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Reproductive decisions under threat of predation: squirrel treefrog (*Hyla squirella*) responses to banded sunfish (*Enneacanthus obesus*)

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Abstract We tested whether the presence of a predator (non-lethal effect) could produce patterns of prey distribution and abundance attributed historically to direct mortality. Sixteen experimental ponds (1,000 l cattle watering tanks) were established; eight containing seven enclosed banded sunfish, *Enneacanthus obesus*, and eight predator-free controls. Ponds were colonized by ovipositing squirrel treefrogs, *Hyla squirella*, and a total of 33,128 eggs and tadpoles were recovered from the experimental ponds. Significantly more eggs and tadpoles (94.8%) were recorded from the predator-free treatments. These data support an alternative mechanism, based primarily on maternal behavior, explaining classic patterns of anuran species composition across a landscape of breeding sites.

Keywords Oviposition · Non-lethal effects · Predation · Reproduction · Anuran

Introduction

Predation is a critical determinant of species composition, species richness, and hence community structure in aquatic ecosystems (Brooks and Dodson 1965; Morin 1983; Kerfoot and Sih 1987; Power 1990; Resetarits and Fauth 1998). Invasions by vagile predators into previously unoccupied habitats may alter species abundances, eliminate species, and inhibit (or facilitate) colonization or persistence. In particular, predatory fish can have dramatic but varied effects on prey species, including amphibians. Predatory fish are essential for the persistence of certain amphibians (e.g., Magnusson and Hero 1991; Werner and McPeek 1994), while predation on eggs and larvae (e.g., Semlitsch 1987; Gamradt and Kats 1996) can decimate populations of many others (Heyer et al. 1975; Kurzava and Morin 1998).

In addition to mortality from predation, fish and other predators can induce suites of behavioral anti-predator defenses in amphibian larva including reduced activity and shifts in habitat use (Kats et al. 1988; Lawler 1989; Resetarits 1991). Anti-predator defenses incur costs such as decreased growth, extended larval periods, and reduced size at metamorphosis (Resetarits 1991; Skelly 1995; Werner 1998) that may affect survivorship, age and size of first reproduction, and fecundity. Thus, the composition and structure of amphibian assemblages should reflect both lethal and non-lethal impacts of predators (Morin 1999). This is best exemplified by characteristic species compositions correlated with the presence and abundance of predatory fish (Wellborn et al. 1996). However, these patterns are typically ascribed to direct predation (Bradford 1989; Bronmark and Edenhamn 1994; Fisher and Shaffer 1996; Tyler et al. 1998; Azevedo-Ramos et al. 1999).

A critical, yet poorly understood, non-lethal effect of predators is habitat selection in the form of oviposition site choice (Rausher 1983; Resetarits and Wilbur 1989; Resetarits 1996). Oviposition sites determine hatching success, larval development, survivorship of offspring, and ultimately fitness. Thus, oviposition decisions will directly affect species composition and patterns of community assembly in natural systems. Predators are a critical determinant of reproductive success and should elicit avoidance (or attraction) by ovipositing females of many species. This may be especially true for small, freshwater systems in which patches (e.g., ponds), and thus the distribution of predators, are often relatively discreet.

Natural selection should favor females that can: (1) detect and assess the fitness consequences of ovipositing in particular localities, and then (2) correctly avoid or select breeding sites based on their consequences. The entomological literature provides numerous examples of non-random female oviposition choice resulting in increased larval growth and survivorship (Rausher 1983; Papaj and Rausher 1987; Singer et al. 1988; Craig et al. 1989; Blaustein and Kotler 1993; Sherratt and Church 1994; Nylin et al. 1996; Blaustein 1999), yet only a handful of

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studies have examined oviposition site choice in other groups of organisms (Bernardo 1996). Even fewer studies have examined oviposition responses to variation in species composition, which on a local scale may be spatially and temporally more variable than abiotic conditions.

We examined reproductive behavior under threat of fish predation by quantifying female oviposition site selection in squirrel treefrogs, *Hyla squirella*, in the presence and absence of a caged fish predator, *Enneacanthus obesus*. *H. squirella* is a small, locally abundant treefrog common in the Coastal Plain of the southeastern United States. It breeds in ephemeral aquatic habitats that vary greatly seasonally in both duration and species composition. *E. obesus* is a dwarf sunfish common in a variety of habitats, both permanent and semi-permanent, in the same areas, and is a very effective predator on larval *H. squirella* (D. Chalcraft and W. J. Resetarits, unpublished data). Seasonal flooding plays a large role in the distribution of fish predators (including *E. obesus)* in these Coastal Plain habitats, creating a spatially and temporally shifting mosaic of predation risks and habitat suitability for breeding amphibians. This variability should select for the ability to detect and avoid unfavorable habitats (e.g., habitats with predatory fish). Physically separating the predator from *H. squirella* allowed us to quantify the non-lethal behavioral effects of predation unconfounded by the direct lethal component, thus specifically examining the response of ovipositing frogs to the perceived risk of predation.

Materials and methods

We established 16 experimental ponds (two rows of eight) using cattle watering tanks (Morin 1983) at the Grice Marine Biological Laboratory (GMBL) on James Island, Charleston, South Carolina (henceforth referred to as pools, to delineate them from natural ponds). All pools were 2 m from each other and each column of pools comprised a block for analysis (total=8). We filled all pools (0.61 m deep×1.52 m diameter) with tap water (approximately 1,000 l total volume) and allowed them to sit for several days before 2 kg of commercial pine straw was added to each pool. We inoculated pools with zooplankton collected from fishless temporary ponds located in the Francis Marion National Forest (FMNF) in Charleston and Berkley Counties, South Carolina. Pools were kept covered with fiberglass mesh lids (mesh size 1 mm) to prevent colonization by aquatic insects (Morin 1983).

We constructed fish enclosures from 115 l plastic trashcans by removing two 25×50 cm side sections and replacing these with fiberglass screening (Resetarits, in press). One enclosure was placed in each of the 16 pools. We collected *E. obesus* from a temporary pond and a permanent ditch located in the FMNF and added seven small randomly selected *E. obesus* to one randomly selected enclosure in each block. This predator density fell well within the wide range of natural densities encountered in the field (personal observation). Use of enclosures eliminated all physical interactions between predators and *H. squirella,* but allowed for nonlethal communication (chemosensory, visual, and/or mechanical). *Enneacanthus* were added to four blocks on 1 July 1998 and to the remaining four on 3 July 1998. Mean (±1 SE) total length (4.7±0.11 cm) and mass (1.4±0.14 g) of the predators did not differ among blocks (ANOVA, P=0.914 and P=0.882, respectively). Immediately after adding fish, and once a week thereafter, we slowly raised all enclosures (fish and fishless) out of the pools and then forced them back into the water to enhance water flow and chemical communication between the enclosures and the pools. Fish were not fed prior to, or during the experiment, but most likely consumed zooplankton. Five fish from five different pools died at some point during the experiment. These were not replaced because their death was not discovered until after the pools were drained.

H. squirella is the only anuran that uses experimental pools at GMBL and is the only *Hyla* heard calling on the property. On nights with heavy rain, we removed lids from all pools to permit *H. squirella* breeding. Every 2 h we assayed pools for amplectant pairs using a headlamp and recorded the number at each pool. This procedure took <5 min and did not appear to disturb oviposition behavior. This methodology could not determine if oviposition assessment behavior involved entering pools. Male calling site choice was not analyzed since approximately 50% of located males called from sites other than the experimental pools (other cattle tanks, trees, boats etc.) and thus could not be assigned to a specific treatment. This general lack of correlation between male calling and female oviposition sites has been documented for other *Hyla* (Resetarits and Wilbur 1991). Pools were recovered with the fiberglass mesh lids at sunrise after reproductive activity had ceased. We removed eggs later the same morning and placed them in separate containers (one for each pool) before transportation to the College of Charleston. Eggs were refrigerated and counted over the next several days. Complete removal of all eggs was impossible because *H. squirella* deposits eggs in small clusters, strings, or singly, and eggs sink as they are laid (personal observation). Thus, several times a week we checked for, removed and counted any remaining tadpoles using two different handheld dipnets (one for fish pools and one for fishless pools). Only a few individual tadpoles remained in several of the pools on the nights when oviposition occurred. The experiment was terminated on 6 August 1998.

We examined the effect of treatment (fish vs. fishless) and block on the number of amplectant pairs and number of eggs deposited. Response variable means were square root transformed to meet assumptions of normality and homogeneity of variances before being analyzed using ANOVA. Data were analyzed using SAS for Windows version 6.11 (SAS Institute 1994) with type III sums of squares and α=0.05.

Results

Due to limited precipitation, *H. squirella* bred on only three nights during July 1998. On nights when it rained, males began calling from the pools soon after sunset and their numbers increased throughout the night. Number of calling males peaked at approximately 0130 hours and declined thereafter. Amplectant pairs were never recorded before 0130 hours and number of mating pairs peaked at approximately 0330 hours. Male calling and female oviposition did not cease until sunrise.

The presence of *E. obesus* had dramatic effects on the reproductive behavior of female *H. squirella*. Significantly fewer amplectant pairs ($F_{1,7}$=68.1, P<0.0001) were recorded and eggs and tadpoles recovered ($F_{1,7}$=82.7, P<0.0001) from the fish pools than the fishless controls (Figs. 1, 2). There were no significant block effects ($F_{7,7}$=2.91, P=0.09 and $F_{7,7}$=2.57, P=0.12, respectively) for either of these response variables. A total of 27 amplectant pairs (90.0% of the total) were observed in the fishless pools, compared to three from pools containing *E. obesus* (Fig. 1). A total of 31,401 eggs and tadpoles, (94.8% of the total), were recovered from the fishless pools, compared with 1,727

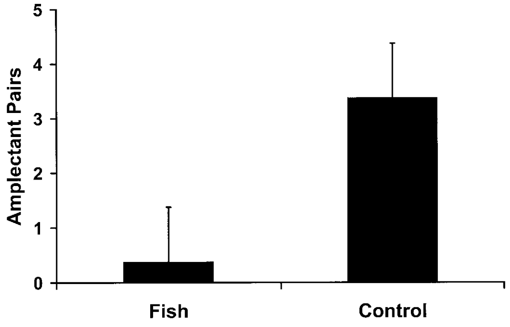

Fig. 1 Mean number (+1 SE) of amplexed *Hyla squirella* pairs recorded from pools containing *Enneacanthus obesus* and fishless controls

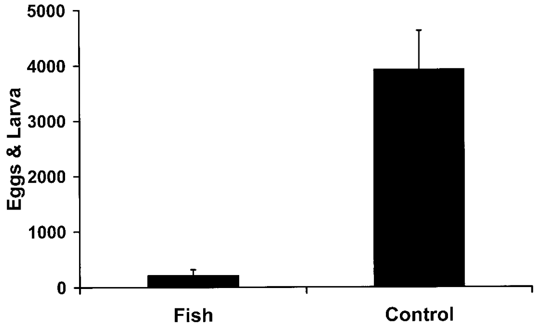

Fig. 2 Mean number (+1 SE) of *H. squirella* eggs and tadpoles recovered from pools containing *E. obesus* and fishless controls. *E. obesus* could not prey upon either eggs or tadpoles (see Materials and methods)

from pools containing *E. obesus* (Fig. 2). Most eggs were laid in predator pools during the third night of reproduction (83.4% of 1,727).

Discussion

E. obesus is a very effective predator on larval *H. squirella*, capable of eliminating it from experimental ponds (D. Chalcraft and W. J. Resetarits, unpublished data). *E. obesus* has also been shown to eliminate other species of *Hyla* (Kurzava and Morin 1998). Most North American *Hyla* species do not possess anti-predator mechanisms, such as noxious eggs and larvae or reduced activity and increased refuge use, that allow other anurans to persist with fish (Kats et al. 1988; Lawler 1989). Therefore, the presence of *E. obesus* at the time of oviposition is a reliable indicator of reproductive failure for *H. squirella* females, and avoidance should increase offspring survival and female fitness. The natural oviposition environment for *H. squirella* (with respect to fish predators) is highly dynamic and strongly spatially and temporally heterogeneous. Thus, the ability to detect and respond to such heterogeneity and discriminate among sites should be selected for versus indiscriminate oviposition or philopatry. In this experiment female *H. squirella* responded to the threat of predation by strongly avoiding pools containing *E. obesus*, depositing 94.8% of eggs in predator-free pools (Figs. 1, 2). Clearly, this is one of the strongest oviposition responses yet recorded for an amphibian.

These results expand on previous work on oviposition site selection in anurans and other amphibians in response to fish (e.g., Resetarits and Wilbur 1989; Kats and Sih 1992; Hopey and Petranka 1994; Holomuzki 1995; but see Laurila and Aho 1997) by clearly establishing that *H. squirella* can respond to the threat of predation in the absence of any physical interaction. Oviposition site choice thus provides an alternative mechanism to explain the negative correlations between fish presence and amphibian population density that are usually attributed to contemporary predation (Bradford 1989; Brönmark and Edenhamn 1994; Fisher and Shaffer 1996; Tyler et al. 1998; Azevedo-Ramos et al. 1999). Our findings clearly indicate that contemporary allopatric distribution patterns could be partly or entirely driven by female avoidance of predators, rather than strictly by direct predation, and that these avoidance behaviors need not require actual physical interaction.

Evolution of oviposition site choice requires heritable genetic variation in avoidance behavior, sensory capability to detect variation in aspects of the breeding environment that have positive or negative fitness effects, and reliable and exploitable variation in the factors themselves. Fish (Resetarits and Wilbur 1989; Werner and McPeek 1994), salamanders (Morin 1983), conspecifics (Wilbur 1997; Resetarits and Wilbur 1989), strong interspecific competitors (Morin 1987; Alford 1989; Morin et al. 1990; Lawler and Morin 1993) and parasites (Kiesecker and Skelly 2000) present in potential breeding ponds might be avoided if their presence is a reliable indication of reduced egg and larval survivorship. For example, salamander (*Ambystoma tigrinum*) larvae can eliminate entire populations of anurans from experimental pools (Morin 1983). Thus, this species should elicit a strong avoidance response in anurans as did *Ambystoma maculatum* in *Hyla chrysoscelis* (Resetarits and Wilbur 1989). The negative effects of both intraspecific and interspecific competition (Wilbur 1997; Morin 1987; Morin and Johnson 1988) as a result of breeding phenology and priority effects (Alford 1989; Morin et al. 1990; Lawler and Morin 1993) could also be ameliorated by oviposition site selection. *H. chrysoscelis* females avoided pools containing conspecific tadpoles just as strongly as they avoided a fish predator (Resetarits and Wilbur 1989), suggesting that the presence of conspecifics might not be used by females as a correlate for habitat safety or quality as documented in several mosquito oviposition studies (see Bentley and Day 1989 for review). However, the relative importance of predation versus competition in eliciting avoidance responses remains untested.

While only a handful of studies document oviposition site selection by anurans based on the biotic composition of the breeding site (Resetarits and Wilbur 1989; Crump 1991; Petranka et al. 1994; Hopey and Petranka 1994; Spieler and Linsenmaier 1997), it appears widespread both phylogenetically (Hylidae, Ranidae, Bufonidae, Dendrobatidae) and geographically (New World and Old World Tropics, New World Temperate). Its importance in structuring aquatic communities, however, is largely untested. Oviposition site selection can reduce the frequency of specific predatory and competitive interactions while increasing the frequency of an entirely different set of interactions, thus impacting the assembly of aquatic communities on the scale from individual ponds to larger regional landscapes (Resetarits, 2001). However, predicting larval distribution patterns at larger temporal and spatial scales requires viewing the choice of oviposition sites as a specific form of habitat selection.

Habitat selection models, such as the ideal free distribution (Fretwell and Lucas 1970; Fretwell 1972), or minimization of mortality rate/growth rate (Werner and Gilliam 1984), suggest that habitats (breeding ponds) with the highest potential fitness are chosen first, but as conditions change (increase in predator or competitor density), the use of alternative breeding sites will occur. For example, strong avoidance of ponds containing *E. obesus* by *H. squirella* could result in the saturation of primary breeding sites with conspecific larva. If these ponds elicit density-dependent avoidance behavior (Resetarits and Wilbur 1989), available breeding sites for *H. squirella* are reduced further. Reproduction might conceivably switch back to areas containing fish predators (eggs must be laid somewhere). But how many of these breeding compromises actually lead to the production of successful offspring? The resulting distribution pattern of oviposition might suggest lack of avoidance when in fact the mechanism of strong oviposition site choice is still operating, but compromised (see Rosenzweig 1985, 1986; Rosenzweig and Abramsky 1985). In addition, the quality of ephemeral breeding sites can be rapidly “reset” to higher values for ovipositing anurans as ponds dry and re-fill, and differences in effective hydroperiod can be detected by some species of anurans (Spieler and Linsenmaier 1997; but see Fegraus and Marsh 2000). Clearly, examining the role of oviposition site choice in community assembly should enhance our understanding of species diversity patterns in wetland and aquatic systems on a variety of spatial and temporal scales.

The mechanisms that structure anuran assemblages in aquatic ecosystems have become an ecological “model” for testing and generating hypotheses applicable to many biological communities (Wilbur 1997; Werner 1998; Resetarits and Fauth 1998). The common experimental design places varying densities of eggs and tadpoles in either microcosm, mesocosm or field enclosures under different levels of competition and/or predation. The responses of these life stages to treatments (e.g., Wilbur 1997), as well as associated costs of producing anti-predator defenses (e. g. Kats et al. 1988; Skelly 1995) are then quantified. Oviposition site choice is thus obviated. Such studies focus on elucidating the nature of species interactions. However, the critical choice defining the extent of species interactions may be made at the oviposition stage. Non-lethal effects of predators might largely explain variation in the distribution and abundance of larval anurans across a landscape of breeding sites. By incorporating oviposition site choice, we have now expanded and refined the scope of this model system to include adult female behavior, and thus gain a more complete picture of the assembly of natural communities.

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