

REPORT

Island biogeography at the mesoscale: Distance from forest edge affects choice of patch size by ovipositing treefrogs

William J. Resetarits Jr.  | Kevin M. Potts  | Reed C. Scott 

Department of Biology and Centers for Water and Wetlands Resources and Biodiversity and Conservation Research, The University of Mississippi, University, Mississippi, USA

Correspondence

William J. Resetarits Jr.
Email: wresetarits@gmail.com

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Abstract

Diversity in habitat patches is partly driven by variation in patch size, which affects extinction, and isolation, which affects immigration. Patch size also affects immigration as a component of patch quality. In wetland ecosystems, where variation in patch size and interpatch distance is ubiquitous, relationships between size and isolation may involve trade-offs. We assayed treefrog oviposition at three patch sizes in arrays of two types, one where size increased with distance from forest (dispersed) and one with all patches equidistant from forest (equidistant), testing directly for an interaction between patch size and distance, which was highly significant. Medium patches in dispersed arrays received more eggs than those in equidistant arrays as use of typically preferred larger patches was reduced in dispersed arrays. Our results demonstrated a habitat selection trade-off between preferred large and less-preferred medium patches across small-scale variation in isolation. Such patch size/isolation relationships are critical to community assembly and to understanding how diversity is maintained within a metapopulation and metacommunity framework, especially as wetland habitat becomes increasingly rare and fragmented. These results bring lessons of island biogeography, writ large, to bear on questions at small scales where ecologists often work and where habitat restoration is most often focused.

KEYWORDS

colonization, compromise designs, habitat restoration, habitat selection, island biogeography, patch isolation, patch size, trade-offs

INTRODUCTION

Tension between the roles of patch size and patch isolation in determining species richness is a central feature of the equilibrium theory of island biogeography (MacArthur & Wilson, 1967), with isolation playing the

major role in determining immigration rate and size playing that role in extinction rate. But it is not a pure dichotomy; larger patches may also have greater immigration rates (target area hypothesis) (Connor & McCoy, 1979; Hanski, 1999), and less isolated patches may have lower extinction rates via rescue effects

Kevin M. Potts and Reed C. Scott contributed equally to this work.

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(Brown & Kodric-Brown, 1977; Gotelli, 1991). However, the role of patch size in immigration rate is even more complex because organisms may have preferences for patches of different sizes and possess different dispersal capabilities. Patch size functions as a niche dimension for ovipositing treefrogs (Resetarits et al., 2018), mosquitoes (Bohenek et al., 2017), and a diverse assemblage of aquatic insects (Resetarits et al., 2019). Different species express preferences for patches of different sizes, leading to species sorting at the immigration stage. Thus, depending on the taxa, the effects of patch size preferences can be either synergistic with or antagonistic to the passive effects of patch size on extinction or colonization rates. Similarly, the effect of distance injects complexity into the extinction side of the equation because of both variation in patch preferences and dispersal capabilities. If preferred patch types are also closer to the source of colonists, the potential exists for greater extinction rates because negative density dependence overcomes rescue effects. This extends to the community level if preferred patch types and dispersal abilities/tendencies are shared among species, resulting in a concentration of colonists in a subset of patches. The alternative is also true—differences in dispersal abilities/tendencies could result in species sorting among patches differing in isolation.

Cope's gray treefrog, *Hyla chrysoscelis*, has demonstrated a strong preference both for fishless habitats and larger patch size when choosing among relatively small patches (Resetarits et al., 2018; Resetarits & Wilbur, 1989), which are common in natural systems (Semlitsch & Bodie, 1998) and frequently the only fishless habitats available. Also, given a choice between open- and closed-canopy ponds, both *H. chrysoscelis* and *Hyla squirella* strongly prefer an open canopy (Binckley & Resetarits, 2007), and anuran population persistence is often negatively affected by canopy closure (Skelly et al., 1999). Oviposition within forested habitats by the cryptic sister taxon of *H. chrysoscelis*, *Hyla versicolor*, declined rapidly from core areas (consisting of existing breeding ponds) beginning at 5 m (Johnson & Semlitsch, 2003).

The effects of distance on treefrog oviposition arise from three factors: (1) difficulty in locating more distant ponds, (2) energetic and predation risk costs associated with movement, and (3) risk of desiccation. Thus, all else being equal, less distant ponds are better. But what happens when all else is *not* equal, and ponds vary in other factors that themselves generate strong impacts on oviposition (Resetarits, 2021)? We utilized a unique compromise design (Resetarits, 2021) that allowed us to examine how distance from a core habitat area, in this case forest, affected treefrogs' strong preference for large patches. We handicapped patches of the preferred patch type (large)

by placing them at a greater distance from the forest edge and enhanced the potential attractiveness of small and medium patches by placing them closer to the forest, allowing us to test specifically for a size \times distance interaction. We placed patches of three sizes in two configurations (equidistant and dispersed, which is the terminology we will use hereafter), either arrayed linearly along the forest edge (equidistant patches—control on distance effects) or arranged roughly perpendicular to the forest edge (dispersed patches) in reverse order of preference (small < medium < large) (Figure 1a). We were guided by three specific hypotheses based on prior work (Resetarits et al., 2019):

1. Oviposition in small patches, which are virtually ignored when larger patches are available, would substantially increase in dispersed arrays.
2. Medium patches, which normally receive just a fraction of the eggs deposited in large patches, would experience an increase in dispersed arrays because they are preferred over small patches and closer than large patches.
3. Large patches more distant from the forest edge would receive fewer eggs than those adjacent to the forest edge (Figure 1b).

MATERIALS AND METHODS

Our experiment was conducted in a large, treeless old field at the University of Mississippi Field Station, Lafayette County. We constructed mesocosm arrays (blocks) of two types using three pool sizes (1.13, 2.54, and 5.73 m²), hereafter referred to as small, medium, and large; pools were of the same material, color, and shape (cylindrical). The largest pools were 13 cm taller, which we compensated for by filling all pools to the same depth (50 cm). Dispersed arrays were arranged in two spatial blocks, with four replicates in each block of small, medium, and large pools placed at increasing distances from the forest edge (5, 15, and 25 m, respectively) ($N = 24$) (A, B in Figure 1a). Additionally, we set up four equidistant arrays, each with one small, medium, and large pool arranged in linear blocks with all pools adjacent to the forest and positions randomly assigned ($N = 12$). Thus, we could compare preferences for patch size when all patches were equally accessible (controls) to those same patch sizes with distance as a factor. Equidistant pools (along with two dedicated interceptor pools) also served to intercept colonists coming from directions other than the primary direction of interest in the two dispersed arrays (Figure 1a), which were established

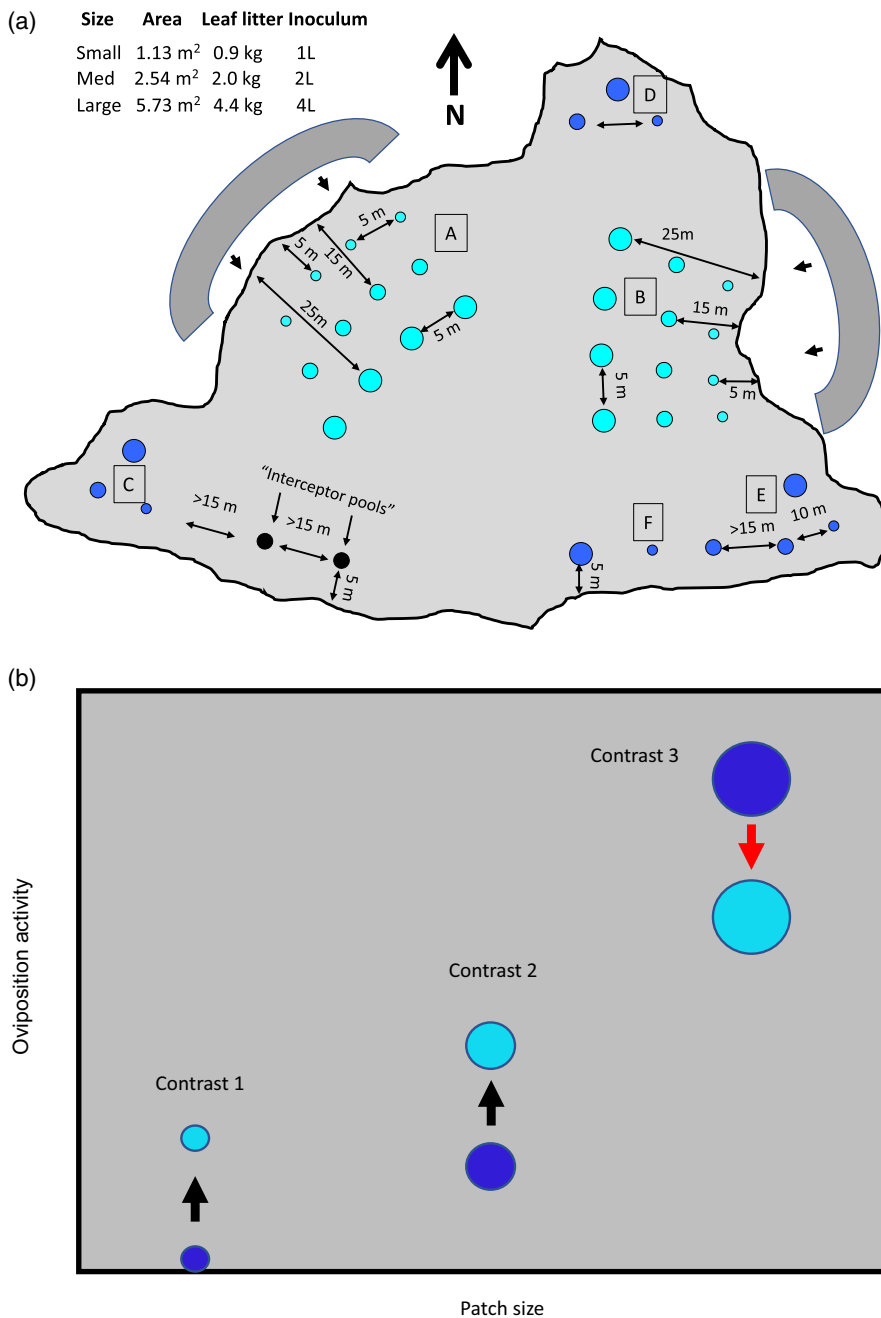


FIGURE 1 (a) Physical layout and treatment summary of experimental landscapes in an old field at University of Mississippi Field Station, approximately to scale. Blue = equidistant, cyan = dispersed, black = dedicated interceptor pools (not included in analysis). Letters indicate spatial blocks. Gray arc indicates expected direction of arrival of female treefrogs in dispersed arrays, based on prior experiments. (b) Schematic of results of a previous experiment/expectations for equidistant patches (blue) and expected results for mean total eggs in dispersed patches (cyan). Hypothesis tests consist of three, one-tailed, a priori contrasts comparing equidistant to dispersed for each patch size (see *Methods*). Arrows indicate predicted direction of effects (direction of one-tailed test): black = positive, red = negative

based on previous experiments. This was necessary in order to actually implement the distance component because of the limited size of our site. It was successful in that large “corner” pools, which were roughly equidistant to forest in two directions, did not receive more eggs than large “interior” pools.

We filled pools with well water from 5 to 7 May 2020. 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, and 4.4 kg, respectively). On 9 May all pools received aliquots of pond water (1, 2, and 4 L, respectively) to serve as a

zooplankton and phytoplankton inoculum, and screen lids were submerged to begin the experiment. We checked every morning and eggs were removed, photographed, and placed in rearing tanks or natural fishless ponds. We counted eggs from photographs using ImageJ (Bohenek & Resetarits., 2017; Schneider et al., 2012). The experiment was ended 1 week early, on 23 July, because of increasing local COVID-19 infection rates.

Our experiment was a nested design, with size nested within treatment (dispersed or equidistant), which precludes independent tests of size or distance effects but tests for an interaction between size and distance. The primary response variable was the mean total number of eggs/patch, which we decomposed into two components, total breeding events (eggs in a patch on a night), and mean deposition per patch (eggs/event). Our main hypothesis tests were a series of orthogonal, a priori one-tailed (two-tailed for mean deposition) contrasts testing three specific hypotheses:

1. Small patches in dispersed arrays would have more total eggs and breeding events than small patches in equidistant arrays.
2. Medium patches in dispersed arrays would have more total eggs and events than medium patches in equidistant arrays.
3. Large patches in dispersed arrays would have fewer total eggs and events than large patches in equidistant arrays (Figure 1b).

Our hypothesis for mean deposition was that there would be no differences between equidistant and dispersed patches of any size, because once females chose a patch, they would deposit their entire clutch. Egg counts were log transformed and events square-root transformed in a general linear mixed model analysis of variance (ANOVA), with size nested within distance (dispersed or equidistant) as a fixed effect and block as a random effect, using PROC MIXED (SAS Institute 2016) in SAS version 9.4 (SAS Institute 2016) with Type III sums of squares and $\alpha = 0.05$.

RESULTS

Treefrogs laid 185,152 eggs, spread over 38 nights, with 344 breeding events in 25/36 patches. As expected, patch size (nested within treatment) was highly significant for mean total eggs ($F_{5,26} = 5.88$, $p = 0.0009$) (Figure 2a; Appendix S1: Table S1). One of our three a priori contrasts for mean total eggs was significant, with medium patches getting significantly more eggs in the dispersed patches than in the equidistant patches, as predicted ($df = 26$, $t = 1.85$, $p = 0.0376$, Cohen's $d = 0.67$), with a moderately

large effect size, while the contrast for small ($df = 26$, $t = 0.37$, $p = 0.3578$, Cohen's $d = -0.01$) and large patches ($df = 26$, $t = 0.92$, $p = 0.8168$, Cohen's $d = -0.20$) were not significant, with no detectable effect in the small patches and a very small effect size in large patches. The increase in the mean number of eggs in medium dispersed patches (1496) closely mirrored the mean reduction in eggs in the large dispersed patches (1913), but the latter comparison (Contrast 3) was complicated by extremely high variance among large equidistant patches, including one large patch that received no eggs (Block F), which never happened before this. Exclusion of this block did not change the results, but it does suggest that the distance effect may be stronger than shown here, as the highly significant interaction would suggest.

Decomposing mean total eggs into its two components, mean breeding events and mean deposition, we get a clearer picture of how eggs were parsed among patch types. Size (nested within treatment) was highly significant for both events ($F_{5,26} = 7.22$, $p = 0.0002$) and mean deposition ($F_{5,26} = 5.07$, $p = 0.0020$) (Figure 2b,c). None of the contrasts was significant for mean events (Appendix S1: Table S1a). For mean deposition, the medium contrast was marginally nonsignificant ($df = 26$, $t = 1.99$, $p = 0.0574$, Cohen's $d = 0.88$), with a large effect size, and nonsignificant for small and large (Appendix S1: Table S1b,c).

The distance effect is shown clearly in the cumulative proportion plot in which, for half of the experiment, large equidistant patches got 100% of the eggs in equidistant patches, and the proportion fell to no lower than 88% at the end, while large dispersed patches fluctuated around 80% of the total laid in dispersed patches throughout the experiment, finishing at 78%, with the remainder in medium patches (Figure 2d).

DISCUSSION

Patch size and isolation are central concepts in ecology, and understanding the interplay between the two is important to understanding patterns of distribution and diversity, as well as preserving and restoring that diversity. We often think of size variation and variation in isolation at larger scales, for example, larger patch sizes and greater isolation, but smaller-scale variation may be critically important for both size and isolation. The theory of island biogeography, while classically used to describe immigration and extinction on larger-habitat islands, has been applied at smaller scales from microscopic organic aggregates (Lyons et al., 2010), to holes in glacier surfaces (Darcy et al., 2018), to the study presented here looking at the scale of a few meters. A variety of aquatic taxa, including treefrogs, mosquitoes, beetles, and true bugs,

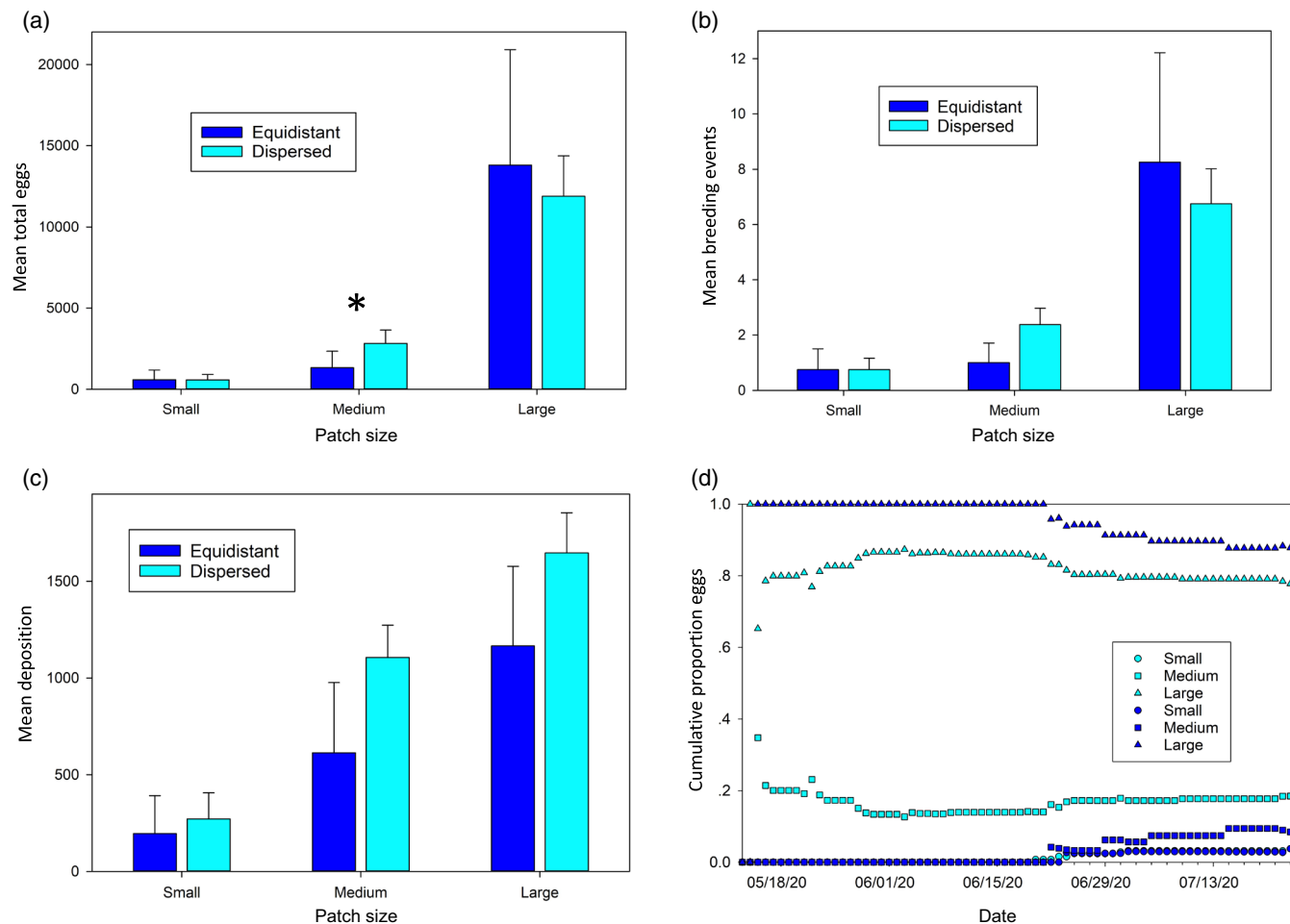


FIGURE 2 Data for (a) mean total egg number, (b) breeding events (egg/pool/night), and (c) mean deposition (eggs/breeding event); asterisks indicate significantly different contrasts. (d) Plot of cumulative proportion of total eggs distributed between patch sizes in equidistant (blue) and dispersed treatments (cyan). Very few eggs were laid in small patches.

have strong preferences among patch sizes at the small end of the scale (~1–6 m²), and that variation in preferences generates species sorting across a gradient of patch sizes (Bohenek et al., 2017; Resetarits et al., 2018, 2019). Ovipositing gray treefrogs strongly prefer the largest patches in this range (Resetarits et al., 2018) and also show some sensitivity to patch isolation, distance from either a source pond (Johnson & Semlitsch, 2003) or forest edge (unpublished data). Gray treefrogs also strongly prefer open-canopy ponds when available (Binckley & Resetarits, 2007). We took advantage of the preference for larger and more open patches, along with dispersal tendencies, to test the distance/patch size trade-off over a spatial scale in the tens of meters.

Contrary to expectations, small patches in the dispersed arrays did not receive more eggs than in the equidistant arrays, suggesting that the difference in perceived habitat quality between small patches and larger patches is quite robust—small patches are avoided if there are any available options. In contrast, medium patches

benefitted from being closer to the forest edge compared to large patches. Though the contrast is not significant, the decrease in the large patches largely matches the increase in medium patches (Figure 2). This is produced by the higher mean deposition in medium dispersed patches, and those increases come at the expense of large patches. Increases observed in mean deposition in more distant patches may result from more females/night or eggs/female (larger females). The cumulative proportion plot (Figure 2d) clearly shows the distance effect on large and medium patches.

For desiccation-prone organisms like treefrogs, venturing out into open, drier, treeless habitat carries considerable risk (Schmid, 1965; Watling & Braga, 2015; Wells, 2010). Besides desiccation, movement to and between patches also involves significant predation risk, as well as inherent energy costs, which are particularly high for gravid females (Wells, 2010). Here we attempted to estimate how greater distance from forest habitat (where treefrogs live) affected habitat preferences.

Though effects were not large, neither were the distances, so we would expect much greater effects at larger distances from the forest than we can generate at our site. Why is this important? To understand species distributions on the landscape scale, it is important to have a grasp of the absolute and relative dispersal abilities of the component species, their habitat preferences, the specific characteristics of a patch, where that patch is located, what other habitat patches are available, and at what distances. We also know that context is important in terms of the terrestrial matrix (Deans & Chalcraft, 2017; Richter-Boix et al., 2007; Vandermeer & Carvajal, 2001). Distance costs would be reduced in a forested landscape because less ground travel is required, so there is less exposure to terrestrial (vs. arboreal) predators, and because higher humidity reduces water loss (Watling & Braga, 2015). In pre-Columbian times, the vast majority of breeding sites for gray treefrogs in Eastern North America were in forested landscapes with various degrees of canopy closure. However, with massive increases in human impacts, that dynamic has dramatically changed, and, coupled with the gray treefrog's strong preference for open-canopy ponds, distance effects become more important as breeding increasingly occurs in human-altered landscape habitats (Hocking & Semlitsch, 2007; Semlitsch et al., 2009).

Consideration of patch size and isolation has been central to the development of nature reserve design, an area where there is growing interest in the role of patch quality, particularly in the context of climate change, thus altering the nature of the single large or several small (SLOSS) debate (Cody & Diamond, 1975). The equilibrium theory of island biogeography is central to the SLOSS debate, supporting dynamic approaches to modeling species diversity (Tjørve, 2010). This recent shift in focus to include patch quality in conservation planning emphasizes the need to better understand the relative contribution of these critical factors (size, quality, and connectivity) and their effects on colonization rates and resulting population, community, and metacommunity dynamics (Doerr et al., 2011; Hodgson et al., 2009, 2011; Mortelliti et al., 2010). Dispersal capabilities are a critical consideration but must be linked to habitat preferences of target organisms. If aquatic habitats are being managed or constructed to maintain or increase landscape-scale (beta) diversity, dispersal abilities and habitat preferences of the entire suite of species must be considered. Providing variety in patch size, location, duration, and other measures of quality are critical considerations for maintaining and generating biodiversity.

H. chrysoscelis females can assess many sources of variation in patch quality directly. Though we can speculate on factors that might vary with patch size, very little is actually known regarding variation among patches

at this smaller end of the size spectrum (where *H. chrysoscelis* frequently breed) in terms of, for example, predator density, permanence, and productivity. An obvious choice is density (Wilbur, 1987), but a strong preference for larger patches can lead to higher, not lower, densities. Permanence may scale positively with patch size, but in natural systems, hydroperiod is more dependent on depth, vegetation, and underlying hydrology (Eason & 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 these directly (Alford & Wilbur, 1985; Binckley & Resetarits, 2007, 2008; Pintar & Resetarits, 2017; Seale, 1980). *H. chrysoscelis* are also capable of directly assessing the presence/absence of fish, and younger ponds may be a better predictor of the presence/abundance of nonfish predators than pond size (D. W. Schneider & Frost, 1996), though both may be important (Spencer et al., 1999; Woodward, 1983). It remains to be determined what sources of variation in expected fitness *H. chrysoscelis* are tracking in larger patches.

For gray treefrogs, the passive aspects of larger patch size (target-area effect) and the active, habitat selection aspects are in sync. Larger patch size leads to a passive increase in colonization, and colonizing individuals also actively select larger patches. Patch size is a component of perceived patch quality for treefrogs, while distance is a cost. Factoring in distance suggests that this reinforcement may dilute distance effects versus a situation where no preference exists or where the passive and active effects are opposed, as seen in several beetle species and mosquitoes that prefer smaller patches (Bohenek et al., 2017; Resetarits et al., 2019). The effects of distance also depend on how organisms locate suitable habitat. For treefrogs the assumption is that they use chemical cues. The Field of Dreams hypothesis ("if you build it, they will come") (Palmer et al., 1997) is well supported by work on ovipositing treefrogs (e.g., Binckley & Resetarits, 2003, 2005; Kraus & Vonesh, 2010; Resetarits et al., 2018; Resetarits & Wilbur, 1989; Vonesh et al., 2009). Despite the conventional wisdom that amphibians are highly philopatric (Duellman & Trueb, 1986), treefrogs very quickly colonize newly constructed ponds if local populations exist, making restoration of habitat feasible. Alternatively, ponds can be "seeded" with larvae to establish new or restore locally extinct populations. Our experiment suggests that both size and distance are important considerations in any restoration strategy.

Again, the important message here is that a trade-off between distance and patch size/quality in habitat selection exists and is important even at small scales, and that effect is accentuated in the highly variable mosaic

landscapes of wetlands. Studies of habitat preferences should take distance from source population or source habitat into account to avoid confounding the passive effects of distance or size with active preferences. Unconventional experimental designs can be useful to tease apart components of both passive immigration effects and habitat selection across multiple axes. Habitat preferences can be very strong along a given axis of patch quality (e.g., size, predators, canopy cover), obscuring variation that could arise from other factors (Binckley & Resetarits, 2007; Resetarits et al., 2018). The use of two different factors, patch size and distance, and two different array types, dispersed and equidistant, in a “compromise” design that could not be truly interspersed allowed us to identify the interaction of size and distance and identify a relatively weak, but meaningful, effect of distance at a small scale. This brings the lessons of island biogeography, writ large (Losos & Ricklefs, 2009; MacArthur & Wilson, 1967; Santos et al., 2016), to bear on questions posed at the small to moderate scales, where ecologists often work and where habitat restoration efforts are most often focused.

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DATA AVAILABILITY STATEMENT

Data (Resetarits et al., 2022) are available in Dryad at <https://doi.org/10.5061/dryad.6t1gljx1v>.

ORCID

William J. Resetarits Jr.  <https://orcid.org/0000-0002-0197-1082>

Kevin M. Potts  <https://orcid.org/0000-0001-7293-7087>

Reed C. Scott  <https://orcid.org/0000-0003-2843-6095>

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SUPPORTING INFORMATION

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