling site and female oviposition site. We were interested in how successful reproduction depends on a set of coordinated responses to an array of environmental stimuli, and how important the behavior of the opposite sex is as one of those stimuli. In a previous paper (Resetarits and Wilbur 1989) we discussed the role of predators and competitors of larvae in the choice of oviposition sites by female *Hyla chrysoscelis*. We found that females discriminate among potential oviposition sites based on the species present and suggested that choice of oviposition site can affect a female's reproductive success, as well as the structure of ecological communities (Resetarits and Wilbur 1989). In this paper we examine data from the same experiment focusing on the male responses to larval predators and competitors, and on the relationship between male choice of calling sites and female choice of oviposition sites.

MATERIALS AND METHODS

Hyla chrysoscelis (Anura: Hylidae) breeds during late spring and summer in small ponds and temporary pools and is abundant at the site of our experiments at the Duke Zoology Field Station, Durham County, North Carolina. Males call from near the edge of temporary ponds, overflow pools, and flooded ditches. There they are visited by females who choose an individual male, approach him, initiate amplexus, and then choose an oviposition site (Fellers 1979a, Godwin and Roble 1983; W. J. Resetarits, Jr., and H. M. Wilbur, *personal observation*). *Hyla chrysoscelis* is the only large treefrog at the study site and the only summer-breeding anuran that readily oviposits in open experimental tanks. Its eggs are laid in floating packets and are easily distinguished from those of other species in the area. Male *Hyla chrysoscelis* readily call from the rims of the experimental ponds and are easily distinguished from other species in the area on sight or by call.

Experimental design

The experiment used 45 plastic wading pools, 1.38 m in diameter and 0.29 m deep, arranged in five circular arrays of 9 pools each. The entire procedure was repeated for a total of 90 experimental units in 10 blocks. A block represents a location (5 circular arrays) and a time (early or late). Arrays were located at least 25 m apart in an open field surrounded by old-growth pine and hardwood forest. Pools were covered with 0.05×0.05 m mesh poultry netting, successfully reducing odonate colonization to a few haphazardly scattered individuals. Vegetation in the array was kept mown, preventing anurans such as *Gastrophryne carolinensis* and *Acris crepitans* from climbing into the pools.

All pools within a block were filled with city water on the same day and allowed to stand for 24 h before the addition of 0.35 kg of dried litter raked from the bottom of a temporary pond.

The experiment employed a randomized complete block design for variance analysis with replication of controls within each block. Each of six experimental treatments and three controls were assigned at random to the nine pools in each of 10 blocks. Treatments consisted of the addition of known numbers of potential competitors or predators of *Hyla* eggs or larvae to the pools (Table 1). The six species used were: adult newts *Notophthalmus viridescens dorsalis* (Caudata: Salamandridae), larval *Ambystoma maculatum* (Caudata: Ambystomatidae), larval *Tramea carolina* (Odonata: Libellulidae), adult *Enneacanthus chaetodon* (Perciformes: Centrarchidae), larval *Rana catesbeiana* (Anura: Ranidae), and larval *Hyla chrysoscelis*, plus control pools receiving no predators or competitors. The first four additions were known predators, the latter two were known competitors. All six species would be expected to negatively effect larval performance of *Hyla*. *Rana*, *Hyla* and *Ambystoma* were collected from Duke Forest, Durham County, North Carolina. *Notophthalmus*, *Enneacanthus* and *Tramea* were taken in the Sandhills Game Management Area, Scotland County, North Carolina.

The experiment began on 2 May 1985 with five blocks of nine pools each and continued until 31 May. The

TABLE 1. Summary of treatments.

Treatment	Species introduced	Number of individuals		Number of replicates
		Blocks 1–5	Blocks 6–10	
Control	None	...	...	30
Ambystoma	A. maculatum larvae	15	9–15	10
Enneacanthus	E. chaetodon adults	2	2	10
Hyla	H. chrysoscelis larvae	550	550*	10
Notophthalmus	N. viridescens adults	2	2	10
Rana	R. catesbieana larvae	100	100	10
Tramea	T. carolina larvae	50	25†	10

* 333 in Block 10.
† 21 in Block 8.

experiment was then dismantled and all pools completely assayed and emptied. Treatment positions were re-randomized and the experiment restarted on 2 June, again with five blocks of nine pools each, with slight modification in initial numbers of predators and competitors due to availability of animals (Table 1). The second phase of the experiment continued until 24 June and used the same locations of arrays as the first phase.

On each of 26 nights a survey of calling males was made between 2100 and 2330, recording the calling location (by pool number) of each male. Eggs were removed from individual pools as early as possible each morning and placed in numbered dishpans. Each collection was spread to a monolayer in a photographing tray and photographed for later counting using a fixed sampling grid. Estimates of the number of eggs laid in tanks were within 7% of complete counts on 10 test photographs. Numbers and sizes of predators in the experiment were kept small to eliminate any significant effects of egg consumption. There was no evidence of eggs being removed from the jelly envelopes, and the time available (<12 h) between oviposition and collection precluded any significant impact of egg predation on the results.

Data analysis

Three response variables measured different aspects of choice of calling site by males. "Mean male activity" is defined as the number of calling males per pool per night that any males were calling in the block. It is a measure of the relative attractiveness of a treatment on nights when males were calling from a block. "Active nights" is defined as the number of nights on which ≥1 male called from a pool. "Males per active night" is defined as the mean number of males calling per night in which a pool had ≥1 male calling. The latter two variables comprise the variance in mean male activity. The response variable for choice of oviposition site by females, "mean female activity," was the mean number of eggs per pool on any night that eggs were laid in a block. Mean female activity was square-root transformed, and all data were analyzed for main effects using analysis of variance (ANOVA).

Hypothesis testing was done using Dunnett's procedure (Dunnett 1955), a test designed specifically for analysis of experiments in which each of a number of treatment means is compared to a control mean. Dunnett's procedure allows correction for unequal variances (as in a Student's t test), and uses Satterthwaite's procedure to determine the appropriate degrees of freedom for individual comparisons (Dunnett 1964, Steel and Torrie 1980). The resultant statistic is designated t_d. Dunnett (1955, 1964) suggests using a higher number of replicates for the controls, the optimum being the square root of the number of treatments excluding controls. Dunnett (1964) provides adjustment factors for critical values for both unequal variances and unequal replication. The test controls the experimentwise Type I error rate. The one-tailed alternative was used in all tests, the a priori hypotheses being that the treatment means would be less than the control mean for all comparisons.

A G test with Williams' correction was used to test whether the presence of eggs in a pool was independent of the presence of calling males in that pool the previous night. The same test was used to determine whether the presence of calling males was independent of the presence of eggs in a pool that morning. Pearson's product–moment correlation coefficient was used to test the relationship between the number of calling males on a given night at a pool and the number of eggs in the pool the next morning, using a subset of the data from individual pools where both males were calling and eggs were laid on a given night.

The correlation between male and female choice was investigated with respect to three sources of variation: (1) the faunal composition of the pools in a block ("treatment"), (2) the joint location–time that defined the blocks ("block"), and (3) the spatial location of the blocks ("location"). The appropriate variables for comparing male and female response to treatments are mean male activity and mean female activity. The total numbers of males and eggs were used as the measures of response to block and location. Pearson's product–moment correlation was used to determine the correspondence between the values for male and female responses. Spearman's rank correlation was used to test the correspondence between the relative ranking of treatments by males and females.

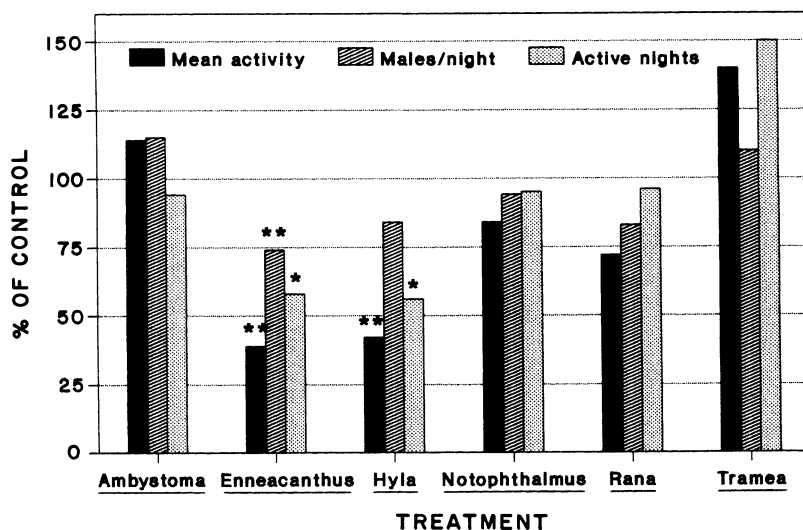Data analysis used the Statistical Analysis System

FIG. 1. Values of mean male activity, mean number of males per active night, and number of active nights for *Hyla chrysoscelis* as a percent of their respective control values for each of these three response variables. An asterisk indicates mean significantly different from control (*P < .05, ** P < .01), using Dunnett's procedure.

(SAS Institute 1982) installed at the Triangle Universities Computation Center and the Statgraphics Statistical Graphics System site-licensed to Duke University (Statistical Graphics Corporation 1986). Dunnett's t statistics and approximate degrees of freedom for comparisons (using Satterthwaite's procedure [Steel and Torrie 1980]) were calculated by hand.

RESULTS

The experiment ran a total of 52 nights yielding 1170 pool-nights of observations on males (26 of the 52 nights) and 2340 pool-nights of observations for eggs (52 of 52 nights). Surveys of calling males yielded 409 calling-site observations. We observed 109 oviposition events (new eggs found in a pool), distributed over 19 nights, yielding a total of >145 000 *H. chrysoscelis* eggs. Based on a mean clutch size of ≈1500 (W. J. Resetarits, Jr., and H. M. Wilbur, *unpublished data*), this number represents about 97 clutches. No other anuran oviposited in the pools or called from the pools during the experiment.

Male responses

Treatments had a highly significant (P = .0105) effect on mean male activity (Fig. 1, Table 2). Block effects were also highly significant (P = .0011), indicating that certain blocks (location and time components) were preferred over others as calling sites. The block × treatment interaction was not significant (P = .92); therefore responses to treatments did not vary across blocks.

Comparisons between treatment means and the controls using Dunnett's procedure (Dunnett 1955, 1964) revealed highly significant differences between the *Hyla* (df = 38, t_d = 3.55, P < .01) and *Enneacanthus* (df = 38, t_d = 3.74, P < .01) treatments and the controls, indicating that these treatments were discriminated

against as calling sites. *Ambystoma, Notophthalmus, Rana,* and *Tramea* treatments were not significantly different from the controls.

Treatments also had a highly significant (P = .0014) effect on the number of active nights (Fig. 1, Table 3), indicating that treatment had an effect on the relative number of nights on which pools were used as calling sites. Block effects were also highly significant (P = .0001). Block × treatment interactions again were not significant (P = .19).

There were significant differences between the *Enneacanthus* treatment and the controls (df = 28, t_d = 2.62, P < .05) and between the *Hyla* treatment and the controls (df = 30, t_d = 2.77, P < .05) for the variable active nights. Pools with these treatments were used as calling sites on relatively fewer nights than the controls and the four other treatments. None of the other treatments were significantly different from the controls using the a priori criterion of a one-tailed test.

The treatments had a suggestive (P = .074), but not significant effect on the number of males per active night (Fig. 1, Table 4). Perhaps treatments had an effect on the mean number of males calling from a pool when calling occurred in that pool. Block effects were significant (P = .023), further indicating the importance of differences between different location and time combinations. Block × treatment interactions were not sig-

TABLE 2. Summary of ANOVA for mean male activity.

Source	df	SS	MS	F	P
Block	9	8.39	0.932	5.15	.0011
Treatment	6	4.16	0.693	3.83	.0105
Block × Trt	54	5.94	0.110	0.61	.9245
Error	20	3.62	0.181		
Total	89	22.11			

TABLE 3. Summary of ANOVA for number of active nights.

Source	df	ss	MS	F	P
Block	9	2.29	0.255	7.99	.0001
Treatment	6	1.09	0.182	5.71	.0014
Block × Trt	54	2.45	0.045	1.43	.1933
Error	20	0.64			
Total	89	6.48			

nificant ($P = .67$). Paired comparisons between treatments and the controls showed highly significant differences between the *Enneacanthus* treatment and the control for the number of males per active night (df = 38, $t_d = 3.69$, $P < .01$). None of the other treatments were significantly different from controls. Thus *Hyla* males did not aggregate at the *Enneacanthus* treatment pools to the same extent as in the other pools.

Female responses

Female responses are treated in detail elsewhere (Resetarits and Wilbur 1989). Here we will concentrate on the variable "mean female activity," which is analogous to mean male activity as a measure of response to treatments. Mean female activity is the mean number of eggs laid per pool per night that any eggs were laid in that block. Treatments had a highly significant ($P = .0007$) effect on this variable (Fig. 2, Table 5), indicating that females responded to the treatments in their choice of oviposition site. Blocks also had a highly significant effect ($P = .0002$), indicating that some blocks were preferred over others. Block treatment interactions were not significant, that is, female responses to treatments were consistent across blocks.

Comparisons between treatments and controls revealed highly significant differences between the *Enneacanthus* (df = 27, $t_d = 4.27$, $P < .01$), *Ambystoma* (df = 24, $t_d = 3.85$, $P < .01$), and *Hyla* (df = 20, $t_d = 3.31$, $P < .01$) treatments and the controls for mean female activity (Fig. 2). The other treatments were statistically indistinguishable from control values.

Correlations between male and female responses

Comparisons between the mean male and female responses to treatments (Fig. 2) revealed a nonsignificant positive correlation between the variables mean male activity and mean female activity ($n = 7$, $r = 0.53$, $P = .22$). Comparisons between responses to blocks (location–time) (Fig. 3) showed no correlation ($n = 10$, $r = -0.0051$, $P = .99$). However, comparison of rank preference for blocks showed a significant negative correlation between male and female preferences ($n = 10$, Spearman's rank correlation = -0.65, $P = .05$). These results indicate that males and females respond differently both to treatments and to the combination of location and time that defines blocks. The correlation between activity of males and females by location shows no significant relationship between actual numbers of males and eggs ($n = 5$, $r = 0.60$, $P = $
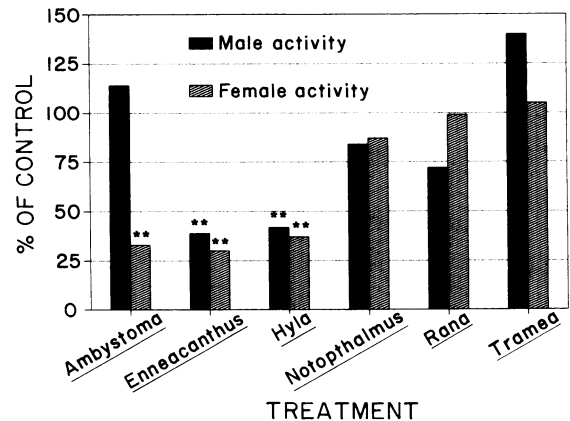

FIG. 2. Comparison of male and female responses to treatments for *Hyla chrysoscelis*. Response variable is mean activity for both sexes. Asterisks indicate highly significant ($P < .01$) difference from control values using Dunnett's procedure (see *Materials and methods: data analysis*).

.29) or between relative ranks ($n = 5$, Spearman's rank correlation = -0.10, $P = .84$). We further tested the correlations between male and female preferences by examining the responses to the control tanks only, which provide a backround uncomplicated by treatment differences and allow testing with greater statistical power. The correlation between the number of calling males and the number of eggs laid in the control tanks was negative and not significant ($n = 30$, $r = -0.20$, $P = .28$; Fig. 4). Using relative rank, the correlation is again negative and not significant ($n = 30$, Spearman's rank correlation = -0.29, $P = .12$). An analysis of variance reveals that the number of calling nights per control pool explains 19% of the variance in the number of eggs laid in the control pools ($F_{12,8} = 1.27$, $P = .38$). The results are similar for early pools (blocks 1–5) and late pools (blocks 6–10) (Fig. 4), with the early pools showing greater variance in the number of eggs per pool. Correlations between calling males and number of eggs are also negative and nonsignificant for both early blocks ($n = 15$, $r = -0.10$, $P = .72$) and late blocks ($n = 15$, $r = -0.36$, $P = .18$).

The interaction between male response and female response was further studied by examining the data from the 50 occasions on which males were observed calling from a pool and eggs were present in that pool the next morning. There was no correlation between the number of males calling and the number of eggs

TABLE 4. Summary of ANOVA for number of males per active night.

Source	df	ss	MS	F	P
Block	9	5.50	0.611	2.88	.0234
Treatment	6	2.95	0.491	2.31	.0735
Block × Trt	54	9.94	0.184	0.87	.6707
Error	20	4.24	0.212		
Total	89	22.62			

TABLE 5. Summary of ANOVA for mean female activity, i.e., the mean number of eggs laid per pool per night that any eggs were laid in that block (square-root transformed) (Resetarits and Wilbur 1989).

Source	df	ss	ms	F	P
Block	9	3776	420	6.68	.0002
Treatment	6	2387	398	6.34	.0007
Block × Trt	54	3891	72	1.15	.3787
Error	20	1256	63		
Total	89	11 310			

present ($n = 50$, $r = 0.097$, $P = .504$). A G test showed no significant deviation from random expectations with regard to the presence of calling males in a pool on a given night and the presence of eggs the following morning ($n = 106$, $\chi^2_1 = 0.34$, $P = .60$). The distribution of calling males on a given night did not predict the location of eggs the next morning.

A test of the relationship between the presence of eggs in a tank on a given morning and the presence of males calling from that tank on the following night shows no deviation from that expected if males called from pools at random. Number of males calling from a tank the night after eggs were laid shows a small, significant positive correlation with the number of eggs laid ($n = 22$, $r = 0.44$, $P = .043$).

Fig. 5 shows the distribution of males and eggs by location for the four most active nights of breeding on which surveys of males were done (four of the six nights with >10 000 eggs). This is illustrative of the highly variable relationship between the choice of calling sites and the choice of oviposition sites in *Hyla chrysoscelis*.

DISCUSSION

This study was designed to determine whether the species present in a pond affect the choice of calling sites by males of *Hyla chrysoscelis*, and to examine how the choices made by males relate to the choices made by ovipositing females. We are interested in how successful reproduction depends on a set of coordinated responses to an array of environmental stimuli,
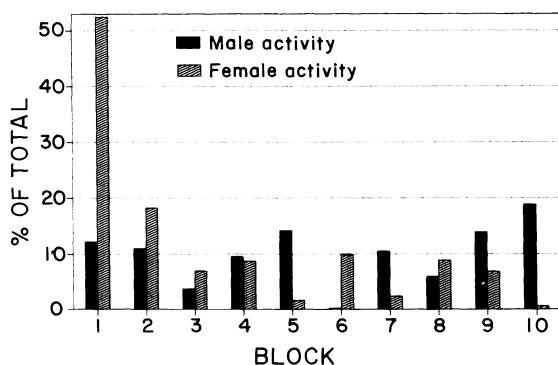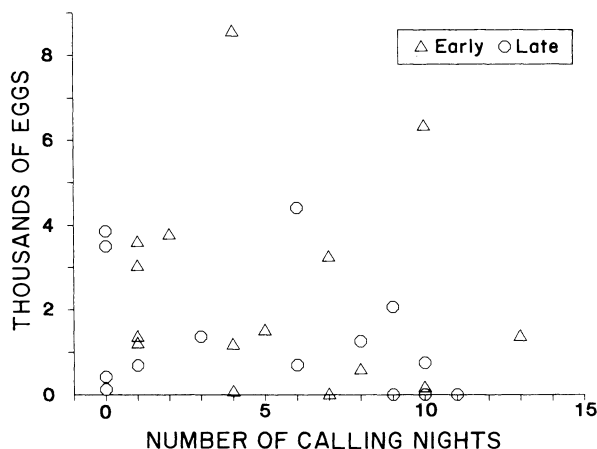

FIG. 4. Relationship between the number of *Hyla chrysoscelis* eggs laid in control pools and the number of calling nights per control pool for both early and late blocks.

and how important the behavior of the opposite sex is as one of those stimuli. Males and female are subject to potentially conflicting selection pressures; males are presumably maximizing the number of mates obtained, while females are presumably maximizing the quality of the mate obtained and the environment provided to their offspring (Halliday 1978, 1983). This, combined with considerations such as physical stress, energetics, and exposure to predation, may create different selective pressures on adult males and females that uncouple aspects of male and female reproductive behavior.

The breeding system in *Hyla chrysoscelis* appears dominated by female choice (Fellers 1979*a*, Godwin and Roble 1983; W. J. Resetarits, Jr., and H. M. Wil-
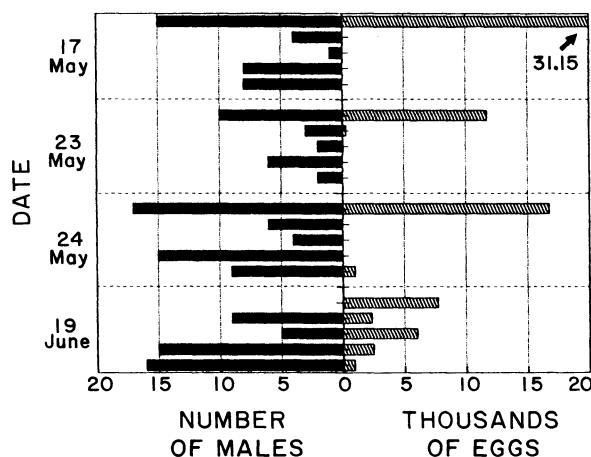

FIG. 5. Comparison of male distributions (solid bars) and egg distributions (hatched bars) by location for *Hyla chrysoscelis* on the four most active nights of oviposition on which data were also available for calling males. Individual nights are separated by dotted lines. Within a night the five potential pairs of bars represent the five locations.

FIG. 3. Comparison of male and female responses to blocks for *Hyla chrysoscelis* using total number of eggs and males recorded from each block.

bur, *personal observation*). Females appear to select a mate, or at least a chorus from which to garner a mate, and subsequently select a site for oviposition. Given the predominance of female choice in this system, the importance of oviposition site for offspring performance, and the high energy cost of calling (Taigen and Wells 1985), selection should favor the ability of males to predict the oviposition sites preferred by females, if there is any female bias towards males calling nearer preferred sites. Pairs may suffer increased risk of predation or reproductive failure when moving considerable distances between the site at which amplexus is initiated (calling site) and the female's preferred site of oviposition. Selection may favor males calling from sites that correspond to females preferences, and, conversely, females may be constrained or prefer to choose a male calling near the intended site of oviposition. Depending on the sequence of choice (male chosen first or site chosen first), the reverse may be true; once a male is chosen, a female is constrained to a limited array of potential oviposition sites.

This experiment demonstrates that male *Hyla chrysoscelis* discriminate among potential calling sites based on the species present. Males are able to some extent to assay the fauna of a pool and reduce their calling activity at certain pools containing "avoided" species. Males show similar, though not identical, responses to those made by females in choosing oviposition sites (Resetarits and Wilbur 1989). Both sexes avoid pools containing *Enneacanthus* or conspecific tadpoles. A major difference appears, however, in that females show a strong avoidance of pools containing larvae of the salamander *Ambystoma maculatum*, whereas males show no response to the presence of this species. The difference between the responses of the sexes to this species is striking, and supports the hypothesis that cues other than the behavior of the opposite sex are important in determining preferences.

Our results suggest a limited response by males to female preferences, but clearly demonstrate that this is not strictly the case. In responses to treatments, blocks (location and time), and location, male and female responses show weak correlation. On a proximate level, male calling site provides little information on how females will distribute their eggs. Conversely, female behavior has only slight predictive value in regard to calling sites of males. These data suggest that the two sexes are responding independently to environmental stimuli, and although there is interaction between the choices made by both sexes, neither sex directly determines the behavior of the other. This is of interest because it suggests an altered view of anuran breeding systems. It becomes more important to understand the specific cues affecting the choices made by males and females, and how responding to those cues rather than directly to the behavior of the opposite sex enhances fitness.

To emphasize the differences between the sexes we can look in detail at a subsample of the data. On the four nights having the most eggs laid on which there was also a survey made of calling males (four of the six nights with >10 000 eggs), over half of the males active were calling from locations in which their chances of obtaining a mate were extremely low (Fig. 5). On three of the four nights, locations with the largest number of eggs also had the largest number of males. However, on one of those nights, the location with the second largest number of males (15 vs. 17) received no eggs, and on the fourth night the largest number of males occurred at the location with the fewest eggs. Location five had the largest total number of calling males over the course of the experiment, yet received the fewest eggs.

This lack of correspondence raises two question regarding the calling behavior of male *Hyla chrysoscelis*: (1) why are males so poor at predicting the oviposition site preferences of females, expressed in this system in terms of treatment, block, and location? and (2) why are males unable to predict which nights females will choose to breed? Phrased in terms of male behavior, why do males spend so much time calling at sites that are not preferred by females and on nights that are not suitable for oviposition? These two questions are important because of the presumed value of being at the right place at the right time for males, and because of the tremendous energy costs (Taigen and Wells 1985), and risks of predation (Ryan 1985) that may be incurred by calling males.

Unpredictability of female arrival is the presumed mechanism behind the extended choruses of *Rana catesbeiana* and *Rana clamitans,* but both of these species are primarily aquatic throughout the year, and defend resource-based territories (Wells 1977*b,* Howard 1978*a, b*). *Hyla chrysoscelis* is arboreal when not at the breeding sites and has only ephemeral territories (Fellers 1979*a,* Godwin and Roble 1983; W. J. Resetarits, Jr., and H. M. Wilbur, *personal observation*). Male *H. chrysoscelis* should call only on nights when obtaining a mate is likely. Even the satellite behavior observed in male gray treefrogs (Fellers 1979*a, b,* Godwin and Roble 1983; W. J. Resetarits, Jr., and H. M. Wilbur, *personal observation*) may be costly in terms of lost feeding time and exposure to predation. Males should attempt to minimize time spent at the breeding site under these conditions. Males that correctly predict the nights on which females choose to breed will be as likely to obtain mates, less likely to be preyed upon, and have a net gain in energy. Data on gray treefrogs are variable with regard to the relationship between number of nights calling and mating success. Fellers (1979*a, b*) found no relationship between these factors for *H. versicolor,* and Godwin and Roble (1983) found a highly significant relationship for *H. chrysoscelis.* However, the latter study lumped all males calling >5 nights, and their data indicate that males achieved a plateau of mating probability by calling at least 4 nights

during the season. This is striking considering that males called up to a maximum of 27 nights ($\bar{X} \pm 1$ SD = 4.2 $\pm$ 4.44, median = 3; Godwin and Roble 1983) (see also Woodward 1982, Ryan 1985). Given the above conditions it becomes even more surprising that male behavior is so poorly coupled to female behavior. Theory generally invokes aspects of male–male interactions to explain this seeming paradox (Fellers 1979a, b). However, no one has yet demonstrated that male–male interactions result in movement of males to entirely different, and presumably less preferred, sites seldom visited by females: in *H. versicolor* subordinate males remain close to "preferred" calling sites (Fellers 1979a, b). Nor has it been demonstrated that male–male interactions require supernormal temporal and spatial coverage for their resolution. Furthermore, the relationship between number of nights calling and reproductive success is not well established for gray tree frogs specifically (Fellers 1979a, b, Godwin and Roble 1983), or anurans in general. We cannot test the hypothesis of size or status segregation among sites with our data, but our impression is that calling sites at the preferred location are not saturated, and that there is no obvious size stratification among locations. All of this suggests that we need to look more closely at how environmental factors, including both intraspecific and interspecific interactions, impinge on the idealized breeding systems inferred for many anurans.

It was our intention to provide frogs with an array of clear choices in as close to natural conditions as possible, while achieving sufficient statistical and inferential power to answer the questions we posed. Those questions revolve around the degree of correspondence between the choices made by males and females. Do males and females share the same criteria for their choices of calling and oviposition sites? Is female activity a direct response to male activity, or do female frogs respond to multiple environmental cues in choosing an oviposition site? Do males chose their calling sites in response to the preferences of females for oviposition? The limited correspondence between male choice of calling site and female choice of oviposition site observed in this study may partly result from the novelty of the breeding habitat and the patchiness of the resources among our experimental pools. This, however, lends support to our contention that neither sex is responding directly to the behavior of the other, and underscores the importance of exogenous environmental factors in the breeding system of *Hyla chrysoscelis*. Male–female correspondence in site-related breeding behaviors appears to be accomplished through partially correlated, coordinated responses to a set of environmental cues; the behavior of the opposite sex is only one of these cues. Such proximate cues may also interact with past experience at local breeding sites to refine the correspondence between male and female behavior and increase the efficiency of reproductive behavior in *Hyla chrysoscelis*.

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