LARVAL PERFORMANCE AND OVIPOSITION SITE PREFERENCE ALONG A PREDATION GRADIENT

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Abstract. The ability of females to assess habitat quality for offspring can strongly influence individual reproductive success as well as population dynamics and community assembly. However, the specific relationship between oviposition site selection and larval performance is often unclear. Ovipositing females of several species of treefrogs (*Hyla*) avoid predatory fish. The fish density required to elicit such avoidance and its relationship to larval performance are central to our understanding of how behavior can drive population dynamics and community assembly in complex landscapes. We conducted experiments investigating both oviposition preference and larval performance in pinewoods treefrogs (*Hyla femoralis*) along a density gradient of predatory fish (0–6 *Umbra pygmaea*). Female *H. femoralis* detected and strongly avoided the nonlethal presence of even a single 2-g fish, ovipositing almost exclusively in predator-free controls. In a separate experiment, larval performance largely matched adult preferences; larvae were totally eliminated in all but the lowest fish density. Given a landscape of breeding sites of varying risks, ovipositing *H. femoralis* behaviorally partition available habitats into those with and without fish, largely matching the associated fitness consequences.

Key words: anurans; ephemeral ponds; female preference; fish; habitat selection; Hyla femoralis; *ideal free distribution; larval performance; oviposition site selection; predation.*

INTRODUCTION

Oviposition site selection is a form of habitat selection in which a female chooses habitat for her offspring, rather than for herself (Rausher 1983, Resetarits and Wilbur 1989, Blaustein 1999). A female's choice of where to place her eggs determines the quality of her offspring's environment and ultimately dictates larval performance and adult fitness, since breeding sites directly affect resource quantity and quality, levels of predation and competition, and the abiotic environment experienced by offspring (Rausher 1983, 1993, Singer 1984, Resetarits and Wilbur 1989, Thompson and Pellmyr 1991, Renwick and Chew 1994, Resetarits 1996, Blaustein 1999, Smith et al. 2000, Murphy 2003*a*). Habitat selection is presumed to be an adaptive response to variation in habitat quality (e.g., Fretwell and Lucas 1970, Pulliam and Danielson 1991, Morris 2003), thus theory suggests that adults should choose oviposition sites that maximize offspring performance. Given variation in resources and risk, females should exhibit various oviposition responses depending on the predicted performance of their offspring and their sensory capabilities. If larval mortality is a linear decreasing function of some factor, females may show a linear dose response. Alternatively, females may demonstrate a threshold response, which may reflect actual offspring performance or derive from detection thresholds in the specific cues used to assess habitat quality. The nature and form of performance and preference curves and their degree of correspondence have important implications for how oviposition behavior affects individual fitness, population dynamics, and community assembly.

Studies of oviposition preference and larval performance have focused largely on insect–plant relationships, where females utilize specific host plants as breeding sites and exhibit a hierarchy in host preference when multiple host plants are present (see e.g., Rausher [1993], Renwick and Chew [1994], and Mayhew [1997] for reviews). Oviposition choices can lead to increased larval growth and survivorship when females avoid low quality host plants, or little relationship may exist between preference and performance, indicating that multiple factors determine this relationship in insect-host plant systems (see Thompson and Pellmyr 1991); little data exists for other types of consumer–resource systems.

The importance of any specific factor in determining larval performance should manifest itself in the strength of covariance between female preference and larval performance. While factors influencing growth and related measures of performance may certainly contribute to variation in fitness, factors that directly influence offspring mortality should have greater net impacts on fitness and are more likely to drive the evolution of oviposition behavior.

Predatory fish simultaneously eliminate and facilitate numerous taxa in aquatic systems, producing distinct patterns between habitats with and without these

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predators (e.g., Hurlbert and Mulla 1981, Morin 1984, McPeek 1990, Wellborn et al. 1996). Prey species lacking specific defenses must therefore reproduce in fishless habitats. In complex natural landscapes, spatial and temporal variation in fish presence and density generates a mosaic of variation in predation risk. While random patterns of oviposition can provide a degree of habitat matching (matching specific phenotypes with suitable habitat), females of many anurans behaviorally avoid breeding sites containing a variety of fish species (Resetarits and Wilbur 1989, Hopey and Petranka 1994, Binckley and Resetarits 2002, 2003). We exploited this propensity to examine the specific relationships between adult oviposition preference and fish density, larval performance and fish density, and the resulting correspondence between adult preference and larval performance.

MATERIALS AND METHODS

Hyla femoralis, the pinewoods treefrog, is a small (2.5–3.8 cm) treefrog common across much of the southeastern United States, including our site in southeast Virginia. Breeding occurs from June to late August during nights with heavy rain when males and females locate breeding sites and females select males from established choruses. Females deposit an average of ~700 eggs per breeding event (D. Chalcraft, *unpublished data*) in numerous floating surface packets of 50 to 200 eggs, and are capable of moving among ponds once egg deposition commences. Females are likely capable of producing multiple, temporally spaced clutches in a breeding season under favorable conditions, but the frequency of this behavior is unknown. Eggs hatch within 24 hours and metamorphosis typically occurs after four weeks.

Umbra pygmaea is a small (4–11.5 cm), locally abundant fish native to the region, and is known to prey upon larval anurans (Chalcraft and Resetarits 2003). *Umbra* can tolerate large fluctuations in water temperature, low pH, and low dissolved oxygen levels, allowing them to invade and persist in conditions typical of many ephemeral/semipermanent ponds used by *H. femoralis* (J. Rieger, *personal observation*).

We conducted experiments at the Naval Security Group Activity Northwest (NSGA) in Chesapeake, Virginia. This 1467-ha facility is located on a remnant of the Great Dismal Swamp and contains a network of agricultural fields, old fields, and woodlands that have been extensively ditched for drainage. Experiments were conducted in an old field surrounded by loblolly pine forest (*Pinus taeda*) and containing a large natural population of *H. femoralis*

Oviposition preference

We used 56, ~400-L, plastic wading pools (1.50 m diameter, 0.29 m deep) arranged in seven spatial blocks, each consisting of a circular array of eight pools spaced 1 m apart; blocks were separated by >20 m (Resetarits

and Wilbur 1989). Between 14 and 21 May, we filled all pools with water from a nearby borrow pit, filtered through mesh screening (2 × 2 mm). We collected leaf litter from surrounding forest and randomly added 0.35 kg to each pool. All pools were covered with mesh screening (2 × 2 mm) to reduce aquatic insect colonists.

We used a randomized complete block design with replication of controls within blocks. Replicated controls reduced the potential for egg saturation. Each block contained eight pools, two fish-free controls plus six fish-density treatments (one to six *U. pygmaea* per pool). This encompasses the lower end of natural densities for this species (J. Rieger, *personal observation*). Fish were measured to the nearest 0.01 g and only individuals ranging from 1.78 g to 2.56 g were used. By using similar sized fish we were able to control for variation in both mass (density) and surface area of fish, the latter an important consideration since cues are likely chemical (Kats and Dill 1998, Berendonk 1999, Angelon and Petranka 2002, Binckley and Resetarits 2003). Fish were added to pools one block at a time between 17 and 23 May; on 24 May, 1-L aliquots of pond water containing algae and microcrustaceans were added to enhance the background community. Fish were not supplementally fed during the experiment, nor did they have access to larval anuran eggs or larvae. The experiment was begun on 27 May.

On nights with precipitation, screens were submerged into the pools preventing harassment of adults and consumption of *Hyla* eggs by fish, but allowing for passage of chemical cues. Eggs were collected from atop the screens the following morning, placed into separate containers by pool, and counted by hand. The experiment was terminated on 23 August.

Data analysis.—We used analysis of variance to evaluate the effect of block and predator density on the mean number of eggs deposited per experimental unit, this is an estimate of relative oviposition activity (type III sums of squares, $\alpha = 0.05$, total df = 55, total number of pools = 56). Data were square root transformed to meet ANOVA assumptions. Block and block × treatment interaction were not close to significant in any analysis (all $P > 0.36$) and were rolled into the error term (Hines 1996). Treatment means were compared using a Ryan-Einot-Gabriel-Welsch multiple stepdown F (REGW-F) test, which controls for experimentwise Type I error rates (Toothaker 1991).

Larval performance

On 31 May, we established 30 plastic wading pools in five rectangular spatial blocks of six pools each spaced ~0.08 m apart in a large abandoned field, using the same protocols as the oviposition experiment. On 6 June, we collected 10 *H. femoralis* egg masses and allowed them to reach Gosner stage 25; 15 tadpoles from each were randomly assigned to individual pools to establish an initial larval density of 150 tadpoles and

to ensure that genetic diversity did not differ among pools.

We employed a randomized complete block design where a single control plus five fish treatments (one to five, free-swimming, ~2-g *U. pygmaea* per tank) were replicated five times (total = 30 experimental units). The six-fish treatment was excluded due to expected high tadpole mortality. Predator treatments were randomly assigned to experimental units within blocks two days after introduction of tadpoles.

Pools were checked daily to collect *H. femoralis* metamorphs (defined as emergence of a single forelimb), which were returned to the laboratory and weighed to the nearest 0.0001 g after tail reabsorption. The experiment was terminated on 18 August when larval dragonflies were discovered in some control tanks (no dragonflies occurred in any fish treatments). All surviving tadpoles were collected and counted at that time.

Data analysis.—We evaluated the effects of predator density on total survival (surviving tadpoles plus metamorphs), mass at metamorphosis, and proportion of survivors that reached metamorphosis. We used ANOVA (as above) to analyze total survival after arcsine transformation to meet assumptions, and REGW-F to compare treatment level means. Proportion metamorphs and mass at metamorphosis from treatments containing zero and one fish were analyzed using MANOVA; no individuals survived in other treatments. Proportion metamorphs was arcsine transformed and mass at metamorphosis reciprocal transformed. As above, block was not near significance (all $P > 0.36$) and was dropped from all analyses. We also performed post hoc ANCOVAs on proportion metamorphs and mass at metamorphosis using total number of survivors as a covariate to examine the role of thinning vs. direct predator effects in the responses of metamorphs.

RESULTS

Female oviposition preference

Hyla femoralis bred on five nights between 2 June and 23 August resulting in 27 175 eggs in controls and 4388 eggs in all other treatments combined (total = 31 563). Estimates of *H. femoralis* clutch sizes from NSGA suggest this represents ~44 females (D. Chalcraft, *personal communication*). On evenings with moderate oviposition activity (e.g., 2 June and 23 June), egg deposition was exclusively limited to control pools; on nights with elevated activity (e.g., 6 June, 16 June, 29 July) a small proportion was also collected from pools containing fish (Fig. 1a). On only three occasions were the number of eggs laid in a pool containing fish greater than the minimum observed clutch size (496; D. R. Chalcraft, *unpublished data*).

Distribution of eggs was significantly skewed among treatments ($F_{6,49} = 9.65$, $P < 0.0001$). Fishless pools received 86.6% and one-fish pools 7.8%, respectively, of the total eggs deposited (Fig. 1b). The combined
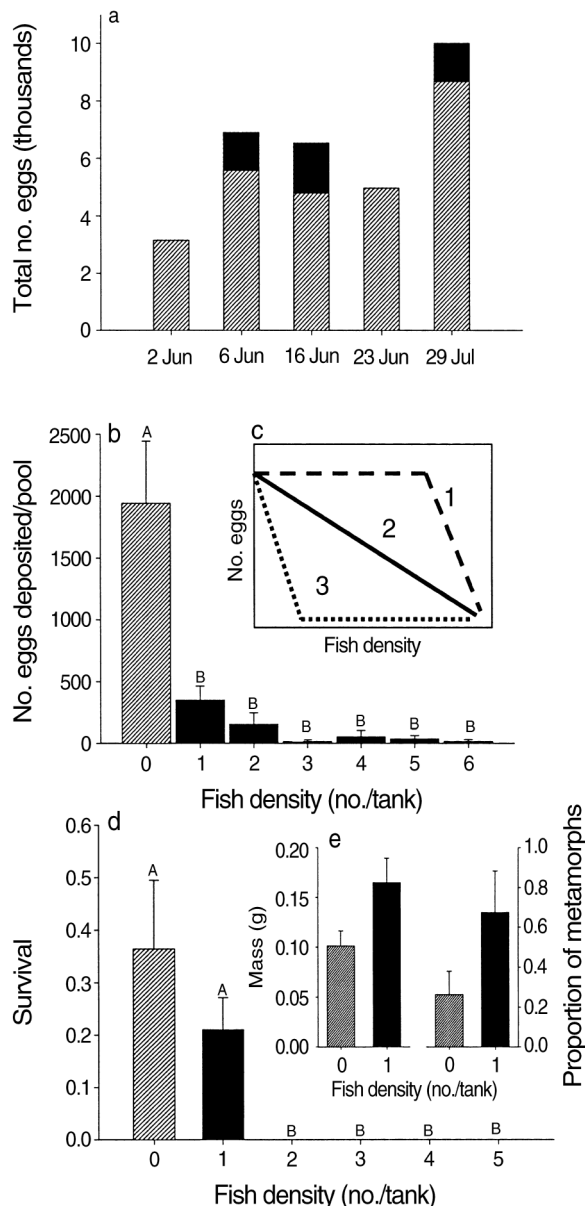

FIG. 1. Solid bars represent fish treatments; hatched bars represent fishless treatments. (a) Egg distribution in fish and fishless pools during the five nights of oviposition. (b) Number (mean + 1 SE) of *Hyla femoralis* eggs deposited in pools with varying densities of *Umbra pygmaea*. Uppercase letters above the bars identify pairs of means that are significantly different using REGW-F. (c) (inset) Three possible oviposition responses along a predator gradient: (1) step function in which females possess a high oviposition threshold, (2) linear response, and (3) step function with low oviposition threshold. The observed response matches line 3. (d) Number (mean + 1 SE) of *H. femoralis* survivors recovered from pools containing varying densities of *U. pygmaea*. Note the close agreement with the oviposition response (see Fig. 2). Uppercase letters above the bars identify pairs of means that are significantly different using REGW-F. (e) (inset) Mean (+ 1 SE) mass of metamorphs (left) and proportion of survivors that reached metamorphosis by the end of the experiment (right) from fishless controls and one-fish treatments. Differences between zero- and one-fish treatments were significant.

percentage of eggs in pools containing more than one fish represented <6% of the total. Comparisons among treatments (REGW-F) indicated fishless pools differed significantly from all fish densities, but comparisons among fish densities were not significantly different (Fig. 1b).

Larval performance

Fish significantly reduced total survival ($F_{5,24} = 13.88$, $P < 0.0001$), with treatments containing more than one fish producing no survivors (Fig. 1d). Mean total survival (tadpoles + metamorphs) was higher in fishless control pools compared to one-fish pools (36% and 21%, respectively), but the difference was not significant. Fish had a significant effect on proportion of metamorphs and size at metamorphosis (MANOVA: Wilks' $\lambda = 0.36$, $F_{2,6} = 5.25$, $P = 0.049$; proportion metamorphs $F_{1,7} = 11.24$, $P = 0.01$; mass $F_{1,7} = 5.51$, $P = 0.05$). Pools containing one fish had a greater proportion of metamorphs, which were, in turn, larger than in fishless pools (Fig. 1e). ANCOVAs using total number of survivors as a covariate suggest that effects on proportion metamorphs likely derive from both thinning (covariate, $F_{2,6} = 5.49$, $P = 0.058$) and direct effects of predators on survivors (treatment, $F_{2,6} = 10.07$, $P = 0.019$), but effects on size at metamorphosis derive only from direct effects (covariate, $F_{2,6} = 0.00$, $P = 0.947$; treatment, $F_{2,6} = 5.12$, $P = 0.0643$).

DISCUSSION

The ability of females to assess habitat quality prior to oviposition will strongly influence their overall reproductive success, as factors influencing larval mortality and performance are highly variable both spatially and temporally (Resetarits and Wilbur 1989, Resetarits 1996, Blaustein 1999, Murphy 2003a). Reproductive strategies involving minimal post-oviposition parental care with dispersal limited larvae (including most anurans) should select for females who choose oviposition sites maximizing larval performance (assuming risk to breeding adults is comparable). In the present context, the consequence of incorrect choices is often complete reproductive failure if larvae lack antipredator mechanisms against predatory fish, as documented for aquatic larvae across a broad spectrum of taxa (e.g., Heyer et al. 1975, Morin 1984, McPeek 1990, Brönmark and Edenhamn 1994, Hecnar and M'Closkey 1997, Eason and Fauth 2001, Abjornsson et al. 2002; see review by Wellborn et al. 1996).

Female anurans select breeding sites based on abiotic characteristics such as pond depth, water temperature, and pond density (e.g., Seale 1982, Spieler and Linsenmair 1997, Marsh 2001), and biotic factors such as the presence of predators and competitors (e.g., Resetarits and Wilbur 1989, Crump 1991). Especially striking is the response to predatory fish by species with fish-intolerant larvae (e.g., Resetarits and Wilbur 1989, Hopey and Petranka 1994, Binckley and Resetarits 2002, 2003). However, studies have not deter-

mined the minimum predator density needed to affect oviposition, the pattern of response females elicit when presented with habitats of varying predation risk, and the relationship between oviposition preference and larval performance. These issues are critical for understanding the role of oviposition site choice in complex landscapes where predator distribution and density are highly variable both spatially and temporally.

In our study, *H. femoralis* females detected and avoided fish at very low density (<0.5 g fish/100 L) and demonstrated a low threshold response to perceived predation risk (curve 3 in Fig. 1c). The specific avoidance pattern observed could conceivably reflect detection limits for the environmental cues associated with fish (presumably chemical; Kats and Dill 1998, Berendonk 1999, Angelon and Petranka 2002, Binckley and Resetarits 2003), or the actual fitness function as determined by *U. pygmaea* predation. In this case, female preference corresponded very closely to larval performance; fish densities allowing larval survival (0 and 1) received 94% of the reproductive effort in this population of *H. femoralis*. Correspondence between preference and performance for the zero- and one-fish treatments is not as strong, but interpretation is complicated by the fact that larval dragonflies established only in fish-free pools and had substantial impact on survival before they were detected. Thus, observed survival in zero-fish pools (Fig. 1d) results in a conservative estimate of fish effects, and other differences between zero- and one-fish pools may also partly reflect responses to dragonflies vs. fish (Relyea 2002).

Moderate levels of predation often have a positive effect on size at and time to metamorphosis (Brockelman 1969, Morin 1983, Smith 1987, Wilbur 1987), so that the actual expected fitness derived from zero- and one-fish treatments would vary depending on other factors, such as rate of pond drying, as well as the presence of other predators (e.g., larger larval dragonflies) typically excluded by fish. The ability of females to integrate across such complex sets of variables may be limited, so we expect preference–performance relationships to weaken where differences in expected fitness are subtle or highly context dependent (Murphy 2003a, b), as at our lowest fish densities.

A primary focus of habitat selection models, such as the ideal free distribution (IFD), is variation in habitat suitability and how individuals select habitats based on perceptions of habitat quality (Fretwell and Lucas 1970). Habitat quality is determined by resource and/or predator levels (among other things), and modified by variation in conspecific density. We can use this conceptual framework to examine the perception of the habitat landscape from the perspective of female *H. femoralis*. Initial habitat suitability is represented by fish density; controls should have the highest quality and the predicted oviposition pattern should reflect a preference hierarchy: 0 fish > 1 > 2 > 3 > 4 > 5 > 6 fish. However, the behavior of ovipositing females indicates that *H. femoralis* only distinguished two hab-
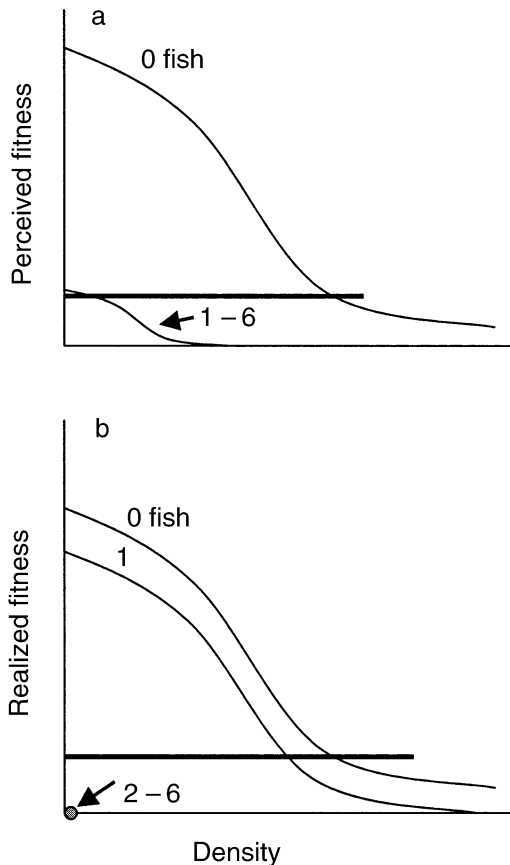
FIG. 2. Fitness vs. conspecific density sensu the ideal free distribution (IFD); horizontal lines connect points of equal fitness. (a) Perceived fitness (utility function) for ovipositing female *Hyla femoralis*. The landscape is perceived as consisting of only two habitat types: fish and fishless. (b) Realized fitness for *H. femoralis* ovipositing in various habitat types. Expected fitness is similar for zero- and one-fish pools, but zero for all other fish densities. The correspondence between perceived and realized fitness is striking but not perfect, suggesting that females err on the side of caution with regard to habitats containing evidence of fish.

itat types, pools with and without fish (Figs. 2a, 1b), and this distinction closely reflects the actual variation in larval performance (Figs. 2b, 1d, 1e). Distribution of eggs in pools containing fish across nights of varying breeding intensity (Fig. 1a) agrees with results from prior work on a closely related species, *H. chrysoscelis* (Resetarits and Wilbur 1989, Binckley and Resetarits 2003), and suggests that conspecific density may also play a role in perceived habitat suitability and the resulting distribution of propagules among habitat types (sensu IFD), although it is clearly subordinate to the dominant effect of fish (Resetarits et al. 2004). Observed responses suggest that oviposition behavior of *H. femoralis* is an adaptive response to variation in expected fitness.

Direct consumption of anuran larva by fish has historically been the hypothesized mechanism by which

fish intolerant species are restricted to fishless habitats (e.g., Brönmark and Edenhamn 1994, Wellborn et al. 1996, Hecnar and M'Closkey 1997, Smith et al. 1999). However, a growing number of studies suggest that oviposition site selection is an alternative mechanism determining the distribution of species in the absence of typical, "face to face" interactions and directly induced mortality (e.g., Resetarits and Wilbur 1989, Hopey and Petranka 1994, Blaustein 1999, Resetarits 2001, Blaustein et al. 2004, Resetarits et al., *in press*). Prior results (Binckley and Resetarits 2002, 2003) suggest that behavioral avoidance is a response to fish in general, rather than to specific species. Ponds containing 0.5 g/100 L of any fish may not only repel *H. femoralis* but limit suitable oviposition sites for a number of anurans and aquatic insects (Resetarits 2001, Abjornsson et al. 2002, Angelon and Petranka 2002), which forces greater covariance among species that share avoidance (or attraction) behavior (Resetarits et al., *in press*). Thus, it is becoming increasingly clear that many aquatic species use fine-scale predator cues to evaluate habitats for themselves and/or their offspring, and that habitat selection behavior plays an important role in the assembly of natural communities at the local and landscape level (Resetarits and Wilbur 1989, Blaustein 1999; Resetarits et al., *in press*).

Our study has shown that the success of *H. femoralis* offspring at a breeding site depends upon the ability of females to detect and avoid even very low densities of predatory fish, and that female behavior in choosing oviposition sites directly reflects the observed variation in larval performance. Oviposition site choice by *H. femoralis* appears to be an adaptive response to spatial and temporal variation in the distribution of fish and the resulting variation in the quality of breeding habitats. This reinforces the importance of habitat selection behavior in the assembly of natural communities and has important implications at levels from the evolution of individual behavior to metacommunity dynamics.

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