Oviposition behavior partitions aquatic landscapes along predation and nutrient gradients

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That individuals attempt to minimize the ratio of mortality risk/growth rate (μ/g) when foraging within individual habitat patches is well established. Do species partition among spatially discrete communities embedded in complex landscapes in a similar manner? We investigated how 3 ovipositing species (2 *Hyla* treefrogs and a hydrophilid beetle, *Tropisternus lateralis*) responded to simultaneous gradients of nutrients and predation risk. Species partitioned our experimental metacommunity primarily by reducing oviposition with fish. *Tropisternus* positively responded to increased nutrients, but the effect decreased with increasing risk, as predicted by μ/g theory. Use of fish habitats by *Tropisternus* was unrelated to breeding intensity. In contrast, *Hyla* showed no nutrient response but oviposited with fish only on nights with high breeding activity. Behavioral responses to the spatial distribution of resources and risk among discrete patches generated substantial variation in habitat-specific colonization rates, which has been identified as a primary mechanism generating both community and metacommunity structure. *Key words:* colonization, dispersal, habitat selection, minimize μ/g, oviposition, predation risk. *[Behav Ecol 19:552–557 (2008)]*

How the movement of individuals, species, and materials across habitat boundaries affects ecological dynamics has become a major focus of research in ecology (Polis et al. 1997; Hanski 1999; Leibold et al. 2004; Loreau and Holt 2004). The importance of the metapopulation, metacommunity, and spatial subsidy themes in ecology collectively derives from the question of the independence, or interdependence, of what typically have been viewed as distinct communities. The metacommunity concept, for example, specifically examines how spatially discrete local communities are linked by dispersal and colonization of multiple species into larger functional units (Holyoak et al. 2005). Under this view, varying magnitudes of dispersal interact with internal community processes to produce both local community and metacommunity structure (Kneitel and Miller 2003). When emigration and immigration are driven by habitat selection rules, substantial variation in the degree to which communities are linked by dispersal can be generated by the nonrandom colonization of patches (Blaustein 1999; Morris 2003; Resetarits et al. 2005).

Habitat selection is a foraging process and is closely associated with optimal foraging and optimization theory (MacArthur and Pianka 1966; Charnov 1976; Rosenzweig 1991; Sutherland et al. 2001). Habitat selection models based on ideal free theory (Fretwell and Lucas 1970) predict that individuals increase their fitness by nonrandomly choosing habitats for feeding or reproduction (Moody et al. 1996; Sutherland 1996; Kiflawi et al. 2003). The most suitable habitat patches with the highest fitness payoff are colonized first until density dependence sufficiently alters the fitness landscape and forces colonization of secondary habitat types (Fretwell and Lucus 1970; Rosenzweig 1991). Factors that determine habitat suitability are diverse and include resources, predators, habitat complexity, and abiotic factors, the

relative importance of which vary within and among species (Sutherland 1996; Morris 2003). Habitat suitability may also be defined by ratios of factors, including combinations of resources and habitat-specific mortality risk (Moody et al. 1996).

Predators affect most decision-making processes of their prey (Lima and Dill 1990; Lind and Cresswell 2005). Incorporating predator-induced mortality into foraging models produces a general foraging rule, whereby individuals attempt to minimize ratios of mortality (μ) to growth rate (g) (minimize μ/g rule; see Werner and Gilliam 1984; Benard 2004; McPeek 2004). The ecological and evolutionary consequences of utilizing this rule have become a dominant research paradigm in both behavioral and theoretical ecology, and extensive evidence documents the ability of numerous species to minimize μ/g ratios when foraging (for reviews, see Dill 1987; Sih 1987; Lima and Dill 1990; Lima 1998). However, tests of this model are often conducted within the spatial confines of a single community, where predators, prey, and resources spatially co-occur. Whether spatially discrete patches are selected based on their ratio of mortality costs to resource gains and how these interact to influence reproductive decisions are 2 gaps in our understanding of how resources and risks affect decision making and the resulting community and metacommunity structure (Lima and Dill 1990; Lima 1998).

The discrete boundaries of small freshwater habitats (e.g., ponds, tree holes, rock pools, etc.) are ideal for examining processes relating to habitat selection, dispersal, and metacommunities (Resetarits et al. 2005). These systems often comprised of isolated patches linked to each other and to the surrounding terrestrial matrix by species with complex life cycles. The fauna contains the larval stages of many organisms that are (semi)terrestrial as adults or that must leave the water to complete their life cycle (Merritt and Cummins 1984; Duellman and Trueb 1986; Wilbur 1997). Persistence of these species depends on seasonal invasion and oviposition by dispersing adults. The challenge to colonizing/ovipositing species is to match correctly their own capabilities, or those of their offspring, to aspects of the habitat (Rauscher 1983;

Resetarits and Wilbur 1989; McPeek 1990; Blaustein 1999; Binckley and Resetarits 2002).

Colonization and oviposition behavior strongly affect the assembly of individual aquatic communities and are key processes linking communities across habitat boundaries and spatial scales in complex landscapes (Binckley and Resetarits 2003; Eitam and Blaustein 2004; Resetarits et al. 2005). We conducted an experiment quantifying oviposition site selection of 3 species (2 treefrogs and an aquatic beetle) in response to variation in resources and predation risk. These species are excellent model organisms for investigating habitat selection given their abundance and ability to rapidly colonize both natural and experimental ponds (Binckley and Resetarits 2005, 2007). We specifically hypothesized that ovipositing females would accept a greater risk, as indicated by ovipositing in ponds with fish predators, when resource levels (and hence growth potential) are elevated, and we examine the results in the context of habitat selection theory and the emerging paradigms of metacommunity ecology.

MATERIALS AND METHODS

Study organisms

This experiment, conducted at the Naval Security Group Activity Northwest (NSGANW) in Chesapeake, VA, examined how predators and nutrient addition affected oviposition in 2 species of anurans and an aquatic insect. *Hyla chrysoscelis* and *Hyla squirella* are terrestrial treefrogs that deposit eggs in ponds as floating surface rafts (*H. chrysoscelis*) or as small clusters or strings (*H. squirella*) after heavy rains during the late spring and summer. Eggs hatch into herbivorous larvae that forage in their natal pond until metamorphosing into terrestrial juveniles (Wilbur 1997). For *Hyla*, oviposition site selection is a specific form of habitat selection in which adults choose habitat for their offspring (Resetarits and Wilbur 1989; Blaustein 1999; Binckley and Resetarits 2003; Kiflawi et al. 2003; Eitam and Blaustein 2004). These species are 2 of the most abundant anurans on the Coastal Plain of Virginia, where the elevation (ca. 3–4 m above sea level), topography, and precipitation generate numerous wetlands.

Tropisternus lateralis is an abundant hydrophilid beetle with obligate aquatic adults, larvae, and egg cases (Zalom et al. 1979; Resetarits 2001). Adult dispersal occurs after an obligate terrestrial pupal stage along the periphery of ponds, and adults disperse aerially to ponds for feeding (adults are grazers/scavengers) and reproduction (Zalom et al. 1979). Females lay conspicuous silken egg cases (3–4 mm) containing 12–24 eggs that hatch into predacious larvae (Zalom et al. 1979; Resetarits 2001). Egg deposition occurs at our study site from early April to October with most occurring from June to August (Binckley CA, unpublished data). Females deposit many egg cases in a season (Young 1958); however, this number and the time interval between oviposition events are unknown. It is not clear if adults specifically select ponds for oviposition or simply deposit egg cases in the same localities they select for feeding (see Scheirs et al. 2004).

Experimental design and analysis

We established 54 experimental ponds using cattle watering tanks approximately 1.65 m in diameter, 0.61 m in depth, and 1000 l total volume. These experimental ponds are rapidly colonized by natural populations of anurans and aquatic insects for oviposition (Binckley and Resetarits 2005; Resetarits et al. 2005). Ponds were arranged into 6 rectangular blocks of 9 pools each, and tanks within a block were spaced approxi-

mately 1.5 m apart. Blocks were located approximately 30 m apart in 2 fields surrounded by hardwood and pine forest. The 2 fields were 0.5 km apart, 4 blocks were located in one field and 2 in the other. We covered all ponds with tight-fitting fiberglass mesh lids (mesh diameter 2 mm) to prevent premature colonization by anurans and aquatic insects and filled them with water pumped from a nearby creek on 29–30 May 2001. Ponds were allowed to settle for 2 days before 0.75 kg of dried leaf litter (red maple *Acer rubrum*, sweet gum *Liquidambar styraciflua*, and loblolly pine *Pinus taeda* leaves and needles) and 1.0 l aliquots of plankton collected from fishless temporary ponds were randomly added to each pool.

This experiment employed a 2-factor randomized complete block design for analysis of variance (ANOVA). Nine treatments were assigned randomly to the 9 ponds in each of the 6 blocks. Treatments consisted of crossing the nonlethal presence of 0, 3, or 6 adult *Enneacanthus obesus* (Centrarchidae) with 0, 10, or 20 g of nutrient addition (rabbit chow pellets, Forti-Diet). We did not quantify productivity, but periphyton and phytoplankton responded rapidly to nutrient addition and others have repeatedly demonstrated that comparable levels of nutrient addition strongly influence growth of larval anurans and aquatic insects (see Leibold and Wilbur 1992; Blaustein and Kotler 1993; Skelly et al. 2002).

Enneacanthus obesus is a known predator of hylid eggs and larva (Chalcraft and Resetarits 2004) and consumes a wide variety of larval and adult insects, including aquatic beetles (Graham 1986). During spring floods or hurricanes, *Enneacanthus* often invades the ephemeral wetlands used by *Hyla* and aquatic beetles for reproduction using an extensive network of natural creeks and drainage ditches (Binckley CA, personal observation). Thus, *Enneacanthus* is widespread and abundant at NSGANW, and densities used span the wide range of natural densities. Previous experiments have demonstrated that colonizing/ovipositing females of all 3 species avoid *Enneacanthus* (Binckley and Resetarits 2007).

Individuals of *E. obesus* were collected from small ponds at NSGANW using plastic minnow traps and were kept in 1000-l cattle watering tanks inoculated with zooplankton until the experiment began. Fish were stratified by body size among blocks, and average individual mass was 3.8 ± 1.3 g standard deviation ($n = 162$).

Predator/nutrient addition combinations were randomly assigned to pools in each block on 31 May 2001, and the experiment ran until 20 August 2001. On nights with heavy rain, we pushed all lids down into the water to permit access by the natural breeding populations of *Hyla* and *Tropisternus*. Screens eliminated physical interaction between fish and reproducing females and allowed ready collection of eggs and egg cases by simply raising the screens. The morning after rain events, we removed all eggs/egg cases, placed them in separate containers (one for each species at each pond), and did complete counts by hand for all 3 species. Ponds were recovered after collection of eggs/egg cases.

We examined the effect of block, nutrient addition, predator density, and the nutrient × predator interaction on 3 response variables: mean number of *H. chrysoscelis* eggs, *H. squirella* eggs, and *T. lateralis* egg cases. We performed univariate ANOVAs for each response variable using SAS for Windows version 8.0 with type III sums of squares and α = 0.05. This is a conservative analysis, but treating each night that any pond within any block received eggs as replicates to increase power did not change the results. In the absence of significant nutrient × predator interaction, all possible pairwise contrasts (thus nonorthogonal) among the levels of any significant main effect were examined (e.g., 0 vs. 3, 0 vs. 6, and 3 vs. 6 fish predators). All data were square root transformed (square root of $Y + 0.5$) before analysis. This normalized the data, but

considerable heterogeneity of variances persisted given that fish means were at or near zero. This did not affect the overall conclusions; thus, we utilized the transformed analysis common for count data such as ours.

Habitat selection theory predicts colonization of secondary habitat types as density increases in preferred patches (Fretwell and Lucas 1970; Sutherland 1996). We examined this prospect using regression of the number of eggs/egg cases deposited with fish (and low nutrients for *T. lateralis*) versus total number of eggs/egg cases for each night that oviposition occurred (e.g., number of data points equals the number of nights with oviposition). We did not analyze the *H. chrysoscelis* data given that reproduction occurred on only 4 nights.

Treating each pond as a single data point potentially masks any temporal changes in oviposition responses. Given that a time lag in the effect nutrients had on productivity and hence growth potential might have existed, we used correlation analysis to examine if our 3 species increased their proportional use of the 10- and 20-g treatments over the course of the experiment. We could not use repeated measures ANOVA as the number of eggs/egg cases deposited on each night of oviposition was sometimes only a single clutch resulting in zero values for most experimental units.

RESULTS

Hyla squirella bred on 9 nights depositing a total of 41 441 eggs, whereas 4 nights of *H. chrysoscelis* oviposition (all overlapping with *H. squirella*) produced 17 945 eggs. The 2 blocks located in the second field did not receive any treefrog eggs and were removed from analyses. For *Hyla*, only the block (*H. squirella*) and main effect of fish (both species) were significant in the ANOVAs (Table 1, Figure 1). There was no evidence that ovipositing treefrogs responded to one another (correlation between *Hyla* oviposition on night when both species reproduced, $r = -0.14$, $P = 0.71$), which is consistent with other observations (Binckley CA, unpublished data). Contrasts revealed that females avoided oviposition in experimental ponds containing *Enneacanthus*, as predator-free controls received significantly more eggs than those with 3 or 6 predators, which did not differ significantly from each other (Table 1, contrasts, Figure 1). Nutrient addition did not affect treefrog oviposition (Table 1, Figure 1) but resulted in rapid growth of periphyton on the walls of the experimental ponds and phytoplankton in the water column (Binckley CA, personal observation). *H. squirella* showed a classic, ideal free response to increasing oviposition activity, completely avoiding fish when oviposition activity was low ($\lesssim 4000$ eggs/night), but switching to use of both fishless and fish habitats at higher densities, with approximately 22% of eggs deposited with fish. The *H. squirella* data fit a 3-parameter sigmoidal function ($R^2 = 0.95$, $n = 9$; Figure 2).

A total of 405 *T. lateralis* egg cases were deposited on 8 nights of colonization/oviposition activity. In contrast to *Hyla*, *T. lateralis* females showed a strong response not only to fish but also to the gradient of nutrients (Figure 1). All effects were significant in the *T. lateralis* ANOVA including the 2-way fish × nutrient interaction term (Table 1). Significantly more egg cases were deposited in ponds with elevated nutrients, but these differences greatly decreased along the predator density gradient (Figure 1). Nutrient addition had the greatest effect in the absence of fish, caused a slight increase in the intermediate predator treatments, and had no effect at the highest predator level (Figure 1). *Tropisternus lateralis* females did not vary the proportion of egg cases deposited in patches with fish ($R^2 = 0.02$, $P = 0.72$, $n = 8$) or those without

Table 1

Univariate ANOVAs for the effect of block, predatory fish (0, 3, and 6 *Enneacanthus obesus*), nutrient addition (0, 10, and 20 g rabbit chow), and the fish × nutrient interaction on the number of *Hyla chrysoscelis* eggs, *Hyla squirella* eggs, and *Tropisternus lateralis* egg cases

Source	df	Sum of squares	Mean square	F	P
H. chrysoscelis					
Block	3	1369.3	456.4	2.12	0.1244
Fish	2	2768.6	1384.3	6.42	0.0058
Nutrient	2	239.2	119.6	0.56	0.581
Fish × nutrient	4	1671.2	417.8	1.94	0.1365
Error	24	5171.1	215.4		
Total	35	11 219.6			
Contrast					
0 versus 3 fish	1	2326.4	2326.4	10.80	0.0031
0 versus 6 fish	1	1791.6	1791.6	8.32	0.0082
3 versus 6 fish	1	34.8	34.8	0.16	0.6910
H. squirella					
Block	3	4270.4	1423.4	6.8	0.0018
Fish	2	9878.6	4939.3	23.6	<0.0001
Nutrient	2	97.8	48.9	0.2	0.7930
Fish × nutrient	4	837.1	209.2	1.0	0.4261
Error	24	5015.2	208.9		
Total	35	20 099.4			
Contrast					
0 versus 3 fish	1	7166.0	7166.0	34.2	<0.0001
0 versus 6 fish	1	7644.1	7644.1	36.5	<0.0001
3 versus 6 fish	1	7.7	7.7	0.04	0.8492
T. lateralis					
Block	5	33.1	6.6	5.6	0.0005
Fish	2	67.0	33.5	28.3	<0.0001
Nutrient	2	15.7	7.8	6.6	0.0032
Fish × nutrient	4	14.0	3.5	2.9	0.0312
Error	40	47.3	1.1		
Total	53	177.3			

Only the main effect of fish was significant for both *Hyla* species, and contrasts revealed that controls received significantly more eggs than any pond containing predators. All effects were significant for *T. lateralis* oviposition, most importantly the interaction term, indicating that *T. lateralis* deposited more egg cases at higher nutrient levels primarily in the absence of fish. df, degrees of freedom.

added nutrients ($R^2 = 0.10$, $P = 0.42$, $n = 8$) as the total number of egg cases increased (Figure 2).

For all 3 species, there was no evidence of proportional increase in use of ponds with added nutrients as the experiment progressed ($P > 0.18$ for all comparisons). This result held even when analyzing only the non-fish controls where most of the oviposition occurred ($P > 0.23$ for all comparisons). Thus, assessment of productivity was not affected by time.

DISCUSSION

How species behaviorally respond to variation in resources and risk has become a major focus of research in ecology (Brodin and Johansson 2004; McPeek 2004). Within the spatial confines of a single community, many species effectively minimize ratios of mortality to growth (μ/g) (Werner and Gilliam 1984; Lima 1998). An important issue is whether spatially discrete communities comprising potential metacommunities are behaviorally partitioned using similar rules. Our study represents the logical extension of a general paradigm from behavioral ecology to the landscape scale. Evidence that variation in both resources and risk, as well as the application of the minimize μ/g rule, affects habitat selection at this scale further underscores the importance of incorporating habitat selection into our consideration of both
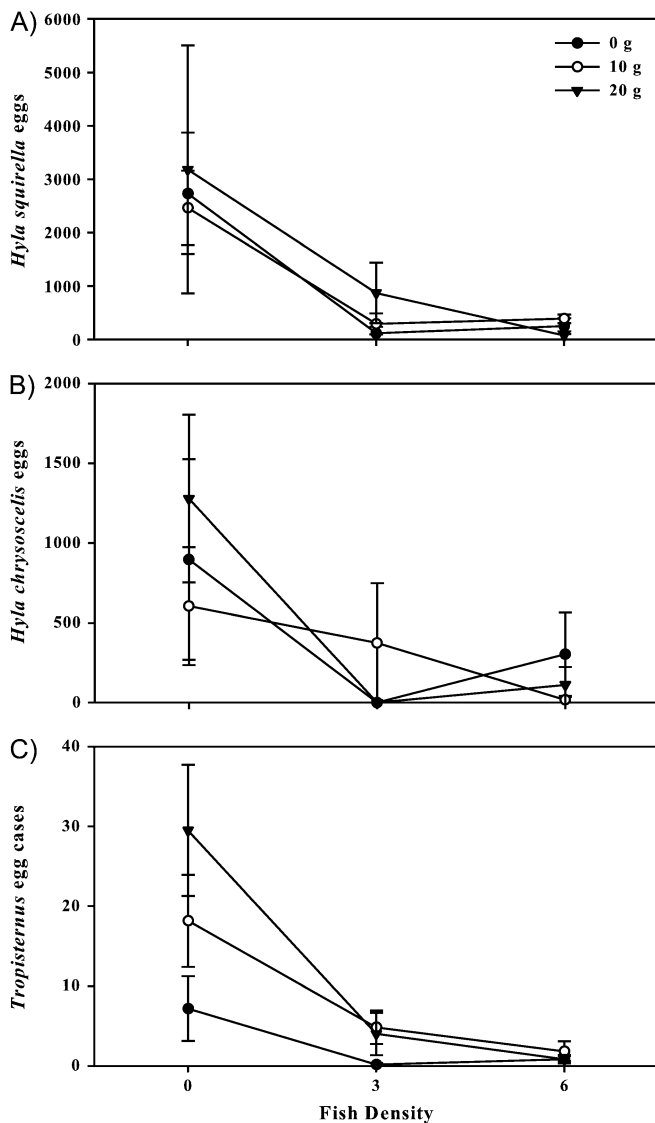
Figure 1
Effects of predator density and nutrient addition on oviposition site selection. (A) Mean number of *Hyla squirella* eggs, (B) *Hyla chrysoscelis* eggs, and (C) *Tropisternus lateralis* egg cases (± 1 standard error) at the 3 nutrient addition levels for each level of predator density. The fish × nutrient interaction and main effect of nutrient addition were not significant for either treefrog species, whereas the presence of fish significantly reduced oviposition. For both *Hyla* species, controls received significantly more eggs than the predator treatments, which did not differ from each other. In contrast, all effects in the model were significant for *T. lateralis* as most egg cases were deposited at 10 and 20 g of nutrient addition when fish were absent and fewer at intermediate predator densities but not at the highest predator abundance.

Figure 2
The proportion of (A) *Hyla squirella* eggs and (B) *Tropisternus lateralis* egg cases in fish treatments versus the total number of eggs for each night when reproduction occurred. (C) The proportion of *T. lateralis* egg cases oviposited at the 0-g nutrient level versus the total number of egg cases oviposited for each night when reproduction occurred. *Hyla squirella* switches to using fish habitats as egg density increases, matching the expectations of the ideal free distribution. In contrast, *T. lateralis* displayed no pattern in the proportion of egg cases placed in fish or low-nutrient habitats with increased egg case density.

community dynamics and the emerging paradigms of meta-community ecology (Holyoak et al. 2005; Leibold et al. 2004; Resetarits et al. 2005).

Our study contrasts responses in species with distinct differences in life history. Adult female *Hyla* spend little time at breeding sites, perhaps a single night/breeding season, and garner no resources from ponds. Predation risk to adults from fish predators is small, except in bodies of water containing fish much larger than *Enneacanthus*. Thus, adults appear to make choices based primarily on consequences for their offspring. This is supported by oviposition responses to other predators
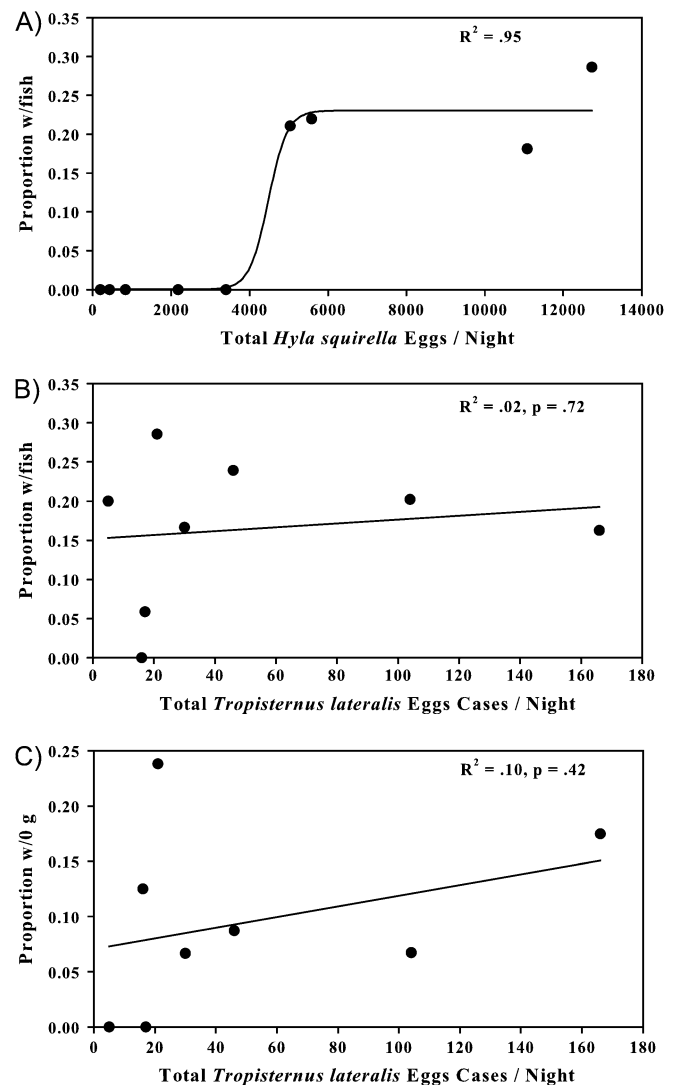
that pose no threat to adults (Resetarits and Wilbur 1989). In contrast, *Hyla* larvae are strongly affected by both variation in resources and risk of fish predation. Increased nutrients should potentially offset the growth cost of oviposition in fish-free ponds that have a strong competitive environment such that high-nutrient/no-fish pools should theoretically maximize larval performance. However, ovipositing treefrogs did not respond to variation in resources, which was surprising considering that nutrient addition has consistently been shown to positively affect larval anuran performance (see Leibold and Wilbur 1992; Skelly et al. 2002). Ovipositing *Hyla* either are incapable of detecting variation in resources or simply do not respond. Responses were very strong to the presence of fish; distribution of *Hyla* eggs was thus exclusively driven by perceived predation risk through females applying

a "minimize mortality" rule (see also Eitam and Blaustein 2004; Rieger et al. 2004).

In the context of habitat selection, presence/absence of predatory fish provides reliable and immediate information concerning mortality, given the limited ability of fish to disperse among ponds. Absence of fish during the breeding season is a good indicator of long-term conditions, corresponding to a low probability that fish will invade later and thus obviate the fitness advantages of selecting fish-free ponds (Resetarits and Wilbur 1989; Resetarits 1996). The only observed concession to potential variation in resource availability was the observed increase in the proportion of eggs laid in pools with fish on nights when breeding activity was high (Figure 2), sensu the ideal free distribution (Fretwell and Lucas 1970; see Kiflawi et al. 2003). Adult *Hyla* avoid conspecific larvae (Resetarits and Wilbur 1989), and perhaps, intraspecific density is a more reliable, or accessible, cue to larval performance than nutrient concentrations. However, our species avoid ponds that are heavily shaded (Binckley and Resetarits 2007), and avoidance of fish predators, typically associated with longer hydroperiod ponds, places many ovipositing species into highly productive, ephemeral water bodies (Odum et al. 1995; Palik et al. 2001) without specifically having to search for these sites.

In contrast, *T. lateralis* responded to both resources and predation risk as predicted by theory. More egg cases were deposited at higher nutrient levels in the absence of fish predators, and the importance of nutrient addition declined with increasing predator abundance (Figure 1). Female mosquitoes (*Culiseta longiareolata*) show a similar response, increasing oviposition in ponds with predatory tadpoles when aquatic resource levels are elevated (Blaustein and Kotler 1993). Yet, despite the significant response of adult *T. lateralis* to variation in nutrient levels, fish clearly dominate oviposition decisions (Table 1, Figure 1).

Both adult and larval *T. lateralis* are obligately aquatic, only leaving ponds for pupation and subsequent adult dispersal flights. However, because of differences in life history, pond conditions affect fitness by generating variation in both adult and larval growth and survival. Females may deposit egg cases in the habitats where they choose to feed (Mayhew 2001; Scheirs et al. 2004) or may specifically seek out sites most suitable for their offspring. Clearly, moving among sites specifically to increase egg/larval survivorship at the cost of adult performance elevates both metabolic and potential mortality costs.

Another informative contrast is the difference in observed responses to increased colonization/oviposition activity. Unlike *H. squirella*, adult *T. lateralis* relegates a highly variable proportion of total breeding activity to "poorer" habitats, unrelated to overall breeding activity (Figure 2). Thus, rather than following an ideal free distribution, the behavior of *T. lateralis* suggests 1) a random error rate by colonizing females, 2) population-level variation in colonization strategy, with certain females actually choosing fish or low-nutrient habitats, 3) a bet-hedging strategy by individual females that lay eggs in different habitat types on different nights, or 4) egg cases simply never reached critical density to induce habitat switching. It is unlikely that individual females laid egg cases in multiple ponds on a given night because they cannot readily redisperse after initially choosing a pond, even if that pond proves to be poor habitat (Resetarits 2001). Which mechanism drives the proportion of egg cases in habitats with predatory fish or low nutrients is unknown.

In its original context, body size was a key parameter in μ/g models as smaller individuals are predicted to require larger "rewards" at any given risk level compared with larger conspecifics (Sih 1982; Werner and Gilliam 1984). The egg stages of our focal species represent their smallest, most vulnerable,

size classes, suggesting that a substantial reward must be available if parents are to modify oviposition site selection along a predation gradient. If large body size differentials between oviposited prey and predators are common, oviposition site selection following a minimize μ/g rule actually should be rare. This may explain the differences in response to nutrients by our focal species. If *Hyla* choose habitats for their offspring based on expectations of the μ/g model, whereas *T. lateralis* choose habitats (at least partially) for themselves, we would expect different responses to resource variation based on where the 2 body size classes fall on the μ/g curve. Clearly, companion studies are needed examining whether female habitat/oviposition preferences match larval and/or adult performance.

A general avoidance of predatory fish by all species, the finer ability of *T. lateralis* to subdivide metacommunities along a second (nutrient) gradient, and species-specific differences in responses to intraspecific density generate substantial variation in patterns of species distribution, community structure, and patch connectivity simply based on the dynamics of habitat selection behavior. Habitat selection is clearly responsive to a broader array of environmental conditions, thus creating the potential for complex behavioral interactions that can have major implications for the structure of communities at both the local and the regional scale (Resetarits and Wilbur 1989; Blaustein 1999; Morris 2003; Resetarits et al. 2005). However, metacommunity ecology currently lacks a mechanistic understanding of how different dispersal/colonization strategies differentially affect community and metacommunity structure (Holyoak et al. 2005; Resetarits et al. 2005). Quantifying how rates of colonization are driven by variation in habitat quality and the resulting differences in the magnitude of mass effects driven by lethal (differential mortality) versus nonlethal (habitat selection) determination of species distributions and abundances will be critical for developing a truly comprehensive and predictive understanding of both community and metacommunity structure. Just as behavioral assessment of the distribution of resources and risk among habitats within a single community is critical for determining the local distribution of organisms (Werner and Gilliam 1984; Lima 1998), behavioral assessment of resources and risk among discrete communities within larger metacommunities is likewise critical in determining the regional distribution of organisms.

REFERENCES

Benard MF. 2004. Predator-induced phenotypic plasticity in organisms with complex life histories. Annu Rev Ecol Syst. 35:651–673.

Binckley CA., Resetarits WJ Jr. 2002. Reproductive decisions under threat of predation: squirrel treefrog *Hyla squirella* responses to banded sunfish *Enneacanthus obesus*. Oecologia. 130:157–161.

Binckley CA, Resetarits WJ Jr. 2003. Functional equivalence of nonlethal effects: generalized fish avoidance determines distribution of gray treefrog, *Hyla chrysoscelis*, larvae. Oikos. 102:623–629.

Binckley CA, Resetarits WJ Jr. 2005. Habitat selection determines abundance, richness and species composition of beetles in aquatic communities. Biol Lett. 1:370–374.

Binckley CA, Resetarits WJ Jr. 2007. Effects of forest canopy on habitat selection in treefrogs and aquatic insects: implications for communities and metacommunities. Oecologia. 153:951–958.

Blaustein L. 1999. Oviposition site selection in response to risk of predation: evidence from aquatic habitats and consequences for population dynamics and community structure. In: Wasser SP, editor. Evolutionary theory and processes: modern perspectives. Dordrecht (NL): Kluwer. p. 441–456.

Blaustein L, Kotler BP. 1993. Oviposition habitat selection by the mosquito *Culiseta longiareolata*: effects of conspecifics, food and green toad tadpoles. Ecol Entomol. 18:104–108.

Brodin T, Johansson F. 2004. Conflicting selection pressures on the growth/predation-risk trade-off in a damselfly. Ecology. 85:2927–2932.

Chalcraft DR, Resetarits WJ Jr. 2004. Metabolic rate models and the substitutability of predator populations. J Anim Ecol. 73:323–332.

Charnov EL. 1976. Optimal foraging: the marginal value theorem. J Theor Popul Biol. 9:129–136.

Dill LM. 1987. Animal decision making and its ecological consequences: the future of aquatic ecology and behaviour. Can J Zool. 65:803–811.

Duellman WE, Trueb L. 1986. Biology of amphibians. Baltimore (MD): Johns Hopkins University Press.

Eitam A, Blaustein L. 2004. Oviposition habitat selection by mosquitoes in response to predator (*Notonecta maculata*) density. Physiol Entomol. 29:188–191.

Fretwell SD, Lucas HL Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheor. 19:16–36.

Graham JH. 1986. Niche ontogeny and progressive deviation in two congeneric sunfishes, *Enneacanthus obesus* and *E. gloriosus* (Centrarchidae) [PhD Thesis]. New Brunswick (NJ): Rutgers University. p. 66.

Hanski I. 1999. Metapopulation ecology. Oxford: Oxford University Press.

Holyoak M, Leibold MA, Holt RD. 2005. Metacommunities: spatial dynamics and ecological communities. Chicago (IL): University of Chicago Press.

Kiflawi M, Blaustein L, Mangel M. 2003. Oviposition habitat selection by the mosquito *Culiseta longiareolata* in response to risk of predation and conspecific larval density. Ecol Entomol. 28:168–173.

Kneitel JM, Miller TM. 2003. Dispersal rates affect species composition in metacommunities of *Sarracenia purpurea* inquilines. Am Nat. 162:165–171.

Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt RD, Shurin JB, Law R, Tilman D, et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecol Lett. 7:601–613.

Leibold MA, Wilbur HM. 1992. Interactions between food-web structure and nutrients on pond organisms. Nature. 360:341–343.

Lima SL. 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. Adv Study Behav. 27:215–290.

Lima SL, Dill LM. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool. 68:619–640.

Lind J, Cresswell W. 2005. Determining the fitness consequences of antipredation behavior. Behav Ecol. 16:945–956.

Loreau M, Holt RD. 2004. Spatial flows and the regulation of ecosystems. Am Nat. 163:606–615.

MacArthur RH, Pianka ER. 1966. On optimal use of a patchy environment. Am Nat. 100:603–609.

Mayhew PJ. 2001. Herbivore host choice and optimal bad motherhood. Trends Ecol Evol. 16:165–167.

McPeek MA. 1990. Determination of species composition in the *Enallagma* damselfly assemblages of permanent lakes. Ecology. 71:83–89.

McPeek MA. 2004. The growth/predation risk trade-off: so what is the mechanism? Am Nat. 163:E88–E111.

Merritt RW, Cummins KW. 1984. An introduction to the aquatic insects of North America. Dubuque (IA): Kendall/Hunt.

Moody AL, Houston AI, McNamara JM. 1996. Ideal free distributions under predation risk. Behav Ecol Sociobiol. 38:131–143.

Morris DW. 2003. Toward an ecological synthesis: a case for habitat selection. Oecologia. 136:1–13.

Odum WE, Odum EP, Odum HT. 1995. Nature's pulsing paradigm. Estuaries. 18:547–555.

Palik B, Batzer DP, Buech R, Nichols CK, Egeland L, Streblow DE. 2001. Seasonal pond characteristics across a chronosequence of adjacent forest ages in Northern Minnesota, USA. Wetlands. 21:532–542.

Polis GA, Anderson WB, Holt RD. 1997. Toward and integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annu Rev Ecol Syst. 28:289–316.

Rausher MD. 1983. Ecology of host-selection behavior in phytophagous insects. In: Denno RF, McClure MS, editors. Variable plants and herbivores in natural and managed systems. New York: Academic Press. p. 223–257.

Rieger JF, Binckley CA, Resetarits WJ Jr. 2004. Larval performance and oviposition site preference along a predation gradient. Ecology. 85:2094–2099.

Resetarits WJ Jr. 1996. Oviposition site choice and life history evolution. Am Zool. 36:205–215.

Resetarits WJ Jr. 2001. Experimental evidence that past predation affects community assembly: fish avoidance in a colonizing/ovipositing aquatic beetle. Oecologia. 129:155–160.

Resetarits WJ Jr., Binckley CA, Chalcraft DR. 2005. Habitat selection, species interactions, and processes of community assembly in complex landscapes: a metacommunity perspective. In: Holyoak M, Leibold MA, Holt RD, editors. Metacommunities: spatial dynamics and ecological communities. Chicago (IL): University of Chicago Press. p. 374–398.

Resetarits WJ Jr, Wilbur HM. 1989. Choice of oviposition site by *Hyla chrysoscelis*: role of predators and competitors. Ecology. 70:220–228.

Rosenzweig ML. 1991. Habitat selection and population interactions: the search for mechanism. Am Nat. 17:s5–s28.

Scheirs J, Zoebisch TG, Schuster DJ, Bruyn LD. 2004. Optimal foraging shapes host preference of a polyphagous leafminer. Ecol Entomol. 29:264–272.

Sih A. 1982. Foraging strategies and the avoidance of predation by an aquatic insect, *Notonecta hoffmanni*. Ecology. 63:786–796.

Sih A. 1987. Predators and prey lifestyles: an evolutionary and ecological overview. In: Kerfoot WC, Sih A, editors. Predation: direct and indirect impacts on aquatic communities. Hanover (NH): University Press of New England. p. 203–224.

Skelly DK, Freidenburg LK, Kiesecker JM. 2002. Forest canopy and the performance of larval amphibians. Ecology. 83:983–992.

Sutherland WJ. 1996. From individual behaviour to population ecology. Oxford: Oxford University Press.

Sutherland WJ, Gill JA, Norris K. 2001. Density dependent dispersal in animals: concepts, evidence, mechanisms and consequences. In: Bullock JM, Kenward RE, Hails RS, editors. Dispersal ecology. Oxford: Blackwell. p. 134–151.

Werner EE, Gilliam JF. 1984. The ontogenetic niche and species interactions in size-structured populations. Annu Rev Ecol Syst. 15: 393–425.

Wilbur HM. 1997. Experimental ecology of food webs: complex systems in temporary ponds. Ecology. 78:2279–2302.

Young FN. 1958. Notes on the care of rearing *Tropisternus* in the laboratory (Coleoptera: Hydrophilidae). Ecology. 39:166–167.

Zalom FG, Grigarick AA, Way MO. 1979. Habits and relative population densities of some Hydrophilids in California rice fields. Hydrobiologia. 75:195–200.