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## CHOICE OF OVIPOSITION SITE BY *HYLA CHRYSOSCELIS*: ROLE OF PREDATORS AND COMPETITORS<sup>1</sup>

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**Abstract.** The role of predators and competitors in the choice of oviposition site by the treefrog *Hyla chrysoscelis* was examined in a randomized complete block experiment using 90 replicated experimental ponds. Control ponds containing neither predators nor competitors were contrasted with treatment ponds into which one of four species of predators (*Ambystoma maculatum* larvae, *Enneacanthus chaetodon* adults, *Notophthalmus viridescens* adults, *Traiea carolina* larvae) or one of two species of competitors (*Rana catesbeiana*, *Hyla chrysoscelis*) was added.

Treatments had significant effects on the mean number of eggs deposited in ponds. Fewer eggs were laid in ponds with *Ambystoma*, *Enneacanthus*, or *Hyla*, as a result of fewer females laying eggs and fewer eggs laid per visit, compared with control ponds. *Notophthalmus*, *Rana*, and *Traiea* had no effect on the number of eggs laid.

Ovipositing *Hyla* discriminated among potential oviposition sites based on the species present. Choice of oviposition site can determine the success of a female's reproductive investment, and it can be a mechanism affecting the structure of ecological communities as well. Our results emphasize the importance of oviposition site choice in the evolution of reproductive patterns and implicate species avoidance by ovipositing females as a mechanism important in generating variability in ecological communities.

**Key words:** *Ambystoma*; amphibian; breeding behavior; competition; *Enneacanthus*; habitat selection; *Hyla*; *Notophthalmus*; oviposition site choice; predation; *Rana*; *Traiea*.

### INTRODUCTION

Choice of oviposition site plays an important role in the reproductive success of temporary pond amphibians. Where a female places her annual, or possibly lifetime, reproductive investment can be as important as how that investment is packaged or the quality of mate she obtains. The suitability of a breeding site directly affects hatching success, larval performance, and, thereby, parental fitness. Selection should be strong for the ability of a female to discriminate potential oviposition sites on the basis of expected larval performance. Factors such as the species present at a pond, and the pond's age, temperature, vegetation structure, and degree of permanence form an interactive complex of characters that influence its suitability as an oviposition site.

The importance of oviposition site choice has been established for many species of insects that use specific host plants (see Rausher 1983 for review). Studies of oviposition site choice in anurans have dealt with physical characteristics of sites in *Rana sylvatica* (Seale 1982), communal oviposition in *Rana sylvatica* (Seale 1982, Waldman 1982), and interactions between a female's choice of oviposition site and attributes of a male's territory in *Rana catesbeiana* (Howard 1978a, b). Female *Rana catesbeiana* reduce predation on their eggs by the predatory leech *Macrobdella decora* by de-

positing eggs in sites with temperatures that increase developmental rate and sites with vegetation structure that reduces the efficacy of predation (Howard 1978a). The direct role of biotic factors, such as the presence of predators and competitors, in the choice of oviposition site has not previously been studied, in spite of its potential importance.

The implications of active choice of oviposition sites based on species composition extend beyond questions of selection on behavioral and physical components of reproduction to questions of colonization and community structure in temporary ponds. The histories of individual ponds can affect the outcome of competitive interactions (Alford and Wilbur 1985, Wilbur and Alford 1985) and perhaps influence the nature of predator-prey interactions (Stenhouse et al. 1983, Stenhouse 1985). Different histories enhance the mosaic nature of potential breeding sites with respect to larval performance (Wilbur and Alford 1985). Choice of oviposition sites based on their species composition provides an additional mechanism for generating differences between communities through the repulsion or displacement of potential colonists.

Predation and competition are important processes affecting temporary pond amphibians (Heyer et al. 1975, Walters 1975, Caldwell et al. 1980, Morin 1981, 1983, 1985, Wilbur 1982, 1984, 1987, Morin et al. 1983, Smith 1983, 1987, Stenhouse et al. 1983, Wilbur et al. 1983, Woodward 1983, Alford and Wilbur 1985, Wilbur and Alford 1985). The composition of the tem-

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TABLE 1. Summary of treatments.

Treatment	Species introduced	Number of individuals		Number of replicates
		Blocks 1–5	Blocks 6–10	
Control	none	0	0	30
<i>Ambystoma</i>	<i>A. maculatum</i> larvae	15	9–15	10
<i>Enneacanthus</i>	<i>E. chaetodon</i> adults	2	2	10
<i>Hyla</i>	<i>H. chrysoscelis</i> larvae	550	550*	10
<i>Notophthalmus</i>	<i>N. viridescens</i> adults	2	2	10
<i>Rana</i>	<i>R. catesbeiana</i> larvae	100	100	10
<i>Traema</i>	<i>T. carolina</i> larvae	50	25†	10

\* 333 in Block 10.

† 21 in Block 8.

porary pond community profoundly affects the larval performance of most species. The larvae of the gray treefrog, *Hyla chrysoscelis*, are sensitive to the presence of predators, competitors, and the density of conspecifics (Morin 1983, Wilbur and Alford 1985, Wilbur 1987). Therefore the presence of such interacting species should impose strong selection for a female's ability to discriminate among potential oviposition sites on the basis of the species present.

We directly manipulated the presence and absence of four species of predators, a larval competitor, and larval conspecifics in replicated experimental ponds to determine the effect of these species on oviposition site choice by the treefrog *Hyla chrysoscelis*. Two questions were addressed: (1) Do females discriminate between potential oviposition sites based on differences in their faunal composition and (2) What species or classes of species are avoided?

#### MATERIALS AND METHODS

*Hyla chrysoscelis* (Anura: Hylidae) is the southern diploid member of the *Hyla versicolor* complex. It breeds during late spring and summer in small ponds and temporary pools on the Piedmont of North Carolina and is abundant at the Duke Zoology Field Station, Durham County, North Carolina, where the experiment was carried out. *Hyla chrysoscelis* is the only large summer-breeding treefrog at the station and the only species that readily breeds in open experimental tanks. Its eggs are laid in floating packets that are easily distinguished from those of other summer breeders in the area, assuring unambiguous identification.

Experiments used 45 plastic wading pools, 1.38 m in diameter and 0.29 m deep, arranged in five circular blocks of nine pools each. Pools within a block were  $\approx 0.3$  m apart. Blocks were located at least 25 m apart in an open field surrounded by old-growth pine and hardwood forest. Pools were covered with  $5 \times 5$  cm mesh poultry netting to reduce colonization by odonates. This technique was successful in limiting odonates to a few stray individuals distributed haphazardly among the pools. Surrounding vegetation 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 dried litter (0.35 kg per pond) raked from the bottom of a natural temporary pond was added. The entire procedure was repeated twice during the summer for a total of 90 experimental units in 10 blocks.

#### Experimental design

The experiment employed a randomized complete block design for analysis of variance with replication of controls within each block. 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 *Traema carolina* (Odonata: Libellulidae), adult *Enneacanthus chaetodon* (Perciformes: Centrarchidae), larval *Rana catesbeiana* (Anura: Ranidae), and larval *Hyla chrysoscelis* (Anura: Hylidae), plus control pools receiving neither predators nor competitors. The first four additions were known predators, the latter two were known competitors. All six species would be expected to negatively affect larval performance of *Hyla*. *Rana*, *Hyla*, and *Ambystoma* were collected from Duke Forest, Durham County, North Carolina. *Notophthalmus*, *Enneacanthus*, and *Traema* were taken in the Sandhills Game Management Area, Scotland County, North Carolina.

The experiment began on 2 May 1985 and ran until 31 May. The experiment was then dismantled, and all pools were completely assayed and emptied. Treatment positions were rerandomized, and the experiment was restarted on 2 June, again with five blocks of nine pools each, with slight modification in initial numbers of predators and competitors due to variation in availability of animals (Table 1). The second phase of the experiment used the same locations of blocks as the first phase and ran until 24 June.

Eggs were removed from individual pools as early as possible the day following oviposition and placed in numbered dishpans. They were then transported to the laboratory, and each collection was spread in a

monolayer in a photographing tray, photographed, and later counted 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 reduce the potential effects of egg consumption. There was no evidence of eggs being removed from their jelly envelopes, and the time (<12 h) available between oviposition and collection of the eggs precluded any significant effect of egg consumption on the results.

The experiment ran a total of 52 nights, yielding 2340 pool-nights of observations. The result was a total of 109 oviposition events (eggs in a pool on a night), distributed over 19 nights, yielding a total of over 145 009 *H. chrysoscelis* eggs. Based on a mean clutch size of  $\approx 1500$  (W. J. Resetarits and H. M. Wilbur, *personal observation*), this number represents  $\approx 97$  clutches. No other anuran oviposited in the pools during the experiment.

A second part of the experiment (W. J. Resetarits and H. M. Wilbur, *personal observation*) consisted of observations of calling males to determine whether they discriminated between potential calling sites on the basis of the species present and whether there were interactions between male choice and the activity of females (see Results: Mean Number of Active Nights per Pool).

#### Data analysis

The choice of oviposition site by a female in this experiment can be partitioned into several components. First she arrives at a set of nine pools (a block) in which she will deposit her eggs. Next she visits a pool (or several pools) and chooses one in which to begin oviposition. She may then deposit her entire egg complement in this pool, or she may distribute her clutch among several pools in the block. At each pool visited she decides whether or not to deposit any eggs and how many to deposit. It is unlikely that ovipositing females moved between blocks.

Three variables were used to assay female oviposition behavior. (1) *Active nights* is the probability that a pool received eggs on a night that any pool in its block received eggs. It is computed as the number of nights a pool received eggs divided by the number of nights that any pool in its block received eggs. Active nights is a measure of the frequency of oviposition in a pool adjusted for the oviposition activity within its block. (2) *Mean activity* is the mean number of eggs deposited in a pool (including zero values) on nights when any pool in its block received eggs. Mean activity is the principal variable of interest because it measures the attractiveness of a treatment, given that a block has been visited and a choice has been made. (3) *Mean deposition* is the mean number of eggs deposited in a pool on nights when the pool received eggs. Mean deposition is a measure of a female's behavior once she has begun laying eggs in a pool. Eggs are laid in clusters

of 20–100, and females have the ability to stop and restart egg deposition several times within a single night (W. J. Resetarits, *personal observation*), controlling the number of eggs laid at any given site. Observations suggest that once amplexus begins, oviposition must be completed in a single night, but females may lay more than one clutch in a summer (H. M. Wilbur, *personal observation*). Variation in mean deposition and active nights produces the overall variation in mean activity.

All three response variables were square-root transformed, and the data were analyzed separately 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 with a control mean. Dunnett's procedure allows correction for unequal variances, as in a Student's *t* test, and uses Satterthwaite's procedure (or that of Cochran and Cox) to determine the appropriate degrees of freedom for individual comparisons (Dunnett 1964, Steel and Torrie 1980). 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* hypothesis being that the treatment means would be less than the control mean for all comparisons.

Analysis of variance used 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

### Mean activity

Treatments had a highly significant ( $P = .0007$ ) effect on mean activity (Fig. 1, Table 2), indicating that females responded to the treatments, resulting in a non-random distribution of eggs. Block effects were also highly significant ( $P = .0002$ ), indicating that more eggs were laid in some blocks than others. The differences among treatments explained 21% of the variance in egg numbers. The highly significant block effect explained 33% of the variation. We deliberately scattered blocks among very different habitats, so this result was not unexpected. The block  $\times$  treatment interaction, however, was not significant ( $P = .38$ ); that is, females did not react to treatments differently in the various blocks.

Pairwise comparisons of treatment means with the control mean for the variable mean activity revealed highly significant ( $P < .01$ ) differences between the

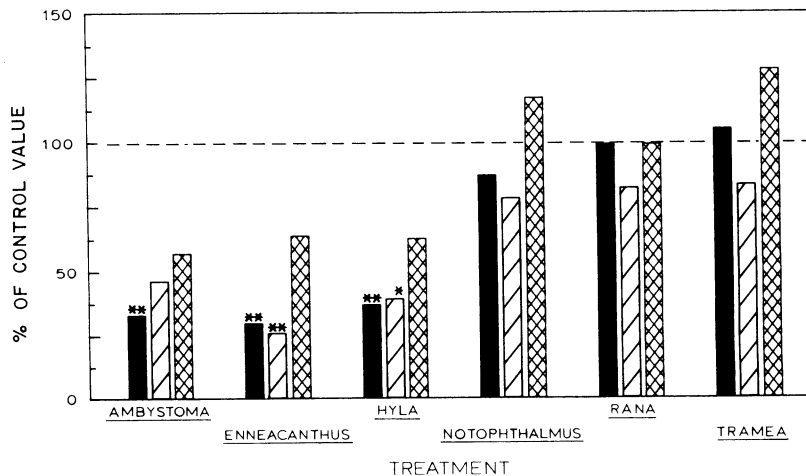


FIG. 1. Variables mean activity (■), mean deposition (▨), and active nights (▩) as a percent of control value (— — —) for each variable. All data were square-root transformed. \* indicates mean significantly different from control at  $\alpha = .05$ ; \*\*  $\alpha = .01$ . All comparisons used Dunnett's procedure (see Materials and Methods: Data Analysis).

*Enneacanthus*, *Ambystoma*, and *Hyla* treatments and the control (Table 3). *Notophthalmus*, *Rana*, and *Tramea* treatments were statistically indistinguishable from the control values. Response to treatments was distinctly dichotomous: treatments elicited either avoidance or neutrality (equivalence to controls).

#### Mean number of eggs per pool per active night

The variable mean deposition (Fig. 1) followed the general pattern shown in the analysis of mean activity. Treatment had a highly significant effect on mean deposition ( $P = .0009$ ; Table 4), as did block ( $P = .00005$ ). The block  $\times$  treatment interaction was not significant ( $P = .55$ ). Females responded to treatments by varying the number of eggs they laid in a pond. Although certain blocks had higher mean deposition, treatment preferences were consistent across blocks.

Pairwise comparison of treatment means with the controls for the variable mean deposition (Table 5) was similar to the results for mean activity. The comparison between the *Enneacanthus* treatment and the control was highly significant ( $P < .01$ ), and that between the *Hyla* treatment and the control was significant ( $P < .05$ ). The *Ambystoma* vs. control comparison was not significant in this case, nor were the comparisons between *Notophthalmus*, *Rana*, or *Tramea*, and the control. The *Ambystoma* treatment was significantly discriminated against in the overall variable of interest, mean activity, but was not significantly discriminated against in mean deposition. Significant overall effects (mean activity) can be produced in different ways; by varying mean deposition, active nights, or both.

#### Mean number of active nights per pool

The ANOVA for the variable active nights (Fig. 1) was highly significant for treatment ( $P = .002$ ; Table

6) and significant for block ( $P = .04$ ). The block  $\times$  treatment interaction was also highly significant ( $P = .009$ ); that is, the effect of treatment on the variable active nights differed significantly among blocks. Though female and male responses to treatments were similar, choice of oviposition sites by females was not closely correlated with the choice of calling sites by males, and male responses showed no block  $\times$  treatment interactions (W. J. Resetarits and H. M. Wilbur, *personal observation*), suggesting that this significant interaction is not the result of responses to variation in male behavior among blocks.

Dunnett's procedure for the variable active nights (Table 7) found no significant differences between any of the treatments and the control values. The pattern of variation in active nights is very similar to that for the other variables (Fig. 1), though the differences are less marked. The significant variation in active nights clearly contributes to both the level and the pattern of variation in mean activity, in spite of the lack of significance of individual comparisons.

## DISCUSSION

The accepted view of anuran breeding systems places a great deal of emphasis on the role of males in deter-

TABLE 2. Summary of ANOVA for mean number of eggs per active block night (mean activity) (data square-root transformed).

Source	df	ss	MS	F	Prob. (> F)
Block	9	3776	420	6.68	.0002
Treatment	6	2387	398	6.34	.0007
Blk $\times$ trt	54	3891	72	1.15	.3787
Error	20	1256	63		
Total	89	11 310			

TABLE 3. Comparisons of all treatments (additions of the indicated species) with the control for the variable mean no. eggs per active block night (mean activity) (data square-root transformed).\*

Comparison	Trt. mean	~df†	$t_D$	Prob. ( $> t$ )
Control	16.52			
<i>Enneacanthus</i> vs. control	4.98	27	4.27	$P < .01$
<i>Ambystoma</i> vs. control	5.38	24	3.85	$P < .01$
<i>Hyla</i> vs. control	6.02	20	3.31	$P < .01$
<i>Notophthalmus</i> vs. control	14.46	not calculated	0.56	NS
<i>Rana</i> vs. control	16.31	not calculated	0.04	NS
<i>Tramea</i> vs. control	17.28	not calculated	0.21	NS

\* Comparisons used Dunnett's (1955) procedure with adjustments for unequal variances of means and allocation of more observations to the control (Dunnett 1964). Dunnett's procedure controls the experimentwise error rate.

† Degrees of freedom for comparisons were calculated using Satterthwaite's approximation (Steel and Torrie 1980) when  $t_D$  values were potentially significant.

mining breeding sites. The data on *Hyla chrysoscelis* (W. J. Resetarits and H. M. Wilbur, *personal observation*) demonstrate that males do exercise choice in regard to calling sites. But the choice of specific oviposition sites by females is largely independent of male choice, and it is the actual choice of oviposition site that is most important in the context of this paper. Choice of oviposition site can directly influence fitness by establishing the conditions for larval development. It is also an important behavioral factor affecting community structure. Although the correlation between male choice of calling site and female choice of oviposition site does have implications for the breeding system of *Hyla chrysoscelis* (W. J. Resetarits and H. M. Wilbur, *personal observation*), here we focus strictly on oviposition site choice as an outcome of the breeding process and the implications of that choice for patterns of reproductive biology and community structure in temporary ponds.

The main objectives of this study were (1) to determine whether ovipositing *Hyla chrysoscelis* are capable of responding to variation in the faunal composition of potential oviposition sites and (2) to characterize what specific faunal elements elicit avoidance behavior. In nature, *Hyla chrysoscelis* is faced with both spatial and temporal variation in the faunal composition of potential oviposition sites (H. M. Wilbur, *personal observation*). The suite of oviposition sites available to *Hyla chrysoscelis* in this experiment consisted of control pools and pools that contained potential predators of eggs and larvae (*Ambystoma maculatum*, *Enneacanthus chaetodon*, *Notophthalmus viridescens*, *Tramea carolina*), a larval competitor (*Rana catesbeiana*), or larval conspecifics. These species are all sympatric with *H. chrysoscelis* and represent major classes of predators and competitors that are important in ponds in the Southeast (H. M. Wilbur, *personal observation*).

The a priori hypothesis was that the control pools, being identical in every respect to the treatment pools except for the presence of potential predators or competitors, should be favored over the treatment pools as oviposition sites. The hypothesis was based on studies that document or suggest the potential impact of

the species chosen on larval performance in *H. chrysoscelis*.

Mean activity (the mean number of eggs laid in a pool on nights when any pool in the block received eggs) was significantly related to some of the experimental treatments, indicating that *H. chrysoscelis* are capable of discriminating between pools containing various species, and that the faunal composition of a pond is a factor in the choice of oviposition site. This is a significant finding in regard to both the evolution of reproductive behavior and the mechanisms by which communities are assembled.

Both a reduction in the number of eggs laid in a pool per active night and a reduction in the number of active nights per pool contributed to the reduction in total number of eggs laid in unfavored treatments, though active nights was not significant for individual comparisons. Since olfaction is the presumed mechanism of discrimination (Petranks et al. 1987), the fact that the distribution of active nights is far more even than the distribution of overall egg numbers (mean activity) suggests that the frogs sample the individual pools fairly closely before a choice is made. This may be an artifact of the proximity of the pools in the circular arrays. It may be difficult for individuals to assess the suitability of pools in the array without visiting them. The importance of avoidance of unfavored treatments might increase as the size and separation of potential sites increases, until interpool distance precludes viable comparisons. An alternative explanation is that the distributing of eggs among pools is an active bet-hedg-

TABLE 4. Summary of ANOVA for mean number of eggs per active pool night (mean deposition) (data square-root transformed).

Source	df	SS	MS	F	Prob. ( $> F$ )
Block	9	12 816	1424	10.11	.00005
Treatment	6	5204	867	6.16	.0009
Blk $\times$ trt	54	7456	138	0.98	.5438
Error	20	2816	141		
Total	89	28 292			

TABLE 5. Comparisons of all treatments with the control for the variable mean eggs per active pool night (mean deposition) (data square-root transformed).\*

Comparison	Trt. mean	~df†	$t_D$	Prob. (> $t$ )
Control	28.18			
<i>Enneacanthus</i> vs. control	7.37	30	4.77	$P < .01$
<i>Ambystoma</i> vs. control	12.85	14	2.12	NS
<i>Hyla</i> vs. control	11.08	18	2.95	$P < .05$
<i>Notophthalmus</i> vs. control	21.93	not calculated	1.18	NS
<i>Rana</i> vs. control	23.22	not calculated	0.66	NS
<i>Tramea</i> vs. control	24.29	not calculated	0.71	NS

\* Dunnett's (1955) procedure with adjustments for unequal variances of means and allocation of more observations to the control (Dunnett 1964). Dunnett's procedure controls the experimentwise error rate.

† Degrees of freedom for comparisons were calculated using Satterthwaite's approximation (Steel and Torrie 1980) when  $t_D$  values were potentially significant.

ing strategy, a possibility suggested, though not directly tested, by those nights when a block contained a clutch ( $\approx 1500$  eggs) spread over several pools.

The comparisons of individual treatments with the controls are of interest both in terms of the avoidance of individual species and in the overall patterns that emerge. The expected avoidance of *Ambystoma maculatum* results from the fact that *Ambystoma* are major tadpole predators in temporary ponds. Experiments with a close congener, *A. tigrinum*, have shown that this species is capable of completely eliminating tadpoles of several species, including *H. chrysoscelis*, from experimental communities (Morin 1983). *Ambystoma maculatum* breeds much earlier in the year than *H. chrysoscelis* (Murphy 1963 and W. J. Resetarits and H. M. Wilbur, *personal observation*); therefore the presence or absence of *A. maculatum* at the time of oviposition is a reliable indicator of the presence or absence of the species during the early larval period of *H. chrysoscelis*. The factor of predictability is as important as the magnitude of the effect in determining the efficacy of selection for avoidance of a particular species. There are costs associated with avoidance; therefore a decision to lay or not must be based on information that reliably predicts not only the immediate but also the longer term conditions within a site.

Much the same argument can be made for avoidance of *Enneacanthus chaetodon*. The effect of predatory fish on anuran eggs and larvae is well documented, especially for temporary pond species such as *H. chrysoscelis*, which lack fish-specific antipredator mechanisms (e.g., Macan 1966, Voris and Bacon 1966, Grubb 1972, Heyer et al. 1975, Werschkul and Christensen 1977, Cecil and Just 1979, Formanowicz and Brodie 1982). The presence of fish usually means complete reproductive failure; therefore it is not surprising that this species elicits the strongest avoidance. As is the case with *A. maculatum*, the presence or absence of *E. chaetodon* at the time of oviposition is a reliable estimator of presence throughout the period of larval development of *Hyla*.

Avoidance by *Hyla chrysoscelis* of pools containing

conspecific larvae presumably results from the avoidance of intraspecific competition in small temporary ponds. Density dependence of survival, growth rate, time to metamorphosis, and size at metamorphosis have been demonstrated for *H. chrysoscelis* (Wilbur and Alford 1985), and potentially affect parental fitness (Smith 1987). In species that oviposit in temporary ponds, density effects may be particularly critical if density slows growth to the point that few or none of the larvae reach minimum size for metamorphosis before the pond dries (Wilbur 1987). Slow growth also increases the exposure time of larvae to gape-limited predators.

The lack of any detectable response to *Notophthalmus viridescens* is surprising in light of the extensive documentation of newts as potent predators of the eggs and larvae of amphibian species, including *H. chrysoscelis* (Morin 1981, 1983, Morin et al. 1983, Wilbur et al. 1983, Wilbur 1987). The key may lie in the predictability of newt presence in temporary or semipermanent ponds. Adult newts are relatively mobile animals that can migrate between aquatic and terrestrial habitats with changing conditions (Harris et al. 1988). The presence or absence of newts at the time of *H. chrysoscelis* breeding may be a poor predictor of conditions over the larval period. This may especially be true in recently filled ponds in which newts may arrive before or after *Hyla* breeds, thus precluding effective avoidance behavior. This, coupled with the local pervasiveness of newts in such habitats may make newts practically unavoidable, and may partly explain the most counterintuitive of the experimental results.

TABLE 6. Summary of ANOVA for mean number of active pool nights (active nights) (data square-root transformed).

Source	df	ss	ms	F	Prob. (>F)
Block	9	0.907	0.101	2.53	.0401
Treatment	6	1.258	0.210	3.45	.0021
Blk $\times$ trt	54	5.711	0.106	1.97	.0093
Error	20	0.796	0.040		
Total	89	8.672			

TABLE 7. Comparisons of all treatments with the control for the variable mean number of active pool nights (active nights) (data square-root transformed).\*

Comparison	Trt. mean	~dft†	$t_D$	Prob. (>t)
Control	0.504			
<i>Enneacanthus</i> vs. control	0.325	not calculated	1.48	NS
<i>Ambystoma</i> vs. control	0.286	not calculated	2.00	NS
<i>Hyla</i> vs. control	0.318	not calculated	1.84	NS
<i>Notophthalmus</i> vs. control	0.588	not calculated	0.87	NS
<i>Rana</i> vs. control	0.501	not calculated	0.02	NS
<i>Tramea</i> vs. control	0.643	not calculated	1.32	NS

\* Dunnett's (1955) procedure with adjustments for unequal variances of means and allocation of more observations to the control (Dunnett 1964). Dunnett's procedure controls the experimentwise error rate.

† Degrees of freedom for comparisons were calculated using Satterthwaite's approximation (Steel and Torrie 1980) when  $t_D$  values were potentially significant.

*Tramea* naiads are effective predators on larval *H. chrysoscelis* (W. J. Resetarits, *personal observation*). However, there is a major difference between this species and the other predators used in this experiment. Though experiments have demonstrated the ability of this species to prey on *H. chrysoscelis* hatchlings and tadpoles of other anurans, *Tramea* is not an effective predator of *H. chrysoscelis* eggs (W. J. Resetarits, *personal observation*). The egg is the most vulnerable stage of *Hyla* to the vertebrate predators used in this experiment (H. M. Wilbur, *personal observation*) and to certain insect predators such as larval dytiscid and hydrophilid beetles (W. J. Resetarits, *personal observation*) common in temporary ponds. The inability of *Tramea* to exploit this highly vulnerable stage may limit its relative impact on *Hyla chrysoscelis*.

This last point may indicate that, even when presence or absence can be reliably determined, all predators are not equal. Several experiments have shown that moderate levels of predation may actually benefit species that breed in temporary ponds, including *Hyla chrysoscelis*, by reducing the levels of competition, thereby increasing growth rate and decreasing time to metamorphosis or increasing size at metamorphosis (Wilbur 1988). Studies have shown that the qualitative and quantitative effects of salamander predation on an anuran assemblage vary with both the species of predator (Morin 1983) and predator density (Morin 1983, Wilbur 1987). In regard to choice of oviposition site, certain predators may be perceived as tolerable or even beneficial, or the response may depend on the predators' density, though the latter implies a much more sensitive assay than detecting presence or absence. Avoidance has a cost that must be weighed against any potential benefits. The lack of responses by ovipositing *Hyla chrysoscelis* to *Notophthalmus* and *Tramea* may result from such differences in the relative impact of predators.

Larvae of frogs of the genus *Rana* have been demonstrated to compete with several hylids, including *H. chrysoscelis* (Wilbur and Alford 1983). It was our original intention to use *R. utricularia* as the competitor in this experiment, but larvae of this species were not

available when the experiment began. *Rana catesbeiana* is an inhabitant of more permanent ponds (generally ones having fish) and for this reason an infrequent associate of *H. chrysoscelis*. We are not aware of data on competition between *R. catesbeiana* and *H. chrysoscelis*. It would be interesting to determine whether *H. chrysoscelis* avoids demonstrated competitors that use the same types of breeding habitats, such as *R. utricularia*, *Bufo americanus*, *Scaphiopus holbrookii*, or competing congeners such as *H. gratiosa* or *H. femoralis*.

The ability to choose between potential oviposition sites on the basis of the species present can be as important in the reproductive success of a female as the more commonly considered reproductive parameters of egg size and egg number. This suggests that selection must act on a complementary suite of both behavioral and physiological characters to approach an optimal or even a successful reproductive pattern (Horn and Rubenstein 1984). Choice of oviposition site and related behavioral factors should be integrated into models of the evolution of reproductive biology to prevent an oversimplified and mechanistic approach to the problems of reproduction in complex physical and biotic environments (Wilbur et al. 1974).

This paper has documented the behavioral avoidance of predators by ovipositing *Hyla chrysoscelis*. The role of predators in determining the composition of communities has been well documented (Macan 1966, Paine 1966, Addicott 1974, Morin 1981, 1983). This study suggests another mechanism whereby predators may affect the composition of communities on a microgeographic scale. The presence of a predator in a particular pond may affect not only that pond by discouraging oviposition, but may increase the densities of *Hyla* in neighboring ponds or perhaps force *Hyla* to ponds where it formerly did not occur. This nonconsumptive effect of a predator (the ghost of predation past?) may result in more far-reaching direct (on *Hyla*) and indirect (on populations with which *Hyla* interacts) effects because the prey is not removed from the system at large but forced into other localities and different competitive and predatory interactions. The ongoing



assembly of communities may be continually influenced by past predator-prey interactions. Colonization by an avoided species may result in a local decrease in a prey species or in a change in its distribution pattern or population structure. Similar effects would result from the avoidance of competitors.

The biotic features of a pond, especially temporary ponds, may vary from year to year, including whether predators, competitors, or conspecifics are present. Community composition may be affected by potential colonists' responses to prior colonists. The presence of a major predator such as *Ambystoma* larvae or centrarchid fish may severely restrict the composition of a community by discouraging colonization by some species, as well as by affecting those that actively attempt colonization. In regard to species such as *Hyla chrysoscelis*, ponds are not islands in the biogeographic sense (MacArthur and Wilson 1967), but patches (Levin and Paine 1974, Whitaker and Levin 1977) containing varying levels of resources and of risk. The processes described above have far-reaching implications for the local distribution and abundance of species that inhabit temporary ponds and the structure of temporary pond communities. These same processes may occur in other temporally or spatially variable habitats and affect a wide range of species.

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