

Spatial contagion of predation risk affects colonization dynamics in experimental aquatic landscapes

WILLIAM J. RESETARITS, JR.,¹ AND CHRISTOPHER A. BINCKLEY

Department of Ecology, Evolution and Natural Resources, Rutgers University, New Brunswick, New Jersey 08901 USA

Abstract. Colonization rate is a critical factor determining abundance and diversity in spatially distinct communities. Beyond simple variation driven by random processes, many species select/avoid habitat patches based on variation in habitat quality. Perceived habitat quality and colonization dynamics of individual patches may be influenced by specific characteristics of neighboring patches. We demonstrate that abundance and diversity of colonizing aquatic beetles is a function of both spatial variation in predator presence/absence and risk contagion generated by the proximity of predator patches to predator-free patches. Spatial contagion of predation risk generated repulsive sources: high fitness patches that were avoided. Thus, colonization dynamics of spatially discrete communities depends not only on intrinsic patch characteristics, but on the specific characteristics of nearby patches. The landscape-level dynamics of communities and metacommunities, as well as the efficacy of habitat restoration and conservation efforts, depends on how habitat quality is assessed, correctly or incorrectly, by colonizing species.

Key words: aquatic beetles; attractive sinks; colonization; ecological trap; experimental landscapes; habitat selection; maladaptive habitat selection; metacommunities; repulsive sources; risk contagion.

INTRODUCTION

Differential rates of colonization and extinction are key factors determining local biological diversity and community structure (MacArthur and Wilson 1967, Hamilton and May 1977, Wellborn et al. 1996, Leibold et al. 1997, Holt and Barfield 2001, Shurin and Allen 2001, Kneitel and Miller 2003). For species capable of habitat selection, theory predicts colonization rates will match variation in habitat quality (Fretwell and Lucas 1970, Pulliam and Danielson 1991, Resetarits 1996, Morris 2003, Resetarits et al. 2005). The critical first step in habitat selection is assessment of the quality (expected fitness) of available habitat patches. Failure to correctly identify spatial variation in habitat quality can transform adaptive habitat selection behavior into fitness neutral or even maladaptive behaviors as a consequence of mismatch between life history phenotype and habitat characteristics (Resetarits 1996). Because individual habitat patches are often clustered, and clusters may contain habitats of different types, perceived habitat quality and resulting colonization dynamics may be directly influenced by the quality of neighboring patches (Resetarits et al. 2005).

Habitat selection models predict that the expected fitness in a given patch, hence its attractiveness to

colonists, is relative to both the inherent quality of a patch and intraspecific density (Fretwell and Lucas 1970, Morris 2003). Thus, patch quality has been viewed as an intrinsic property, even though habitat patches are scattered across larger ecological landscapes in differing densities and proximities to patches of differing habitat types (Fretwell and Lucas 1970, Kennedy and Gray 1993). Assessment of habitat quality necessarily involves cues that serve as indirect indicators of expected performance, and can therefore be complex (Schlaepfer et al. 2002). In addition, habitat context plays an important role in assessing habitat quality. For example, a variety of colonizing/ovipositing species strongly prefer fishless patches over patches containing fish; however, that effect is obviated if fishless ponds occur under closed canopy (Binckley and Resetarits 2007). Similarly, multiple intrinsic factors may interact in determining perceived habitat quality and resulting colonization rate, including ratios of resources to risk. Mosquitoes (*Culiseta longiareolata*) increase their oviposition with predatory tadpoles at increased resource levels (Blaustein and Kotler 1993) and *Tropisternus lateralis* (an aquatic hydrophilid beetle) responds positively to increased productivity, but the strength of the response sharply decreases with increasing density of predatory fish (Binckley and Resetarits 2008). Colonizers may also make habitat decisions at both local (among patches) and regional (among sets of patches) scales (Resetarits 2005), setting up potential conflict between habitat selection operating at different spatial scales (Kneitel and Chase 2004).

Manuscript received 31 March 2008; revised 18 September 2008; accepted 6 October 2008; final version received 20 November 2008. Corresponding Editor: S. P. Lawler.

¹ Present address: Division of Environmental Biology, National Science Foundation, 4201 Wilson Boulevard, Arlington, Virginia 22230 USA. E-mail: wresetar@nsf.gov

The question we address here is whether characteristics of discrete habitat patches themselves affect the perceived quality and colonization rate of other nearby patches in the absence of any changes in actual habitat quality in the latter. Such spatial risk (or conversely, reward) contagion could lead to maladaptive habitat selection, wherein the perceived quality of habitats does not match their actual quality (Remes 2000, Delibes et al. 2001a, b, Resetarits 2005). If low-quality patches negatively affect the perceived quality and resulting colonization dynamics of adjacent high-quality sites, the effective amount of high-quality habitat is reduced by the formation of repulsive sources. Conversely, reward contagion could increase the perceived value of low-quality patches surrounded by high-quality habitats, producing attractive sinks (Remes 2000, Delibes et al. 2001a, b). Spatial contagion could thus generate natural ecological traps, wherein species colonize habitats of lower fitness as a result of the mismatch between perceived and actual habitat quality (Dwernychuk and Boag 1972, Schlaepfer et al. 2002). Such interactions among patches could generate landscape-level variation among communities in abundance, species composition, and levels of biodiversity (Resetarits et al. 2005).

Recent work in aquatic systems has identified habitat selection as an alternative to species sorting based on differential mortality as a determinant of community structure (Resetarits and Wilbur 1989, Blaustein 1999, Kiflawi et al. 2003, Binckley and Resetarits 2005, 2007, 2008, Resetarits 2005, Vonesh and Buck 2007). Thus, identifying factors affecting the choice of alternative habitats is central to bringing a clear understanding of the role of behavior in the formation of natural communities, as well as informing us as to how best to integrate behavior into community and metacommunity models (Resetarits et al. 2005, Abrams et al. 2007). The potential importance of habitat selection in response to species composition is underscored by recent work showing the impact of colonization history on community structure, ecosystem function, and species diversification (Travisano et al. 1995, Chase 2003, Fukami and Morin 2003, Price and Morin 2004, Fukami et al. 2007).

We conducted an experiment that allowed us to test for the presence of risk contagion by examining how aquatic beetles respond to the presence/absence of predatory fish within patches, and whether the proximity of predator patches to those lacking predators reduced their perceived quality and resulting colonization rates. This experiment was originally designed to examine the relative effects of habitat quality vs. quantity on colonization rate and species richness in the context of metacommunity ecology, and an extensive analysis of this issue is forthcoming. Here we focus on a poorly documented aspect of responses of colonizing species to the specific characteristics of individual patches, namely, habitat contagion. We specifically examined whether the colonization dynamics of a diverse assemblage of beetles representing the two most

common aquatic families depends on both landscape-scale spatial variation in predator presence/absence among patches and on the proximity of predators to predator-free patches.

MATERIALS AND METHODS

Typical habitats for a variety of aquatic organisms in our study area are quite small, ranging from $<1 \text{ m}^2$ to a few square meters, and number in the thousands as a result of low elevation and little topography. Such small habitats are important to a variety of species (Semlitsch and Bodie 1998) and individual ponds are capable of supporting a diverse array of aquatic organisms (e.g., aquatic beetles; Matta 1979, Schneider and Frost 1996). Pond frequency/density declines with increasing pond size as is typical of many landscapes (Semlitsch and Bodie 1998). However, limited topographic variation does not mean that these habitats are all interconnected. Even topography of a few centimeters can isolate habitat patches from one another resulting in a mosaic pattern of habitat patches and patterns of potential interconnection that vary with the amount and timing of rainfall events. Thus, certain sets of patches may reliably connect during wet conditions, while others remain reliably isolated, even at distances of a meter or less.

A diverse array of adult aquatic beetles colonize our experimental ponds from early spring to late fall (Binckley and Resetarits 2005, 2007, *in press*), arriving from the myriad aquatic habitats surrounding our experimental site. Most beetles at our study site are predaceous diving beetles (Dytiscidae), with carnivorous adults and larvae, or water scavenger beetles (Hydrophilidae), with primarily omnivorous or herbivorous adults (grazer/scavengers) and carnivorous larvae. They feed and reproduce in water, but initially disperse (fly) to new ponds from terrestrial pupation sites and can abandon a site if conditions change dramatically (Zalom et al. 1979, Layton and Voshell 1991, Sheldon 1992), though individuals (especially females) of some species metabolize flight muscles to fuel reproduction and/or the development of swimming muscles (Johnson 1969), which limits their vagility among sites. It is important to note that adult beetles, unlike many other taxa with complex life cycles (e.g., amphibians, odonates, dipterans), colonize aquatic habitats both for themselves and their offspring (Resetarits 2001).

We established four circular experimental landscapes, each containing six unique localities (combinations of number and type of patch). Each landscape contained 21 discrete patches (each patch was a 1000-L tank that simulated a small pond) distributed among the six localities (Fig. 1). We specifically examine responses to three types of patches: predator-free, predator-associated, and predator-present (Fig. 1), while controlling for variation in the number of patches per locality because predator-present and predator-associated patches can occur in localities with greater total patch number. The number of available tanks and limits on physical size of

arrays prohibited controlling for the alternative that predator-free patches enhanced the perceived quality of patches containing predators.

Each locality consisted of aggregations of all predator-free patches, or predator-present and predator-free patches in a 50/50 ratio. Predator-free localities held 1, 2, or 4 patches; mixed localities held 2, 4, or 8 patches, one-half with predators and one-half without. Patches within localities were separated by 1 m; localities were separated by 13 m. The layout of our experimental landscape captures the spatial dynamics of the habitat choices made by aquatic beetles on our coastal plain sites, at least at the local (among patches) and regional (among localities) scales defined here. Clearly the use of unburied cattle tanks exaggerates the isolation of individual patches from cross-flooding, but it does capture the essential nature of the kinds of clustered, discrete habitat patches we see, and allows us the necessary control over who can colonize (flying insects and treefrogs).

All landscapes were placed in a large mowed old field surrounded by hardwood and pine forest adjacent to a remnant arm of the Great Dismal Swamp in Chesapeake Virginia, USA. Individual patches (mesocosms) were set up using established protocols (Binckley and Resetarits 2005, 2007). On 8 July we covered ponds with a tight-fitting fiberglass screen (2 mm²) to prevent premature colonization by insects and filled pools with water pumped (through fine-mesh screen) from a nearby borrow pit. Two days later, we added randomized aliquots of 0.4 kg of dried leaf litter and 1.0 L of pond water containing concentrated zooplankton and phytoplankton collected from nearby ponds. On 10 July, five predators (banded sunfish, *Enneacanthus obesus*, ~4.5 g each) were placed under screens and screens were pushed underwater in all tanks allowing colonization. This procedure eliminates physical interactions between predators and colonizing organisms, but allows chemical communication and a complete inventory of all but the smallest colonizing beetles. Beetles were collected from the pools on 27 July using dip nets, preserved in ethanol, identified to species (at the Smithsonian Institution using voucher specimens from Chesapeake, Virginia) and counted.

Data analysis.—We analyzed mean number of beetles/patch and mean species richness/patch in separate univariate ANOVAs with landscape (block), number of focal patches/locality, and patch type as our factors. We also analyzed species richness using abundance as a covariate (ANCOVA) to examine the possible dependence of richness effects on abundance. Treatment means were compared using Fisher's Protected LSD following significant main effects. We examined the correlation between beetle abundance and species richness at the patch level, and we analyzed abundance by patch for each of the eight most numerous beetles (all species with >200 total colonists), using univariate ANOVAs and Fisher's LSD. All analyses used SAS

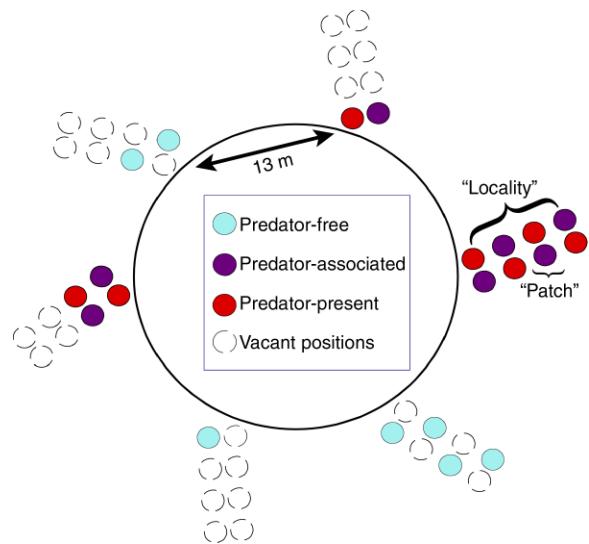


FIG. 1. Diagram of one of four experimental landscapes. Patches were separated by 1 m. Patch number varied among localities to allow assessment of the relative importance of habitat quality and habitat quantity (W. J. Resetarits, Jr., and C. A. Binckley, *unpublished manuscript*).

version 9.1 (SAS Institute 2003) with Type III sums of squares and $\alpha = 0.05$.

RESULTS

Our experiment was colonized by 7299 individuals of 34 species of aquatic beetles: 4588 individuals of 20 species of Dytiscidae, 2696 individuals of 11 species of Hydrophilidae, and one species each of Noteridae (1 individual), Halplidae (2 individuals), and Hydraenidae (12 individuals) (Fig. 2).

Predator location significantly affected both mean beetle abundance/patch (ANOVA, $F_{2,72} = 48.68$, $P < 0.0001$) and mean species richness/patch ($F_{2,72} = 60.55$, $P < 0.0001$) (see Fig. 3). Patches with predators had the fewest beetles, while predator-associated patches were intermediate and significantly different from both predator-present and predator-free patches in mean abundance/patch (Fig. 3a). Species richness in predator-associated patches was significantly lower than predator-present patches, but did not differ from predator-free patches (Fig. 3b). This is because the mean number of beetles/patch was high on the species saturation curve for both predator-free and predator-associated patches (Fig. 3c). An ANCOVA with abundance as covariate confirmed that richness increases were independent of abundance, and results, including effects of patch type ($F_{2,71} = 15.37$, $P < 0.0001$), were unchanged despite the highly significant abundance effect ($F_{1,71} = 150.68$, $P < 0.0001$).

Number of patches per locality did not affect beetle abundance/patch or species richness/patch (abundance, $F_{2,72} = 0.37$, $P = 0.694$; species richness, $F_{2,72} = 0.38$, $P = 0.6825$; Fig. 3a, b), but there was a significant predator

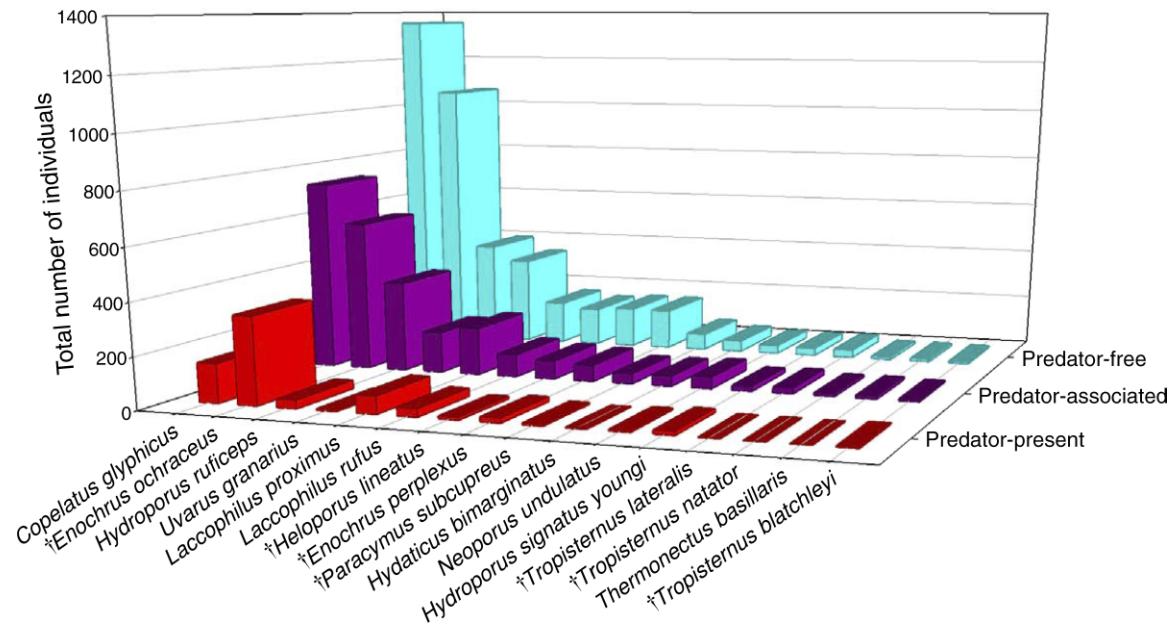


FIG. 2. Total number of colonists of the 16 most abundant beetles (\dagger , Hydrophilidae; others, Dytiscidae) across the three patch types.

treatment \times patch number interaction for species richness ($F_{4,72} = 2.51$, $P = 0.0491$; Fig. 3b). Interestingly, the interaction appears to derive from a change in the relative difference between colonization rates of predator-present and predator-associated patches in localities with four mixed patches vs. two or eight mixed patches; the cause of which is not immediately obvious. Block (landscape) was highly significant for abundance ($F_{3,72} = 10.37$, $P < 0.0001$), but not significant for species richness ($F_{3,72} = 1.39$, $P = 0.2539$).

Six of the eight most numerous species showed significant risk contagion, with abundance in predator-associated sites intermediate between predator-present and predator-free patches (main effect of predators, all $P < 0.02$; Fig. 4). For the two remaining species, *Hydroporus ruficeps* and *Laccophilus proximus*, predator-free and predator-associated were equally preferred over predator-present patches (Fig. 4). In contrast, there were no significant effects of patch number (all $P > 0.24$) or any predator \times patch number interaction (*Heloporus lineatus*, $P = 0.0621$, all others, $P > 0.23$) (Fig. 4). Thus, variation in the number of patches/locality did not affect the colonization rate of individual patches, as observed for the overall beetle response. Responses of six species are straightforward; however, responses of *L. proximus* and *H. lineatus* (Fig. 4e, g) both suggest additional complexities.

Both dytiscids and hydrophilids demonstrated avoidance of predator-present and predator-associated patches (Fig. 3d), and individual species in both families demonstrated a pattern of risk contagion (Figs. 2 and 4). Two congeneric species pairs were included among the eight most abundant species. *Enochrus ochraceus* and *E.*

perplexus showed a very similar pattern of response, with both demonstrating risk contagion (Fig. 4b, h), while *Laccophilus proximus* and *L. rufus* showed contrasting patterns; both species avoided predators, but only *L. rufus* showed contagion (Fig. 4e, f).

DISCUSSION

Here, in a complex experimental landscape colonized by natural populations of a diverse assemblage of aquatic beetles, we show that colonization dynamics depends on both spatial variation in predator presence/absence within discrete habitat patches, and on risk contagion generated by the proximity of predator patches to predator-free patches. Perceived habitat quality was directly influenced by characteristics of neighboring patches (Figs. 1, 3, and 4) independent of changes in actual habitat quality and expected fitness, thus generating strikingly different patch-specific colonization rates, community structure, and inter-patch linkages not predictable from knowledge of intrinsic patch characteristics alone. Beetles avoided patches containing predators, as well as high-quality (predator-free) patches near those containing predators. The signal of risk contagion was observed for aquatic beetles in general, for both of the dominant families of aquatic beetles, and in the responses of a majority of the most numerous species.

Patch quality is typically viewed as a function of intrinsic patch characteristics, and its relative value determined by the frequency/density of patches of differing quality in the landscape, thus, high-quality habitats at low frequency should be heavily colonized (Fretwell and Lucas 1970, Morris 2003). Under a risk

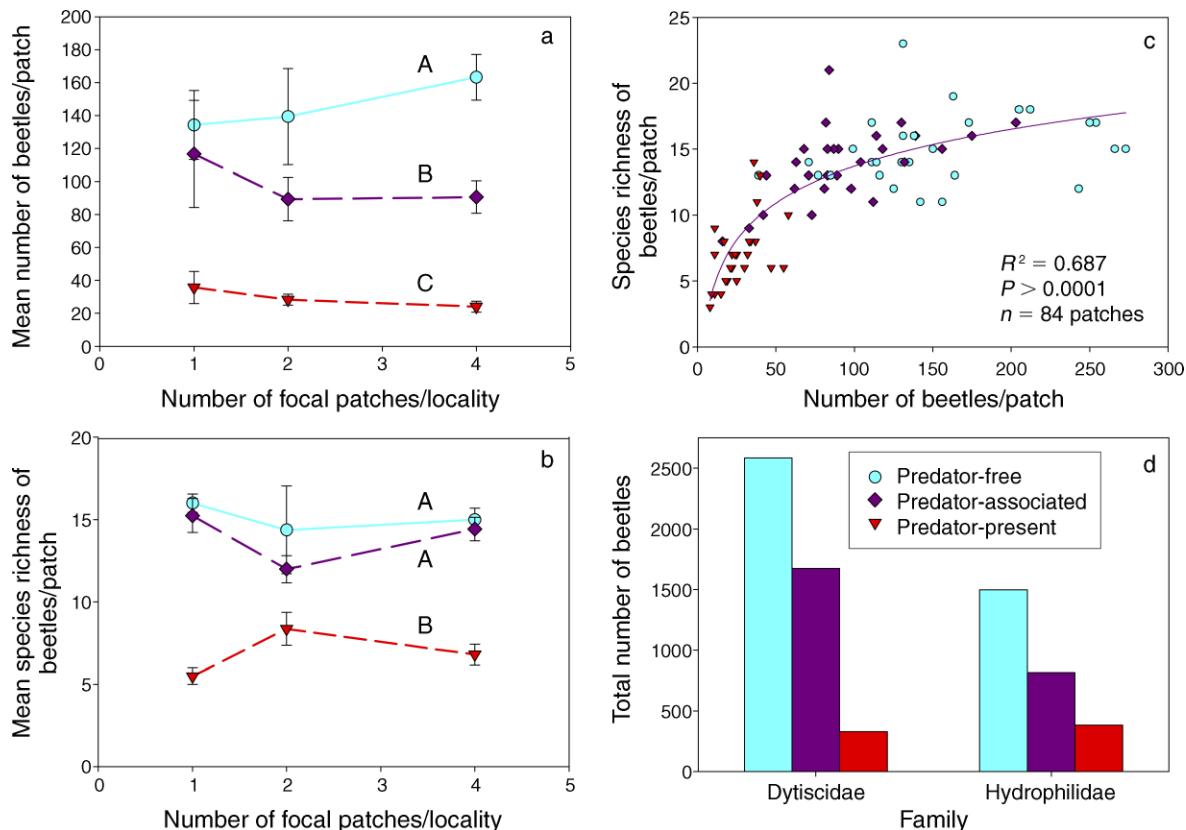


FIG. 3. Aggregate responses of colonizing beetles to three patch types: predator-free (blue circles), predator-associated (purple diamonds), and predator-present (red triangles). Different uppercase letters indicate significant differences among patch types ($P < 0.05$). (a) Number of beetles/patch (mean \pm SE). Predator-associated patches were intermediate between predator-free patches and predator patches, indicating significant overall risk contagion. (b) Species richness/patch (mean \pm SE). Lack of significant difference between the two types of fishless patches is due to the number of beetles/patch for both types approaching the saturation threshold for species richness/patch. (c) Saturation curve for species richness/patch. (d) Responses of the two dominant families of aquatic beetles to predator treatments.

contagion scenario, the perceived quality of a specific patch is a joint function of internal characteristics and characteristics of surrounding habitat patches (Resetarits et al. 2005). In this study, proximity or frequency of predator habitats was a significant factor in determining the perceived habitat quality of predator-free patches; high-quality habitats were devalued by association with low-quality (high risk) habitats.

What is driving this response? In continuous habitats, actual predation risk may be higher in patches spatially associated with predators (Werner et al. 1983, Lima and Dill 1990). In our discrete aquatic habitat patches, predator-associated patches should not necessarily possess a higher risk than predator-free patches, but were nonetheless strongly avoided by colonizing beetles. Several possibilities could explain this pattern. Long-term predation risk may be higher in patches near predators because predators may tend to move into these areas. The limited vagility of fish and the short-lived nature of our colonizers makes this explanation unlikely. Avoidance may also result from misperception; the chemical cues used to assess predation risk may

diffuse into the space surrounding predator-free patches. Many beetles can distinguish between predator and predator-free patches at the scale of a meter or less (Binckley and Resetarits 2005, Brodin et al. 2006), as well as between immediately adjacent predator and predator-associated patches as observed here. Though unlikely, the possibility remains that predator-associated patches may simply be intermediate in fish cue intensity. Last, recognition of nearby predators may alter the perception of high-quality patches in a frequency or density-dependent manner. Thus, the perceived value of a high-quality habitat is reduced based on the distance to or relative frequency of high risk habitats in the surrounding landscape. This seems the most likely scenario, but resolution will require additional experiments. The question of whether this behavior is maladaptive depends on the fitness cost of passing up high-quality habitats and the actual probability of invasion of that habitat essentially a mortality vs. growth rate (μ/g) argument (Werner and Gilliam 1984, Binckley and Resetarits 2008). The response to the proximity of predator patches may have a logical

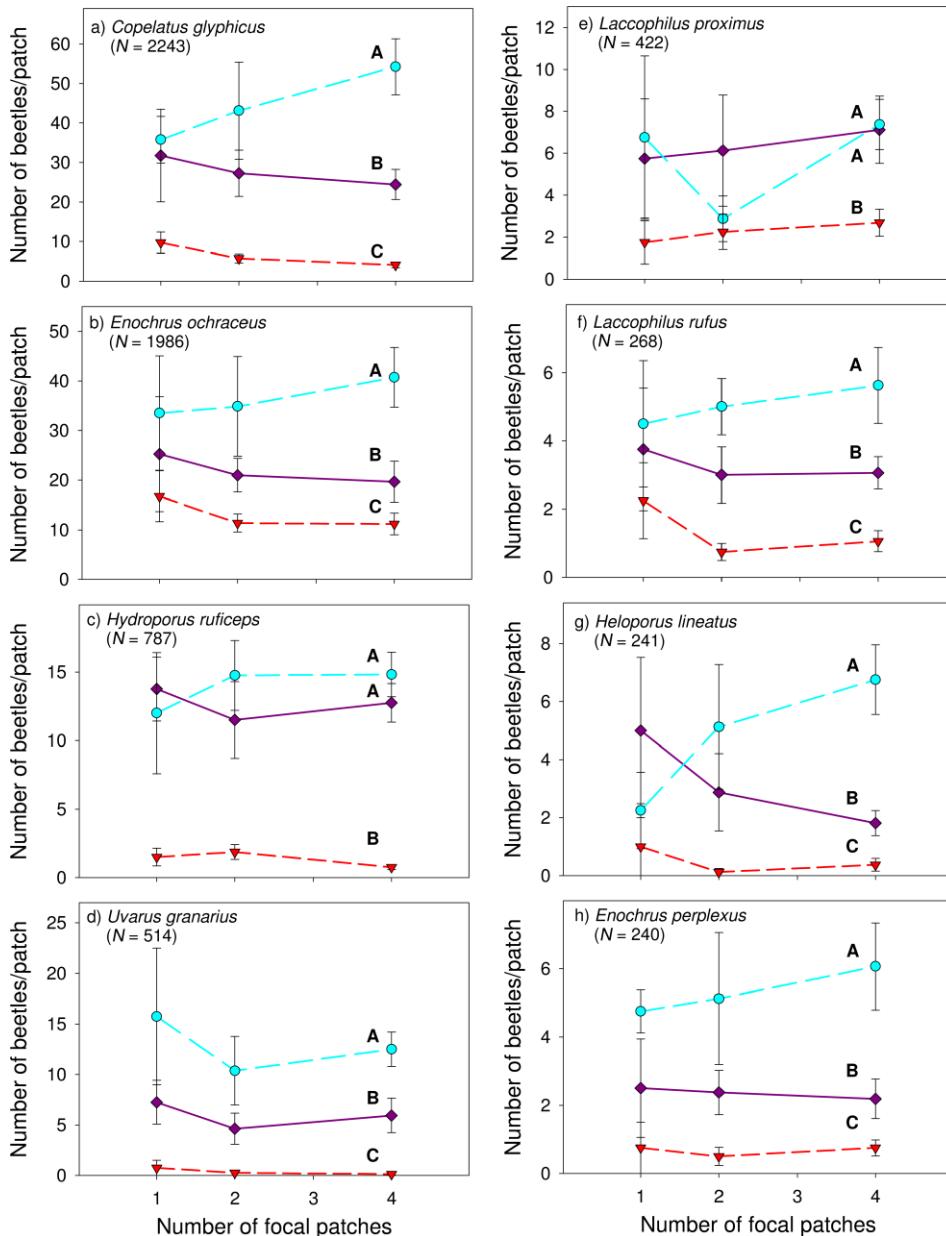


FIG. 4. Abundance (mean \pm SE) of the eight most numerous beetle species (all with >200 individuals) in response to patch type: predator-free (blue circles), predator-associated (purple diamonds), and predator-present (red triangles). Different uppercase letters indicate significant differences among patch types ($P < 0.05$). All eight species showed a significant difference between patches with and without predators. Six showed risk contagion; predator-associated patches were colonized at a lower rate than predator-free patches. For two species (c, e) all patches without predators were statistically equivalent and significantly different from patches with predators.

explanation, but such risk aversion may nonetheless be maladaptive.

The strength of the response both to predator-present and predator-associated patches appeared somewhat stronger among dytiscids than hydrophilids, which is interesting given the life history differences. While the larval life histories of dytiscids and hydrophilids are quite similar and larvae of both are voracious predators, adult dytiscids are also predaceous, whereas adult

hydrophilids are grazers/scavengers. Habitats with fish typically have lower prey abundance and greater stocks of periphyton and phytoplankton as a result of reduction of the density of herbivorous zooplankton and aquatic insects, thus providing a potentially richer growth environment for adult hydrophilids. Fish are thus predators of larvae and adults of both families, competitors of larval and adult dytiscids and larval hydrophilids, but may facilitate adult hydrophilids. This

could explain the stronger responses of dytiscids to both predators and predator-associated patches. As mentioned above, adult *T. lateralis*, a hydrophilid, increases colonization in response to increased resources but the effect is swamped by responses to fish (Binckley and Resetarits 2008). We did not quantify resources, however, this would constitute a minor component of the observed responses.

Larval hydrophilids and dytiscids, along with adult dytiscids, are important predators in temporary aquatic systems. Factors that affect colonization of aquatic habitat patches will doubtless affect the species upon which they prey and with whom they compete. Recent work has demonstrated that variation in the predation regime in aquatic systems can cascade into the surrounding terrestrial systems as well, elevating the importance of species turnover across landscapes of aquatic habitats (Knight et al. 2005). Avoidance of fish habitats appears to be a predictably adaptive response, but individuals or species that avoid otherwise suitable habitats because of proximity to fish habitats not only miss opportunities for themselves, but open up opportunities for individuals/species who exercise a more precise assessment of habitat quality and thereby experience reduced competition and intraguild predation. For example, the two species of *Enochrus* show similar responses, with a resulting covariance in distribution and abundance, while our two species of *Laccophilus* show different responses with a resulting reduction in covariance. Thus, in an environment with increasing frequency of fish, habitat loss proceeds more rapidly for both species of *Enochrus* and *L. rufus* than for *L. proximus* because of risk contagion. Factors and processes that generate variation in patch-specific colonization rates can contribute to local and regional coexistence and landscape-level variation in community structure (Resetarits et al. 2005, Abrams et al. 2007). This reinforces a unique characteristic of habitat selection, in that it simultaneously affects the dynamics of both colonized and avoided habitats (Resetarits 2005).

Recent work in aquatic systems has identified habitat selection behavior as an alternative to species sorting based on differential mortality as a determinant of community structure (Resetarits and Wilbur 1989, Blaustein 1999, Kiflawi et al. 2003, Binckley and Resetarits 2005, 2007, 2008, Resetarits 2005, Vonesh and Buck 2007). Building upon this prior work, the observed responses to the proximity of risk seen in our study have profound implications for both community ecology and conservation biology. Risk contagion complicates any attempt to determine habitat suitability, habitat preferences, or assess habitat availability. Although patch size and isolation remain important factors in metapopulation, community, and metacommunity structure (MacArthur and Wilson 1967, Hanski 1999, Holyoak et al. 2005), understanding the dynamics of specific habitat patches or sets of habitat patches

requires knowledge of both intrinsic patch characteristics and the quality and distribution of neighboring patches. This is especially important if anthropogenic activities decrease the grain size of variation among habitat patches. Local and regional assessment of habitat suitability should consider spatial contagion of risk and reward in determining the status of habitats for species and communities of concern (Pulliam and Danielson 1991, Wellborn et al. 1996, Schlaepfer et al. 2002). Apparently suitable habitats embedded in a matrix of unsuitable habitat patches may not be recognized by colonizing species, thus functionally reducing habitat availability. Conversely, positive contagion may cause unsuitable habitat patches to function as attractive sinks, causing propagule loss, further depressing local and regional populations (Remes 2000, Delibes et al. 2001a, b). Both forms of contagion thus may generate "natural" ecological traps (Dwernychuk and Boag 1972), or may interact with anthropogenic changes to generate or exacerbate classic ecological traps (Schlaepfer et al. 2002). Thus, cryptic processes such as spatial contagion may partly explain observed, seemingly enigmatic, species declines. A more comprehensive understanding of habitat interactions can further aid us in predicting species responses to habitat alteration. Such multifaceted behavioral responses complicate our attempts to understand and model processes of dispersal and colonization, but simultaneously provide a pathway to a more precise understanding of the causes and consequences of species diversity and community structure (Morris 2003, Resetarits et al. 2005, Abrams et al. 2007).

ACKNOWLEDGMENTS

We thank J. Rieger and J. Bolin for assistance, and P. Morin, C. Doncaster, D. Chalcraft, J. Vonesh, and M. McCoy for comments. This material is based upon work supported by the National Science Foundation under Grant Number DEB-0096051 and DEB-0516298.

LITERATURE CITED

- Abrams, P. A., R. Cressman, and V. Krivan. 2007. The role of behavioral dynamics in determining the patch distributions of interacting species. *American Naturalist* 169:505–518.
- Binckley, C. A., and W. J. Resetarits, Jr. 2005. Habitat selection determines abundance, richness and species composition of beetles in aquatic communities. *Biology Letters* 1:370–374.
- Binckley, C. A., and W. J. Resetarits, Jr. 2007. Effects of forest canopy on habitat selection in treefrogs and aquatic insects: implications for communities and metacommunities. *Oecologia* 153:951–958.
- Binckley, C. A., and W. J. Resetarits, Jr. 2008. Oviposition behavior partitions aquatic landscapes along predation and nutrient gradients. *Behavioral Ecology* 19:552–557.
- Binckley, C. A., and W. J. Resetarits, Jr. *In press*. Spatial and temporal dynamics of habitat selection across canopy gradients generates patterns of species richness and composition in aquatic beetles. *Ecological Entomology*.
- Blaustein, L. 1999. Oviposition site selection in response to risk of predation: evidence from aquatic habitats and consequences for population dynamics and community structure. Pages 441–456 in S. P. Wasser, editor. *Evolutionary theory*

- and processes: modern perspectives. Kluwer, Dordrecht, The Netherlands.
- Blaustein, L., and B. P. Kotler. 1993. Oviposition habitat selection by the mosquito *Culiseta longiareolata*: effects of conspecifics, food and green toad tadpoles. *Ecological Entomology* 18:104–108.
- Brodin, T., F. Johansson, and J. Bergsten. 2006. Predator related oviposition site selection of aquatic beetles (*Hydroporus* spp.) and effects on offspring life-history. *Freshwater Biology* 51:1277–1285.
- Chase, J. M. 2003. Community assembly: when should history matter? *Oecologia* 136:489–498.
- Delibes, M., P. Ferreras, and P. Gaona. 2001a. Attractive sinks, or how individual behavioural decisions determine source-sink dynamics. *Ecology Letters* 4:401–403.
- Delibes, M., P. Gaona, and P. Ferrera. 2001b. Effects of an attractive sink leading into maladaptive habitat selection. *American Naturalist* 158:277–285.
- Dwernychuk, L. W., and D. A. Boag. 1972. Ducks nesting in association with gulls—an ecological trap? *Canadian Journal of Zoology* 50:559–563.
- Fretwell, S. D., and H. L. Lucas, Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica* 19:16–36.
- Fukami, T., H. J. E. Beaumont, X. Zhang, and P. B. Rainey. 2007. Immigration history controls diversification in experimental adaptive radiation. *Nature* 446:436–439.
- Fukami, T., and P. J. Morin. 2003. Productivity–biodiversity relationships depend on the history of community assembly. *Nature* 424:423–426.
- Hamilton, W. D., and R. M. May. 1977. Dispersal in stable habitats. *Nature* 269:578–581.
- Hanski, I. 1999. *Metapopulation ecology*. Oxford University Press, Oxford, UK.
- Holt, R. D., and M. Barfield. 2001. On the relationship between the ideal-free distribution and the evolution of dispersal. Pages 83–95 in J. Clobert, E. Danchin, A. Dhondt, and J. Nichols, editors. *Dispersal*. Oxford University Press, Oxford, UK.
- Holyoak, M., M. A. Leibold, and R. D. Holt. 2005. *Metacommunities: spatial dynamics and ecological communities*. University of Chicago Press, Chicago, Illinois, USA.
- Johnson, C. G. 1969. *Migration and dispersal of insects by flight*. Methuen, London, UK.
- Kennedy, M., and R. D. Gray. 1993. Can ecological theory predict the distribution of foraging animals? A critical analysis of experiments on the ideal free distribution. *Oikos* 68:158–166.
- Kiflawi, M., L. Blaustein, and M. Mangel. 2003. Predation-dependent oviposition habitat selection by the mosquito *Culiseta longiareolata*: a test of competing hypotheses. *Ecology Letters* 6:35–40.
- Kneitel, J. M., and J. M. Chase. 2004. Trade-offs in community ecology: linking spatial scales and species coexistence. *Ecology Letters* 7:69–80.
- Kneitel, J. M., and T. E. Miller. 2003. Dispersal rates affect species composition in metacommunities of *Sarracenia purpurea* inquilines. *American Naturalist* 162:165–171.
- Knight, T. M., M. W. McCoy, J. M. Chase, K. A. McCoy, and R. D. Holt. 2005. Trophic cascades across ecosystems. *Nature* 437:880–883.
- Layton, R. J., and J. R. Voshell, Jr. 1991. Colonization of new experimental ponds by benthic macroinvertebrates. *Environmental Entomology* 20:110–117.
- Leibold, M. A., J. M. Chase, J. B. Shurin, and A. L. Downing. 1997. Species turnover and the regulation of trophic structure. *Annual Review of Ecology and Systematics* 28:467–494.
- Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68:619–640.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- Matta, J. F. 1979. Aquatic insects of the Great Dismal Swamp. Pages 200–221 in P. W. Kirk, editor. *The Great Dismal Swamp*. University of Virginia, Charlottesville, Virginia, USA.
- Morris, D. W. 2003. Toward an ecological synthesis: a case for habitat selection. *Oecologia* 136:1–13.
- Price, J. E., and P. J. Morin. 2004. Colonization history determines alternate community states in a food web of intraguild predators. *Ecology* 85:1017–1028.
- Pulliam, R. H., and B. J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *American Naturalist* 137:S51–S66.
- Remes, V. 2000. How can maladaptive habitat choice generate source-sink population dynamics? *Oikos* 91:579–582.
- Resetarits, W. J., Jr. 1996. Oviposition site choice and life history evolution. *American Zoologist* 36:205–215.
- Resetarits, W. J., Jr. 2001. Experimental evidence that past predation affects community assembly: fish avoidance in a colonizing/ovipositing aquatic beetle. *Oecologia* 129:155–160.
- Resetarits, W. J., Jr. 2005. Habitat selection links local and regional scales in aquatic systems. *Ecology Letters* 8:480–486.
- Resetarits, W. J., Jr., C. A. Binckley, and D. R. Chalcraft. 2005. Habitat selection, species interactions, and processes of community assembly in complex landscapes: a metacommunity perspective. Pages 374–398 in M. Holyoak, M. A. Leibold, and R. D. Holt, editors. *Metacommunities: spatial dynamics and ecological communities*. University of Chicago Press, Chicago, Illinois, USA.
- Resetarits, W. J., Jr., and H. M. Wilbur. 1989. Choice of oviposition site by *Hyla chrysoscelis*: role of predators and competitors. *Ecology* 70:220–228.
- SAS Institute. 2003. SAS, release 9.1 version. SAS Institute, Cary, North Carolina, USA.
- Schlaepfer, M. A., M. C. Runge, and P. W. Sherman. 2002. Ecological and evolutionary traps. *Trends in Ecology and Evolution* 17:474–480.
- Schneider, D. W., and T. M. Frost. 1996. Habitat duration and community structure in temporary ponds. *Journal of the North American Benthological Society* 15:64–86.
- Semlitsch, R. D., and J. R. Bodie. 1998. Are small, isolated wetlands expendable? *Conservation Biology* 12:1129–1133.
- Sheldon, A. L. 1992. Colonization dynamics of aquatic insects. Pages 401–429 in J. V. Ward, editor. *Aquatic insect ecology*. Wiley and Sons, New York, New York, USA.
- Shurin, J. B., and E. G. Allen. 2001. Effects of competition, predation, and dispersal on species richness at local and regional scales. *American Naturalist* 158:624–637.
- Travisano, M., J. A. Mongold, A. F. Bennett, and R. E. Lenski. 1995. Experimental tests of the roles of adaptation, chance, and history in evolution. *Science* 267:87–90.
- Vonesh, J. R., and J. C. Buck. 2007. Pesticide alters oviposition site selection in gray treefrogs. *Oecologia* 154:219–226.
- Wellborn, G. A., E. E. Werner, and D. K. Skelly. 1996. Mechanisms creating community structure across a freshwater habitat gradient. *Annual Review of Ecology and Systematics* 27:337–363.
- Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics* 15:393–425.
- Werner, E. E., J. F. Gilliam, D. J. Hall, and G. G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64:1540–1548.
- Zalom, F. G., A. A. Grigarick, and M. O. Way. 1979. Seasonal and diel flight periodicities of rice field Hydrophilidae. *Environmental Entomology* 8:938–943.