Ecology, 99(3), 2018, pp. 661–669

Predation risk and patch size jointly determine perceived patch quality in ovipositing treefrogs, *Hyla chrysoscelis*

William J. Resetarits Jr.,[1] Jason R. Bohenek, Tyler Breech, and Matthew R. Pintar

Department of Biology, Center for Water and Wetlands Resources, The University of Mississippi,
University, Mississippi 38677 USA

Abstract. Two of the most important factors determining community structure and diversity within and among habitat patches are patch size and patch quality. Despite the importance of patch size in existing paradigms in island biogeography, metapopulation biology, landscape ecology, and metacommunity ecology, and growing conservation concerns with habitat fragmentation, there has been little investigation into how patch size interacts with patch quality. We crossed three levels of patch size (1.13 m^2, 2.54 m^2 and 5.73 m^2) with two levels of patch quality (fish presence/absence, green sunfish [*Lepomis cyanellus*] and golden shiners [*Notemigonus crysoleucus*]) in six replicate experimental landscapes ($3 \times 2 \times 6 = 36$ patches). Both fish predators have been previously shown to elicit avoidance in ovipositing treefrogs. We examined how patch size and patch quality, as well as the interaction between size and quality, affected female oviposition preference and male calling site choice in a natural population of treefrogs (*Hyla chrysoscelis*). Females almost exclusively oviposited in the largest fishless patches, indicating that females use both risk, in the form of fish predators, and size itself, as components of patch quality. Females routinely use much smaller natural and experimental patches, suggesting that the responses to patch size are highly context dependent. Responses to fish were unaffected by patch size. Male responses largely mimicked those of females, but did not drive female oviposition. We suggest that patch size itself functions as another aspect of patch quality for *H. chrysoscelis*, and serves as another niche dimension across which species may behaviorally sort in natural systems. Because of strong, shared avoidance of fish (as well as other predators), among many colonizing taxa, patch size may be a critical factor in species sorting and processes of community assembly in freshwater habitats, allowing species to behaviorally segregate along gradients of patch size in fishless ponds. Conversely, lack of variation in patch size may concentrate colonization activity, leading to intensification of species interactions and/or increased use of lesser quality patches.

Key words: colonization; habitat fragmentation; habitat selection; ideal-free distribution; immigration; niche dimensions; oviposition site choice; species sorting.

Introduction

Two of the most important factors determining community structure and diversity within and among habitat patches are patch size and patch quality. Existing paradigms in island biogeography, metapopulation biology, landscape ecology, and metacommunity ecology emphasize patch size, along with patch isolation, as critical characteristics affecting diversity (MacArthur and Wilson 1967, Hanski and Gilpin 1997, Shurin 2001, Kneitel and Miller 2003, Leibold et al. 2004, Kadmon and Allouche 2007). Proportional increases in the abundances and richness of species relative to area is one established law of ecology (Rosenzweig 1991, Gotelli 2008). Interest in how patch size affects populations and species richness precedes the Equilibrium Theory of Island Biogeography (ETIB; e.g., Arrhenius 1921, Gleason 1922, Cain 1938, MacArthur and Wilson 1967, see Connor and McCoy 1979, Bender et al. 1998), however, ETIB and its derivations solidified the central role of patch size in the collective ecological consciousness and its importance has been augmented by the development of metapopulation and metacommunity theories.

That size occupies a central place in ecology and conservation is attested to by the myriad of studies concerning patch size (e.g., McIntyre and Wiens 1999, Öckinger and Smith 2006; review in Bender et al. 1998) and habitat fragmentation (e.g., Golden and Crist 1999, Summerville and Crist 2001; reviews in Debinski and Holt 2000, Mortelliti et al. 2010). Increasing concern with the effects of habitat loss and fragmentation has placed further emphasis on both size and isolation (Debinski and Holt 2000, Hodgson et al. 2009, Ockinger et al. 2010). The effect of patch size on diversity is generally ascribed to its role in extinction rates, with larger patches harboring more species at larger population sizes than smaller patches. However, patch size can also affect the immigration side of the equation. Under random dispersal and

Manuscript received 13 September 2017; accepted 7 December 2017. Corresponding Editor: Mark C. Urban.

[1] E-mail: wresetar@olemiss.edu

colonization, size can increase the probability that a site will be colonized (target area hypothesis; MacArthur and Wilson 1967, Connor and McCoy 1979, Rosenzweig 1991, Hanski 1999). Invoking habitat selection, larger habitat patches may also be more easily detected, cues are more apparent, or may even be preferred. For aquatic systems, cues indicating presence of water, such as reflectance and chemosensory cues, are clearly related to habitat area. Thus, random capture probabilities and active habitat selection may interact; larger "targets" may be proportionally or disproportionately more perceptible or preferable to colonizing species and patch size may be the driving force in colonization dynamics.

Habitat selection theory emphasizes patch quality as a primary determinant of patch-specific colonization rates and resulting patterns of abundance and species richness (Fretwell and Lucas 1970, Wiens 1976, Pulliam and Danielson 1991, Rosenzweig 1991, Morris 2003, Resetarits et al. 2005). Numerous studies have documented the role of habitat quality in driving colonization rates in both terrestrial (Rausher 1983, 1993, Singer 1984, Thompson and Pellmyr 1991, Renwick 1994) and aquatic systems (Resetarits and Wilbur 1989, Resetarits 2001, Kiflawi et al. 2003, Binckley and Resetarits 2005, Vonesh and Buck 2007; review in Blaustein 1999). Likewise, a growing body of theoretical and empirical work suggests that spatial variation in quality should interact with size and isolation to drive colonization dynamics (Armsworth and Roughgarden 2005, Resetarits et al. 2005, Abrams 2007, Abrams et al. 2007). Whereas size and location are relatively stable characteristics of many habitat patches, habitat quality, especially if determined by species composition and intraspecific density, is potentially more dynamic (Resetarits and Wilbur 1989, Wellborn et al. 1996, Leibold et al. 1997). Species capable of assessing relative quality of patches can effectively respond to the shifting mosaic nature of such complex landscapes by directing colonization to current high quality patches (Resetarits and Wilbur 1989, Resetarits 1996).

The presence (and identity) of predators is an important component of patch quality, and predators can have a variety of effects on species diversity and community structure (Paine 1966, Kerfoot and Sih 1987, Wellborn et al. 1996, Crooks and Soule 1999, Terborgh et al. 1999, Prugh et al. 2009, Estes et al. 2011). For example, the transition from fish to fishless habitats is a defining characteristic for freshwater communities (Wellborn et al. 1996). Effects on species distribution and community structure have been primarily attributed to the lethal impacts of predators (but see Lima 1998, 2009, Preisser et al. 2005, Ale and Whelan 2008, Orrock et al. 2008, Peckarsky et al. 2008), but recent work has demonstrated that predators can have dramatic, direct, non-lethal effects on species distribution and community structure via effects on colonization by prey species (Resetarits and Wilbur 1989, Blaustein 1999, Resetarits 2005, Resetarits and Binckley 2009, Vonesh et al. 2009, Kraus and Vonesh 2010, Resetarits and Silberbush 2016). Thus, predators can affect species/area relationships via both extinction rate within patches (Ryberg and Chase 2007) and colonization rate of patches with varying levels of predation risk (Resetarits and Binckley 2013). Patch-specific colonization rates generated by interactions between patch size and patch quality could profoundly affect the equilibrium dynamics of habitat patches and impact both community and metacommunity structure.

Patch size and isolation have been central to the development of nature reserve design and the field of conservation biology. Recently, conservation biologists have expressed a growing interest in the role of patch quality, and concern over the relative weighting of patch quality, size, and connectivity in conservation planning, particularly in the context of climate change. This shift in focus emphasizes the need to better understand the relative contribution of these critical factors and their interaction to colonization rates and resulting population, community, and metacommunity dynamics (Hodgson et al. 2009, 2011, Mortelliti et al. 2010, Doerr et al. 2011).

We conducted an experiment crossing the presence/absence of predatory fish (patch quality) with patch size to examine the specific effects of each factor, and the possible interactions between the two, on the oviposition site choice of naturally colonizing gray treefrogs, *Hyla chrysoscelis*. Our measure of quality was based on observed field patterns of distribution and abundance, and experimentally verified based on behavior of the organisms themselves. Our experimental design directly and independently manipulated both quality and size, allowing examination of their relative importance.

Materials and Methods

Our experiment was conducted in a large oldfield at the University of Mississippi Field Station (UMFS) in Lafayette County, Mississippi, USA. We constructed six rectangular mesocosm arrays (blocks) of six pools each ($N = 36$), crossing three pool sizes (1.13 m^2, 2.54 m^2, and 5.73 m^2) with the presence/absence of fish, specifically green sunfish (*Lepomis cyanellus*) and golden shiners (*Notemigonus crysoleucus*; Fig. 1). Pools were of the same material, color, and shape (cylindrical), though the largest pools were 13 cm deeper than the other two sizes, which we compensated for by filling all pools to the same depth (50 cm). Thus, pools held ~593, 1,334, and 3,002 L, respectively. Treatments were randomly assigned to positions within the array, subject to the caveat that pools of the same size were opposite one another in the two rows of each array, that each row contained alternating fish and fishless pools (Fig. 1), and an equal number of blocks had more fish and fishless pools on the forest side. The green sunfish, *L. cyanellus*, is one of the most widespread fishes in North America, is widely introduced to previously fishless waters both inside and outside of its native range (Lee et al. 1980), and is one of the most abundant fish at UMFS. They are generalist predators that feed at all depths in ponds and strongly repel

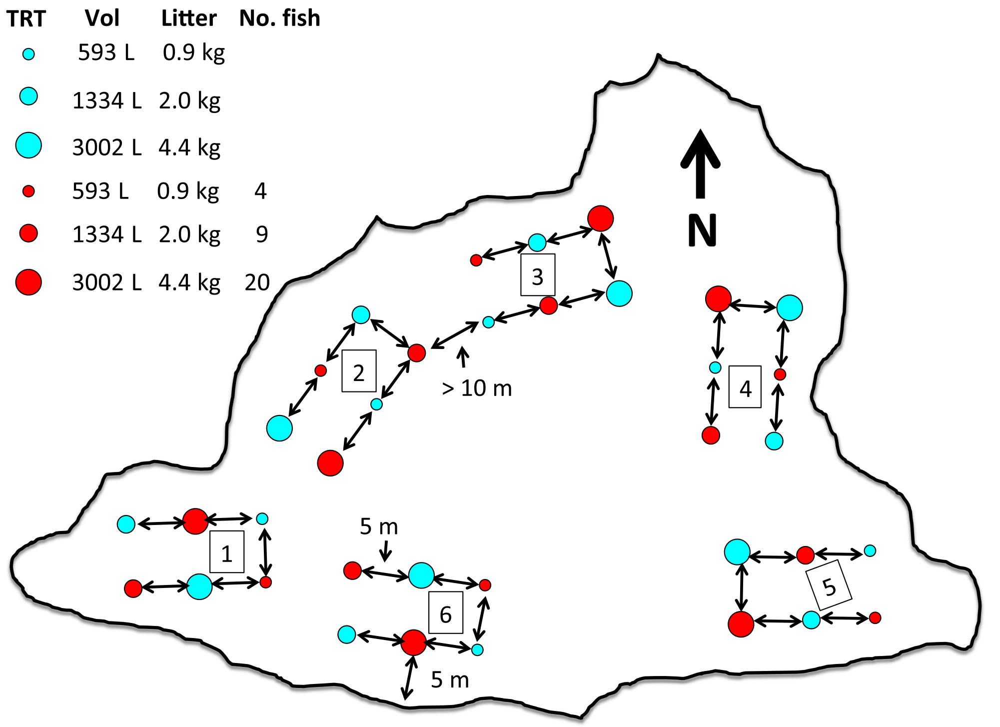

Fig. 1. Physical layout and treatment summary for experimental landscapes in an old field at the University of Mississippi Field Station, approximately to scale; blue, fishless; red, fish. Block 6 attracted very little activity and was eliminated from the analyses.

oviposition by *H. chrysoscelis* (data not shown). The golden shiner, *Notemigonus crysoleucus,* is a small, pelagic, largely planktivorous, gape-limited fish that also strongly repels oviposition by *H. chrysoscelis* (Data not shown). It is also widespread in North America and widely introduced as a forage fish.

We began filling pools with well water on 9 May 2016, one block at a time, completing two blocks per day. Concurrent with filling, dried leaf litter (mixed hardwoods) was added to patches (pools) of different size in proportion to the volume (0.9, 2.0, 4.4 kg, respectively) with all blocks assembled by 11 May. On 11 May, each patch received fish at an initial density of ~2.3 g/100 L: small (1.13 m^2) patches received 4 fish total (2 *N. chrysoleucus* + 2 *L. cyanellus*), medium (2.54 m^2) patches received 9 fish total (4–5 *N. chrysoleucus* + 4–5 *L. cyanellus*), and large patches (5.73 m^2) received 20 fish total (10 *N. chrysoleucus* + 10 *L. cyanellus*). This density is on the lower end of biomass density used in previous experiments and in natural ponds (Mittelbach et al. 1995), but above the threshold that elicits avoidance in *Hyla* species (Rieger et al. 2004; Data not shown). To equalize biomass within blocks, we created eight complementary (one "large" and one "small") pairs within each of the two species for each block (by eye to minimize stress), and randomly assigned the appropriate number of pairs to each fish patch within that block, thus maintaining the same fish density and size structure across patch sizes within blocks. Mean mass of both *N. chrysoleucus* and *L. cyanellus* in the holding tanks from which the experimental animals were haphazardly sampled was ~3.5 g. Because medium patches required an uneven number of fish, each medium patch in blocks 1, 3, and 5 received one extra *L. cyanellus*, while those in blocks 2, 4, and 6 received one extra *N. chrysoleucus.*

On 12 May, screen lids were submerged to begin the experiment. The experiment was checked every morning for eggs, which were removed, photographed, and placed in rearing tanks or natural fishless ponds. They were then counted from photographs using ImageJ (Schneider et al. 2012). On 12 June, after 35,000+ eggs had been laid and clear preferences had been established, we began returning the eggs to the pools in which they were laid to examine whether increasing conspecific density affected oviposition preferences (sensu the Ideal Free Distribution; Fretwell and Lucas 1970). On 17 nights we conducted surveys of calling males. These were conducted beginning 2 June 2016 and occurred on haphazard nights approximately 90 min after sunset and consisted of a single observer walking counterclockwise through the set of blocks and recording the number of males on each patch, which took <15 min. Nights are not independent, as the same males may be recorded on multiple occasions, but surveys provide an estimate of relative calling activity among the patches. Block 6 received only 660 eggs laid in a single patch (large fishless) on one night, and only 11 total observations of male activity. Totals for the other five blocks ranged from 7,419 to 19,832 eggs. Thus, Block

6 clearly informs us that a particular area of our site was not attractive to breeding *H. chrysoscelis*, but provides no information regarding our questions and was thus excluded a priori from the analyses. The experiment was ended on 21 July after five nights of no eggs and an extended forecast of 0% chance of rain for at least 10 d.

Our experiment comprised a randomized complete block design crossing three levels of patch size (size) with two levels of predator treatment (fish). Our primary response variables were the normalized total number of eggs/patch and the normalized male activity/patch (total number of observations of a male on a patch on a night), with individual patches as the unit of analysis. Male activity is an estimate of male calling site preference, since we did not mark males nor survey males each night. The maximum number of observed males on a single night was 40, which serves as a minimum estimate of the number of calling males in the population. Normalization was based on relative surface area and volume, since depth was constant among sizes, and with the scale based on the size of the smallest patches. Egg data was square-root transformed ($\sqrt{X + 0.5}$) and analysed in a generalized linear mixed model ANOVA with block as a random effect, using PROC GLIMMIX (SAS Institute 2016) with a quasi-Poisson distribution and a log link function. The estimate of block effect was zero, and thus block was dropped from the model, resulting in a generalized linear model. The same approach was used for male activity, except we used the raw data with a Poisson distribution, and the small block effect was retained. Treatment means were compared using Fisher's Protected LSD across all treatment combinations only when there was an interaction term with $P < 0.10$, using $\alpha = 0.05$ for individual LSD comparisons. We also examined the correlation (Pearson's Product Moment) between the number of eggs and our estimate of male calling activity. All analyses used SAS v. 9.4 (SAS Institute 2016) with Type III sums of squares and $\alpha = 0.05$.

Results

Eggs

A total of 76,925 eggs were laid in 88 oviposition events (eggs/patch/night) spread over 31 of the 65 nights that comprised the experiment. Eggs were laid in 11 of 30 available patches, with the maximum number of eggs laid on a single night at 8,349. All of the oviposition events in individual patches appeared to contain two clutches or fewer ($\lesssim$2,000 eggs), and only four events appeared to contain less than a typical clutch of eggs (all <300 eggs).

Both patch size ($F_{2,24} = 9.34$, $P < 0.001$) and fish presence ($F_{1,24} = 16.25$, $P < 0.0005$) had significant effects on oviposition, and there was a significant size × fish interaction ($F_{2,24} = 4.12$, $P = 0.029$; Fig. 2a). Females almost completely avoided all fish pools regardless of size, depositing a total of only 2,984 eggs (3.8% raw) spread over four oviposition events in fish patches. Among fishless pools, females showed a strong preference for large pools (normalized mean ± SE, 2,520.2 ± 383.9 eggs), utilized medium pools significantly less (988.98 ± 549.1), and totally avoided small pools (Fig. 2a). Overall 81% of eggs (raw) were laid in large fishless patches. The size × fish interaction resulted from the preference for larger size among the fishless pools, but no preference among the pools with fish: all were avoided equally. Preference for large patches did not decrease after we began returning eggs, in fact, the relative proportion of eggs in large patches increased from 76% to 85%. The most obvious difference after we began returning eggs was a more even distribution of eggs in large predator-free patches among blocks (Appendix S1: Fig. S1).

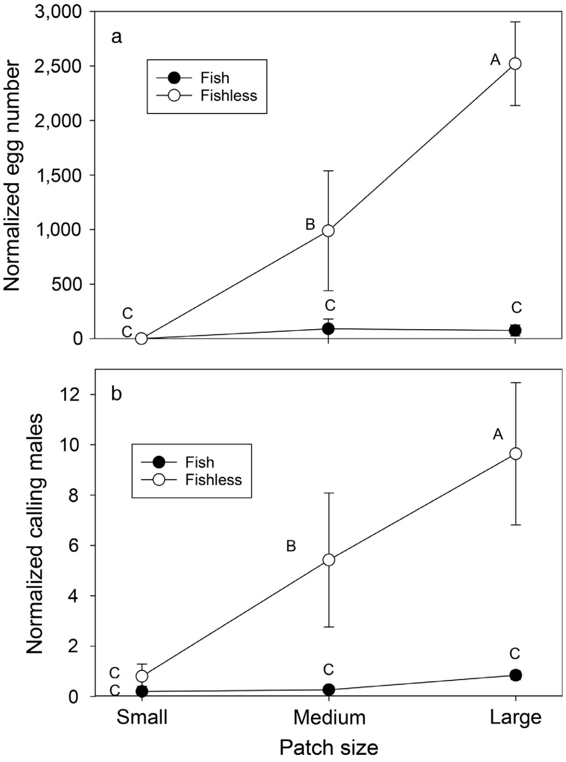

FIG. 2. Data for (a) total egg number and (b) total male activity, both normalized to unit area. Values are means ± 1 SE. Letters indicate significantly different treatments based on Fisher's Protected LSD based on all treatment combinations.

Males

We observed 344 occurrences of male activity (observations of a male on a patch on a night) over the duration of the experiment. Males were observed at patches on 14 of the 17 nights of observation, with nightly totals ranging from 6 to 40.

Patch size ($F_{2,20} = 4.73$, $P < 0.021$) and fish presence ($F_{1,20} = 26.78$, $P < 0.0001$) had significant effects on male activity and there was a significant size × fish interaction ($F_{2,20} = 3.90$, $P = 0.037$; Fig. 2b). Males, like females, almost totally avoided fish pools regardless of size, with only 7.6% of male activity occurring in fish patches. Among fishless pools, males showed the strongest preference for the large pools (normalized mean ± SE; 9.64 ± 2.83 observations), utilized medium pools at a marginally lower rate (5.42 ± 2.66, $P = 0.0634$), and almost totally avoided small pools (0.80 ± 0.49; Fig. 2b). The size × fish interaction resulted from the same pattern as in eggs: preference for larger size among the fishless pools but no preference among the pools with fish. The male preference for large vs. medium patches occurred primarily in earlier observations; later observations (after 24 June) were essentially equivalent in normalized activity between large and medium patches, possibly suggesting a density-dependent response to larval density (Appendix S1: Fig. S2). Large fishless patches accounted for 70% (raw) of male occurrences, while small patches accounted for only 1.5% (raw).

Eggs/male correlation

Totals for male activity and oviposition behavior were strongly positively correlated across patches ($r = 0.911$, $P < 0.0001$, $n = 36$; Fig. 3a), but there was no relationship between the number of eggs laid and total male activity on any given night ($r = 0.0686$, $P = 0.793$, $n = 17$; Fig. 3b). There was also no relationship between the number of eggs on the previous night and male activity ($r = -0.20$, $P = 0.442$, $n = 17$), nor the number of eggs and male activity the previous night ($r = 0.135$, $P = 0.605$, $n = 17$). Thus, males and females are not proximally reacting to current levels of activity, nor to levels of activity on the previous night.

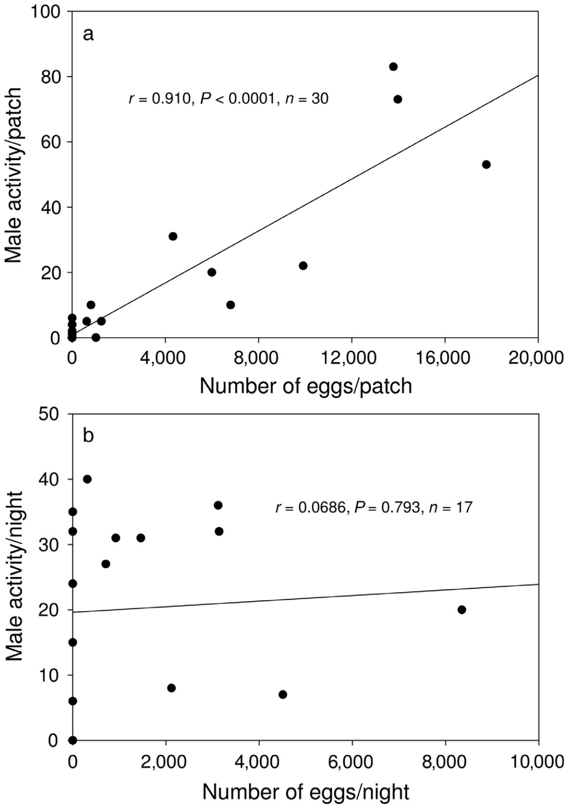

FIG. 3. (a) Correlation between total male activity per patch (raw) and total egg number per patch (raw) for the 30 patches. (b) Correlation between total male activity per night (raw) and total number of eggs per night (raw) for the 17 nights of male activity surveys. Lines are regression lines.

DISCUSSION

Effects of patch quality, patch size, and density on Hyla *oviposition*

We directly manipulated the size and perceived predation risk of available habitat patches to examine the relative importance of those factors and their interaction in the oviposition behavior of gray treefrogs. Our experiment focused on prospection and settlement (colonization), and provides a snapshot of the effects of patch size and quality on early colonization dynamics. This process is critically important because priority effects can strongly influence the trajectories of different communities (Alford and Wilbur 1985, Chase 2003, Kraus and Vonesh 2010) and effects of variation in early colonization carry over into long term community structure (Vonesh et al. 2009).

The response of ovipositing *Hyla* to variation in patch size was contrary to expectations under a passive colonization model based on spatial encounter probabilities (target-area effect), with a strong, size-adjusted, positive response to patch size (Fig. 2a). We initially framed this as a question of patch size vs. patch quality, but clearly patch size itself is a strong component of perceived patch quality. Predation risk, here generated by the presence/absence of fish, produced an expected, but surprisingly strong, pattern of fish avoidance, with a strong patch size × predation risk interaction driven by the total lack of response to variation in patch size in fish patches (Fig. 2a). Given the strength of the preference for large patches, we expected some increase in oviposition in larger fish patches, but this was not the case. Clearly the process is hierarchical, with females (as well as males) choosing based first on predation risk, then on size, and there is no amelioration of the responses to risk by increasing size. The strong active preference for larger patches is not based on an absolute threshold of tolerance, but is a context dependent process, as *Hyla chrysoscelis* readily utilize smaller patches in both natural and experimental systems when larger patches are not available (e.g., Resetarits and Wilbur 1989, Binckley and Resetarits 2003, Pintar and Resetarits 2017; data not shown). All else being equal, female *H. chrysoscelis* simply preferred larger patches, and the preference was quite marked.

There are many sources of variation in patch quality, and *H. chrysoscelis* are capable of assessing many of these directly. While we can speculate on factors that might vary with patch size, very little is actually known regarding variation among patches in predator density, permanence, productivity, etc. at the smaller end of the size spectrum, where *H. chrysoscelis* typically breed. For example, the expectation is that permanence should scale positively with patch size but, in natural systems, this is not necessarily the case, with hydroperiod more dependent on depth, vegetation, and underlying hydrology (Eason and Fauth 2001). Similarly, productivity, from the perspective of *H. chrysoscelis*, is primarily a consequence of pond age, canopy cover, and nutrient profile, and gray treefrogs are capable of assessing age and canopy directly, but do not respond to variation in nutrients (Seale 1980, Alford and Wilbur 1985, Binckley and Resetarits 2007, 2008, Pintar and Resetarits 2017). *Hyla chrysoscelis* are capable of directly assessing the presence/absence of the most important predators, which are fish, and pond age may be a better predictor of non-fish predators than pond size (Schneider and Frost 1996), though both may be important (Woodward 1983, Spencer et al. 1999). It remains to be determined what the source(s) of variation in expected fitness *H. chrysoscelis* are tracking with preference for larger patches.

Conventional wisdom suggests that male calling helps females locate patches and drives female oviposition behavior, but this does not seem the case with *H. chrysoscelis*, where post-amplexus female patch choice appears to dominate (Fellers 1979, Godwin and Roble 1983, Resetarits and Wilbur 1991). In both previous work (Resetarits and Wilbur 1989, 1991) and this study, while patch preferences are strongly correlated on certain axes, there are also striking disconnects between sexes. In the prior study, females avoided a fish (*Enneacanthus chaetodon*), a salamander (*Ambystoma maculatum*), and conspecific tadpoles, while males only avoided fish and conspecific tadpoles. More striking was the disconnect in the spatiotemporal distribution of activity, in which peak male and female activity were poorly correlated, which is also evident here. Males and females share the same preferences for large fishless patches (Fig. 3a), but the activity of females on any given night is not correlated with male activity (Fig. 3b), and male preferences equilibrated between large and medium fishless patches later in the experiment (Appendix S1: Fig. S2), while egg distribution still strongly favored large fishless patches (Appendix S1: Fig. S1).

It is also interesting that we found no evidence of density-dependent oviposition over the range of *Hyla* activity we observed. *Hyla savignyi* in Israel avoid higher densities of conspecific tadpoles when ovipositing (Stein and Blaustein 2015) and, in a previous experiment (Resetarits and Wilbur 1989, 1991), *H. chrysoscelis* avoided ovipositing in pools with high densities of conspecific tadpoles, but we saw no compelling evidence for density-dependent oviposition here, even though some of our large patches eventually contained upward of 5,000 tadpoles. Possibly none of our large pools reached a saturation larval density, or did not reach it until the end of the experiment, or perhaps females respond to the relative stage of the tadpoles in a patch, not simply the total number. Kraus and Vonesh (2010) found that *H. chrysoscelis* avoidance of fish was reduced as communities assembled, but whether this is related to increasing conspecific density in fishless patches is unclear, as predatory insects also accumulate in fish-free pools, and resources are increasingly locked up in less palatable forms of plant biomass. Resolution of this question awaits more focused examination of the interaction between density and the factors determining primary patch quality.

Patch quality vs. patch size in community ecology

The importance of patch quality and how quality interacts with size have a variety of ramifications for how communities are assembled, as well as how communities are potentially linked into larger metacommunities. Structural features of the landscape, such as patch size, number, and isolation, have dominated our view of the role of colonization and extinction dynamics in generating patterns of distribution and diversity (MacArthur and Wilson 1967, Allen 1987, Hanski and Gilpin 1997, Shurin 2001, Kneitel and Miller 2003, Leibold et al. 2004, Binckley and Resetarits 2005, Ryberg and Chase 2007, Resetarits and Binckley 2013). Considering the number of studies addressing size and isolation alone, the longstanding interest in habitat selection (especially in the context of the Ideal-Free Distribution: see Gray and Kennedy 1993, Morris 2003), and current debates over the relative importance of habitat quality, quantity and connectivity in conservation planning (Hodgson et al. 2009, 2011, Mortelliti et al. 2010, Doerr et al. 2011), surprisingly little work has experimentally compared the relative importance (and potential interaction) of patch size and patch quality (Saward-Arav et al. 2016), quality and isolation (but see Thomas et al. 2001), or quality and patch number (but see Resetarits and Binckley 2013) in the context of colonization dynamics. This is partly understandable, as patch size, and to a lesser extent, isolation, are easier to define and measure than patch quality, which must be empirically determined and can differ for each colonizing species. However, we risk a gap in our understanding of colonization dynamics and resulting population/community structure that arises from the failure to incorporate habitat quality into existing paradigms and models (Armsworth and Roughgarden 2005, Resetarits et al. 2005, Abrams 2007, Abrams et al. 2007).

Numerous studies have documented the important role of patch quality in colonization rate both in terrestrial (Rausher 1983, 1993, Singer 1984, Thompson and Pellmyr 1991, Renwick 1994, Mortelliti et al. 2014), and aquatic systems (Resetarits and Wilbur 1989, Resetarits 2001, Kiflawi et al. 2003, Binckley and Resetarits 2005, 2007, 2008, Vonesh and Buck 2007, Vonesh et al. 2009, Deans and Chalcraft 2017, review: Blaustein 1999). However, these studies typically manipulate quality while holding size (and isolation) constant and are rarely designed to compare relative importance. The influence of quality frequently equals or exceeds that of size and distance when explaining population-level patterns of patch occupancy, turnover, and abundance in terrestrial systems (Fleishman et al. 2002, Collinge et al. 2003, Summerville and Crist 2004, Summerville et al. 2005, Mortelliti et al. 2014, but see Moilanen and Hanski 2001). However, size and quality are often confounded when concentrations of limiting resources are correlated with habitat area (see review in Haynes and Cronin 2004, Krauss et al. 2005, Rabasa et al. 2008), thus leaving open the question of which is driving observed patterns. In our study, patch size and patch quality are only confounded because size, along with predation risk, turns out to itself be an important component of perceived quality for ovipositing treefrogs, adding an additional layer of complexity to questions regarding the importance of patch quality vs. patch size and their interaction. The idea that organisms directly assess patch size as a component of patch quality has implications for how we integrate size and quality into conservation planning and how we manage for both individual species conservation and overall biological diversity (Hodgson et al. 2009, 2011, Mortelliti et al. 2010, Doerr et al. 2011).

The fact that in the presence of larger patches smaller patches that are readily utilized when there is no variation in patch size are not utilized reinforces the idea that perceived patch quality and resulting colonization rate are highly context dependent across multiple spatial scales (Resetarits et al. 2005, Resetarits and Binckley 2009, Hughey et al. 2012, Wesner et al. 2012, Deans and Chalcraft 2017, Resetarits and Silberbush 2016). Preferred habitats in one spatial context may be less so in another spatial context, depending upon characteristics of the individual patch, characteristics of surrounding patches (Resetarits et al. 2005), and the larger habitat matrix in which a patch is embedded (Deans and Chalcraft 2017). In this context, patch size itself becomes another niche dimension across which species may behaviorally sort in natural systems. Because of strong, shared avoidance of fish among many colonizing taxa, patch size may be a critical factor in species sorting and processes of community assembly in freshwater habitats, allowing species to behaviorally segregate along gradients of patch size in fishless ponds. Conversely, lack of variation in patch size may concentrate colonization activity, leading to intensification of species interactions and/or increased use of lesser quality, lower fitness patches. The fact that patch size effects on immigration dynamics are not simply a result of passive capture (target-area effect), but are also driven by active habitat selection based on size as a component of perceived patch quality, adds another layer of complexity to how we think about the role of patch size in metapopulation and metacommunity dynamics.

Acknowledgments

B. McDaniel, R. Kroeger, Z. Mitchell and T. Chavez assisted with fieldwork. Support was provided by The University of Mississippi, the Henry L. and Grace Doherty Foundation, and the UM Field Station.

Literature Cited

Abrams, P. A. 2007. Habitat choice in predator-prey systems: spatial instability due to interacting adaptive movements. American Naturalist 169:581–594.

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.

Ale, S. B., and C. J. Whelan. 2008. Reappraisal of the role of big, fierce predators!. Biodiversity and Conservation 17:685–690.

Alford, R. A., and H. M. Wilbur. 1985. Priority effects in experimental pond communities: competition between *Bufo* and *Rana*. Ecology 66:1097–1105.

Allen, L. J. 1987. Persistence, extinction, and critical patch number for island populations. Journal of Mathematical Biology 24:617–625.

Armsworth, P. R., and J. E. Roughgarden. 2005. The impact of directed versus random movement on population dynamics and biodiversity patterns. American Naturalist 165:449–465.

Arrhenius, O. 1921. Species and area. Ecology 9:95–99.

Bender, D. J., T. A. Contreras, and L. Fahrig. 1998. Habitat loss and population decline: A meta-analysis of the patch size effect. Ecology 79:517–533.

Binckley, C. A., and W. J. Resetarits Jr. 2003. Functional equivalence of non-lethal effects: generalized fish avoidance determines distribution of gray treefrog, *Hyla chrysoscelis*, larvae. Oikos 102:623–629.

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.

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. Wasser, editor. Evolutionary theory and processes: modern perspectives. Kluwer, Dordrecht, The Netherlands.

Cain, S. A. 1938. The species–area curve. American Midland Naturalist 41:573–581.

Chase, J. M. 2003. Community assembly: when should history matter? Oecologia 136:489–498.

Collinge, S. K., K. L. Prudic, and J. C. Oliver. 2003. Effects of local habitat characteristics and landscape context on grassland butterfly diversity. Conservation Biology 17:178–187.

Connor, E. F., and E. D. McCoy. 1979. The statistics and biology of the species–area relationship. American Naturalist 113:791.

Crooks, K. R., and M. E. Soule. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400:563–566.

Deans, R. A., and D. R. Chalcraft. 2017. Matrix context and patch quality jointly determine diversity in a landscape-scale experiment. Oikos 126:874–887.

Debinski, D. M., and R. D. Holt. 2000. A survey and overview of habitat fragmentation experiments. Conservation Biology 14:342–355.

Doerr, V. A. J., T. Barrett, and E. D. Doerr. 2011. Connectivity, dispersal behaviour and conservation under climate change: A response to Hodgson et al. Journal of Applied Ecology 48: 143–147.

Eason, G. W., and J. E. Fauth. 2001. Ecological correlates of anuran species richness in temporary pools: A field study in South Carolina, USA. Israel Journal of Zoology 47:347–365.

Estes, J. A., et al. 2011. Trophic downgrading of planet Earth. Science 333:301–306.

Fellers, G. 1979. Mate selection in the gray treefrog, *Hyla versicolor*. Copeia 1979:286–290.

Fleishman, E., C. Ray, P. E. R. Sjögren-Gulve, C. L. Boggs, and D. D. Murphy. 2002. Assessing the roles of patch quality, area, and isolation in predicting metapopulation dynamics. Conservation Biology 16:706–716.

Fretwell, S. D., and H. L. Lucas. 1970. On territorial behavior and other factors influencing habitat distribution in birds I. Theoretical development. Acta Biotheoretica 19:16–36.

Gleason, H. A. 1922. On the relation between species and area. Ecology 3:158–162.

Godwin, G. J., and S. M. Roble. 1983. Mating success in male treefrogs, *Hyla chrysoscelis* (Anura: Hylidae). Herpetologica 39:141–146.

Golden, D. M., and T. O. Crist. 1999. Experimental effects of habitat fragmentation on old- field canopy insects: community, guild and species responses. Oecologia 118:371–380.

Gotelli, N. J. 2008. A primer of ecology. Fourth edition. Sinauer Associates, Sunderland, Massachusetts, USA.

Gray, K., and G. Kennedy. 1993. Can ecological theory predict the distribution of foraging animals? A critical analysis of experiments on the ideal free distribution. Oikos 68:158–166.

Hanski, I. 1999. Metapopulation ecology. Oxford University Press, Oxford, UK.

Hanski, I., and M. E. Gilpin. 1997. Metapopulation biology: ecology, genetics, and evolution. Metapopulation biology. Academic Press, Cambridge, Massachusetts, USA.

Haynes, K. J., and J. T. Cronin. 2004. Confounding of patch quality and matrix effects in herbivore movement studies. Landscape Ecology 19:119–124.

Hodgson, J. A., C. D. Thomas, B. A. Wintle, and A. Moilanen. 2009. Climate change, connectivity and conservation decision making: back to basics. Journal of Applied Ecology 46:964–969.

Hodgson, J. A., A. Moilanen, B. A. Wintle, and C. D. Thomas. 2011. Habitat area, quality and connectivity: striking the balance for efficient conservation. Journal of Applied Ecology 48:148–152.

Hughey, M. C., M. W. McCoy, J. R. Vonesh, and K. M. Warkentin. 2012. Spatial contagion drives colonization and recruitment of frogflies on clutches of red-eyed treefrogs. Biology Letters 8:887–889.

Kadmon, R., and O. Allouche. 2007. Integrating the effects of area, isolation, and habitat heterogeneity on species diversity: a unification of island biogeography and niche theory. American Naturalist 170:443–454.

Kerfoot, W. C., and A. Sih. 1987. Page 386. Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, Germany.

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

Kneitel, J. M., and T. E. Miller. 2003. Dispersal rates affect species composition in metacommunities of *Sarracenia purpurea* inquilines. American Naturalist 162:165–171.

Kraus, J. M., and J. R. Vonesh. 2010. Feedbacks between community assembly and habitat selection shape variation in local colonization. Journal of Animal Ecology 79:795–802.

Krauss, J., I. Steffan-Dewenter, C. B. Müller, and T. Tscharntke. 2005. Relative importance of resource quantity, isolation and habitat quality for landscape distribution of a monophagous butterfly. Ecography 28:465–474.

Lee, D. S., C. R. Gilbert, C. H. Hocutt, R. E. Jenkens, D. E. McAllister, and J. R. Stauffer, editors. 1980. Atlas of North American freshwater fishes. North Carolina State Museum of Natural History, Raleigh, North Carolina, USA.

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.

Leibold, M. A., et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7:601–613.

Lima, S. L. 1998. Nonlethal effects in the ecology of predator–prey interactions. BioScience 48:25–34.

Lima, S. L. 2009. Predators and the breeding bird: Behavioral and reproductive flexibility under the risk of predation. Biological Reviews 84:485–513.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA.

McIntyre, N. E., and J. A. Wiens. 1999. How does habitat patch size affect animal movement? An experiment with darkling beetles. Ecology 80:2261–2270.

Mittelbach, G. G., A. M. Turner, D. J. Hall, J. E. Rettig, and C. W. Osenberg. 1995. Perturbation and resilience: A long-term, whole-lake study of predator extinction and reintroduction. Ecology 76:2347–2360.

Moilanen, A., and I. Hanski. 2001. On the use of connectivity in spatial ecology. Oikos 95:147–151.

Morris, D. W. 2003. Toward an ecological synthesis: A case for habitat selection. Oecologia 136:1–13.

Mortelliti, A., G. Amori, and L. Boitani. 2010. The role of habitat quality in fragmented landscapes: a conceptual overview and prospectus for future research. Oecologia 163:535–547.

Mortelliti, A., G. Sozio, D. Driscoll, L. Bani, L. Boitani, and D. Lindenmayer. 2014. Population and individual-scale responses to patch size, isolation and quality in the hazel dormouse. Ecosphere 5:1–21.

Öckinger, E., and H. G. H. Smith. 2006. Landscape composition and habitat area affects butterfly species richness in semi-natural grasslands. Oecologia 149:526–534.

Ockinger, E., et al. 2010. Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. Ecology Letters 13:969–979.

Orrock, J. L., J. H. Grabowski, J. H. Pantel, S. D. Peacor, B. L. Peckarsky, A. Sih, and E. E. Werner. 2008. Consumptive and nonconsumptive effects of predators on metacommunities of competing prey. Ecology 89:2426–2435.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist 100:65–75.

Peckarsky, B. L., et al. 2008. Revisiting the classics: considering nonconsumptive effects in textbook examples of predator-prey interactions. Ecology 89:2416–2425.

Pintar, M. R., and W. J. Resetarits. 2017. Out with the old, in with the new: oviposition preference matches larval success in Cope's Gray Treefrog, *Hyla chrysoscelis*. Journal of Herpetology 51:186–189.

Preisser, E. L., D. I. Bolnick, and M. F. Bernard. 2005. Scared to death? The effects of intimidation and consumption in predator–prey interactions. Ecology 86:501–509.

Prugh, L. R., C. J. Stoner, C. W. Epps, W. T. Bean, W. J. Ripple, A. S. Laliberte, and J. S. Brashares. 2009. The rise of the mesopredator. BioScience 59:779–791.

Pulliam, H. R., and B. J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. American Naturalist 137:S50–S66.

Rabasa, S. G., D. Gutiérrez, and A. Escudero. 2008. Relative importance of host plant patch geometry and habitat quality on the patterns of occupancy, extinction and density of the monophagous butterfly *Iolana iolas*. Oecologia 156:491–503.

Rausher, M. D. 1983. Ecology of host-selection behavior in phytophagous insects. Pages 223–257 *in* R. F. Denno and M. S. McClure, editors. Variable plants and herbivores in natural and managed systems. Academic Press, New York, New York, USA.

Rausher, M. D. 1993. The evolution of habitat preference: avoidance and adaptation. Pages 259–283 *in* K. Ke Chung and B. A. McPheron, editors. Evolution of insect pests: patterns of variation. John Wiley & Sons, New York, New York, USA.

Renwick, J. 1994. Oviposition behavior in Lepidoptera. Annual Review of Entomology 39:377–400.

Resetarits Jr., W. J. 1996. Oviposition site choice and life history evolution. American Zoologist 36:205–215.

Resetarits Jr., W. J. 2001. Colonization under threat of predation: avoidance of fish by an aquatic beetle, *Tropisternus lateralis* (Coleoptera: Hydrophilidae). Oecologia 129:155–160.

Resetarits Jr., W. J. 2005. Habitat selection behaviour links local and regional scales in aquatic systems. Ecology Letters 8:480–486.

Resetarits Jr., W. J., and C. A. Binckley. 2009. Spatial contagion of predation risk affects colonization dynamics in experimental aquatic landscapes. Ecology 90:869–876.

Resetarits Jr., W. J., and C. A. Binckley. 2013. Patch quality and context, but not patch number, drive multi-scale colonization dynamics in experimental aquatic landscapes. Oecologia 173: 933–946.

Resetarits Jr., W. J., and A. Silberbush. 2016. Local contagion and regional compression: habitat selection drives spatially explicit, multiscale dynamics of colonisation in experimental metacommunities. Ecology Letters 19:191–200.

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

Resetarits Jr., W. J., and H. M. Wilbur. 1991. Calling site choice by *Hyla chrysoscelis*: effect of predators, competitors, and oviposition sites. Ecology 72:778–786.

Resetarits Jr., W. J., 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.

Rieger, J. F., C. A. Binckley, and W. J. Resetarits Jr. 2004. Larval performance and oviposition site preference along a predation gradient. Ecology 85:2094–2099.

Rosenzweig, M. L. 1991. Habitat selection and population interactions: the search for mechanism. American Naturalist 137:S5–S28.

Ryberg, W. A., and J. M. Chase. 2007. Predator-dependent species–area relationships. American Naturalist 170:636–642.

SAS Institute Inc. 2016. Cary, NC, USA.

Saward-Arav, D., A. Sadeh, M. Mangel, A. R. Templeton, and L. Blaustein. 2016. Oviposition responses of two mosquito species to pool size and predator presence: varying trade-offs between desiccation and predation risks. Israel Journal of Ecology and Evolution 62:143–148.

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.

Schneider, C. A., W. S. Rasband, and K. W. Eliceiri. 2012. NIH Image to ImageJ: 25 years of image analysis. Nature Methods 9:671–675.

Seale, D. B. 1980. Influence of amphibian larvae on primary production, nutrient flux, and competition in a pond ecosystem. Ecology 61:1531–1550.

Shurin, J. B. 2001. Interactive effects of predation and dispersal on zooplankton communities. Ecology 82:3404–3416.

Singer, M. C. 1984. Butterfly–hostplant relationships: host quality, adult choice and larval success. Pages 81–88 *in* R. I. Vane-Wright, P. R. Ackery, and E. B. Ford, editors. The biology of butterflies. Published for the Royal Entomological Society by Academic Press, London.

Spencer, M., L. Blaustein, S. S. Schwartz, and J. E. Cohen. 1999. Species richness and the proportion of predatory animal species in temporary freshwater pools: Relationships with habitat size and permanence. Ecology Letters 2:157–166.

Stein, M., and L. Blaustein. 2015. Larval performance and oviposition habitat selection of the tree frog, *Hyla savignyi*, in response to conspecific larval density. Israel Journal of Ecology and Evolution 61:61–66.

Summerville, K. S., and T. O. Crist. 2001. Effects of experimental habitat fragmentation on patch use by butterflies and skippers (Lepidoptera). Ecology 82:1360–1370.

Summerville, K. S., and T. O. Crist. 2004. Contrasting effects of habitat quantity and quality on moth communities in fragmented landscapes. Ecography 27:3–12.

Summerville, K. S., R. M. Steichen, and M. N. Lewis. 2005. Restoring lepidopteran communities to oak savannas: Contrasting influences of habitat quantity and quality. Restoration Ecology 13:120–128.

Terborgh, J., J. Estes, P. Paquet, K. Rails, D. Boyd-Heger, B. Miller, and R. Noss. 1999. The role of top carnivores in regulating terrestrial ecosystems. Pages 39–64 *in* M. E. Soule and J. Terborgh, editors. Continental conservation: scientific foundations of regional reserve networks. Island Press, Washington, DC.

Thomas, J. A., N. A. D. Bourn, R. T. Clarke, K. E. Stewart, D. J. Simcox, G. S. Pearman, R. Curtis, and B. Goodger. 2001. The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. Proceedings of the Royal Society B 268:1791–1796.

Thompson, J., and O. Pellmyr. 1991. Evolution of oviposition behavior and host preference in Lepidoptera. Annual Review of Entomology 36:65–89.

Vonesh, J. R., and J. C. Buck. 2007. Pesticide alters oviposition site selection in gray treefrogs. Oecologia 154:219–226.

Vonesh, J. R., J. M. Kraus, J. S. Rosenberg, and J. M. Chase. 2009. Predator effects on aquatic community assembly: disentangling the roles of habitat selection and post-colonization processes. Oikos 118:1219–1229.

Wellborn, G. A., D. K. Skelly, and E. E. Werner. 1996. Mechanisms creating community structure across a freshwater habitat gradient. Annual Review of Ecology and Systematics 27:337–363.

Wesner, J. S., E. J. Billman, and M. C. Belk. 2012. Multiple predators indirectly alter community assembly across ecological boundaries. Ecology 93:1674–1682.

Wiens, J. A. 1976. Population responses to patchy environment. Annual Review of Ecology and Systematics 7:81–120.

Woodward, B. D. 1983. Predator-prey interactions and breeding-pond use of temporary-pond species in a desert anuran community. Ecology 64:1549–1555.

Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.2130/suppinfo