

Between a rock and a hard place: Ovipositing treefrogs navigate complex trade-offs in the landscape of patch quality

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Citation: Resetarits Jr., W. J. 2021. Between a rock and a hard place: Ovipositing treefrogs navigate complex trade-offs in the landscape of patch quality. *Ecosphere* 12(5):e03524. 10.1002/ecs2.3524

Abstract. Colonizing organisms actively choosing habitats face a bewildering array of choices regarding patch quality, whether choosing for themselves, offspring, or both. Decisions are especially critical when selecting patches for long-term use (demographic habitat selection). Thus, identifying higher quality patches based on available cues, and integrating information across multiple axes of patch quality, is critical to survival, performance, and fitness. Two critical axes of patch quality for ovipositing gray treefrogs, revealed by prior experiments, are predation risk and patch size. We utilized a unique design presenting two, suboptimal patch choices: small fishless pools and large pools with fish. Our goal was to gain an understanding of the relative priority of these two important patch characteristics for treefrogs by presenting only compromise choices and comparing these results to expectations generated by a previous experiment. In the absence of optimal patches, treefrogs increased their use of both large pools with fish and especially small fishless patches, both of which are unused when larger fishless patches are available. These results reaffirm the primacy of predation, especially the presence of fish, vividly illustrating the spatial context dependence of habitat selection behavior, as well as the complexity of the decisions faced by colonizing and ovipositing organisms in complex landscapes.

Key words: colonization; compromise; context dependence; demographic habitat selection; patch quality; predation risk.

Received 11 October 2020; revised 31 December 2020; accepted 14 January 2021; final version received 15 March 2021. Corresponding Editor: Jeff S. Wesner.

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INTRODUCTION

Colonizing organisms that actively choose habitats face a bewildering array of decisions with regard to axes of patch quality. This is true whether they are choosing for themselves alone, for their offspring, or both (Refsnider and Janzen 2010). Thus, the ability to identify indicators of quality habitat patches based on available cues and to integrate information across multiple axes of patch quality is critical to individual survival, performance, and fitness (Singer 1984, Thompson

and Pellmyr 1991, Rausher 1993, Resetarits 1996). However, organisms cannot have perfect knowledge of the potential fitness landscape (*sensu* the Ideal Free Distribution; Fretwell and Lucas 1970), and nature rarely presents an optimal choice, so understanding how and when organisms compromise (Resetarits et al. 2005) is critical to predicting how colonizing organisms distribute themselves across a complex landscape of habitat patches.

Habitat selection is especially critical when patches are selected for long-term use, as exemplified by nest-site selection in birds (Schmidt

2004, Emmering et al. 2018), denning in mammals (Fernández and Palomares 2000, Davies et al. 2016), oviposition site choice in amphibians (Resetarits and Wilbur 1989, Rudolf and Rödel 2005, Touchon and Worley 2015), colonization/oviposition by phytophagous and aquatic insects (Sadeh et al. 2009, Berger et al. 2012, Friberg et al. 2016, Resetarits and Pintar 2016), and even settlement in sessile marine organisms (Price 2010, Dumas et al. 2014). These habitat selection decisions are enduring and may even be permanent, as is the case with many oviposition decisions, and occur at a specific life-history transition point. They constitute demographic, in contrast to transient, habitat selection, because these decisions directly affect population sizes in specific habitat patches. In addition to effects on individual fitness, population demography, and community assembly, modeling suggests that habitat selection has greater adaptive potential than either adaptive plasticity or divergent natural selection (Nicolaus and Edelaar 2018).

Many organisms that colonize freshwater habitats have complex life cycles with terrestrial adults who choose habitat patches for their offspring, and that choice is the only parental care provided. Examples include the majority of amphibians (Duellman and Trueb 1986) and a wide variety of insects (Merritt et al. 2008). Freshwater habitats also exhibit extreme spatial and temporal variation in resources and risk, as well as many physico-chemical parameters, that affect patch quality (Wellborn et al. 1996). Many colonizing/ovipositing organisms can evaluate patch quality and make decisions based on a proximate assessment of quality (Resetarits and Wilbur 1989, Blaustein 1999, Vonesh et al. 2009, Buxton and Sperry 2017). However, the quality of a given patch is not static over time, and quality, as well as perceived quality, is context dependent, depending on both the habitat matrix and the number and characteristics of nearby patches (Resetarits 2005, Resetarits and Binckley 2009, Resetarits and Silberbush 2016, Deans and Chalcraft 2017, Trekels and Vanschoenwinkel 2019). A critical gap in our knowledge is how the components that determine patch quality are weighed and prioritized by colonizers.

We have established the importance of predation risk (Binckley and Resetarits 2003, 2008, Rieger et al. 2004, Resetarits 2005), as well as patch

size (Resetarits et al. 2018), canopy cover (Binckley and Resetarits 2007), and nutrients/resources (Binckley and Resetarits 2008) in oviposition site choice by treefrogs. The difficulty in ranking the importance of these factors and how these factors are integrated and prioritized has been that, when given a set of choices that includes an optimal habitat, the vast majority of females choose that habitat to the exclusion of all others. Thus, in an experiment with Cope's gray treefrogs (*Hyla chrysoscelis*), crossing patch size, and the presence of fish, almost all of the eggs were laid in large fishless patches (Resetarits et al. 2018), even though treefrogs will lay eggs in much smaller patches when larger patches are not available (Resetarits and Wilbur 1989, Rieger et al. 2004, Resetarits 2005). Similarly, when presented with a gradient of canopy cover and nutrients, canopy dominates, swamping the variation in nutrients (Binckley and Resetarits 2007).

One approach to this dilemma is to provide sets of patches that do not contain the optimal type, but provide alternatives that are a compromise across axes of preference. Because of the strength of previously established preferences with regard to patch size and the previously established binary responses to fish (both fish density and species identity; Binckley and Resetarits 2003, Rieger et al. 2004, Resetarits et al. 2018), our design here focused on the extremes of these two gradients—large vs. small and fish vs. fishless. When presented a choice between large and small patches, no eggs are deposited in small patches, and when presented a choice between fish and fishless patches of the same size, <4% are laid in patches with fish (Resetarits et al. 2018). Thus, though a response surface design crossing patch size and predation risk would be more typical, it does not force the kind of difficult compromise we are interested in exploring, and it is also unrealistic because of the threshold response to fish presence. A further complication with presenting a gradient of predation risk is that we simply have no way of knowing that the treefrogs actually perceive the variation in risk, or simply do not perceive the presence of fish below a threshold. Our design also precludes providing a true control, but we can base expectations and compare the results to a prior experiment, conducted at the same site on approximately the same dates, in a prior year,

that unequivocally established these strong preferences (Resetarits et al. 2018).

We conducted an experiment in naturally colonized experimental landscapes to tease apart the relative importance of patch size and predation risk for ovipositing gray treefrogs. We utilized a design that presented two different suboptimal choices, small, fishless pools, and large pools with fish, asking how ovipositing females prioritized these two important patch characteristics in choosing larval habitat. We compare these results to a prior experiment where, in addition to these patch types, the preferred habitat type, larger fishless patches, was available (Resetarits et al. 2018). Our expectation, given the absence of higher quality patches, was that ovipositing females would achieve some form of compromise, either choosing one patch type over the other or distributing eggs across both patch types in some fashion.

MATERIALS AND METHODS

Our experiment was conducted in a large old-field at the University of Mississippi Field Station (UMFS) in Lafayette County, Mississippi. We constructed six triangular mesocosm arrays (blocks) of three pools each ($N = 18$; Fig. 1), partially crossing two pool sizes (1.13 and 5.73 m²) with the presence/absence of a mixed assemblage of green sunfish (*Lepomis cyanellus*), golden topminnows (*Fundulus chrysotus*), and golden shiners (*Notemigonus crysoleucus*; Fig. 1). A similar species combination had been used in a previous experiment and strongly repelled oviposition by *H. chrysoscelis* (Resetarits et al. 2018). Pools were of the same material, color, and shape (cylindrical), though the large pools were 13 cm taller, which we compensated by filling all pools to the same depth (50 cm). Thus, pools held ~525 and 2650 L, respectively. Within each block, there were two small fishless pools and one large pool with fish in order to reduce the effects of density on any given night. A single small pool could quite easily saturate and oviposition spill over into large pools, obviating our main question. Large pools were randomly assigned to a position within each array (Fig. 1).

We filled pools on 20–21 May with well-water, three blocks/day, and on 21 May added size-scaled inocula of pond water (zoops; Fig. 1) from

a fishless pond and aliquots of leaf litter (mixed hardwoods; Fig. 1). On 22 May, we added 18 fish, three of each species, to the large pools, the same density as in the previous experiment (Resetarits et al. 2018). This density is on the lower end of biomass density used in previous experiments and in natural ponds, but above the threshold that elicits avoidance in *Hyla* species (Rieger et al. 2004, Resetarits et al. 2018; W. J. Resetarits, *unpublished data*). On 24 May, screen lids were submerged to allow oviposition and 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 (Bohenek and Resetarits 2017). Block 6 received only 817 eggs laid in a single patch (small fishless) on one night and was excluded a priori from the analyses. The last eggs were laid on 23 July and the experiment terminated on 26 July.

Our primary response variables were the total number of eggs/patch and scaled number of eggs/patch, with individual patches as the unit of analysis. Scaled data were based on relative surface area and volume, since depth was constant among sizes, and scaled to the size of the smallest patches (small = total eggs/1; large = total eggs/5.06). Egg data were log-transformed ($\log_{10}(x + 1)$) and analyzed in a generalized linear mixed model ANOVA with block as a random effect, using PROC MIXED. Repeated-measures analysis of the oviposition pattern for 2019 used log-transformed scaled egg number in a GLMM with patch as a random effect with a negative binomial distribution (due to large number of zeros) and a log-link function. We also regressed number of eggs (untransformed) laid in the non-preferred treatment(s) on a given night vs. total eggs on that night for both years. All analyses used SAS v. 9.4 (SAS Institute Inc., Cary, NC, USA) with type III sums of squares and $\alpha = 0.05$.

RESULTS

A total of 83,772 eggs were laid in the five blocks included in the analyses. There was no significant difference in the mean total number of eggs laid in individual large patches with fish and individual small fishless patches ($F_{1,9} = 0.17$,

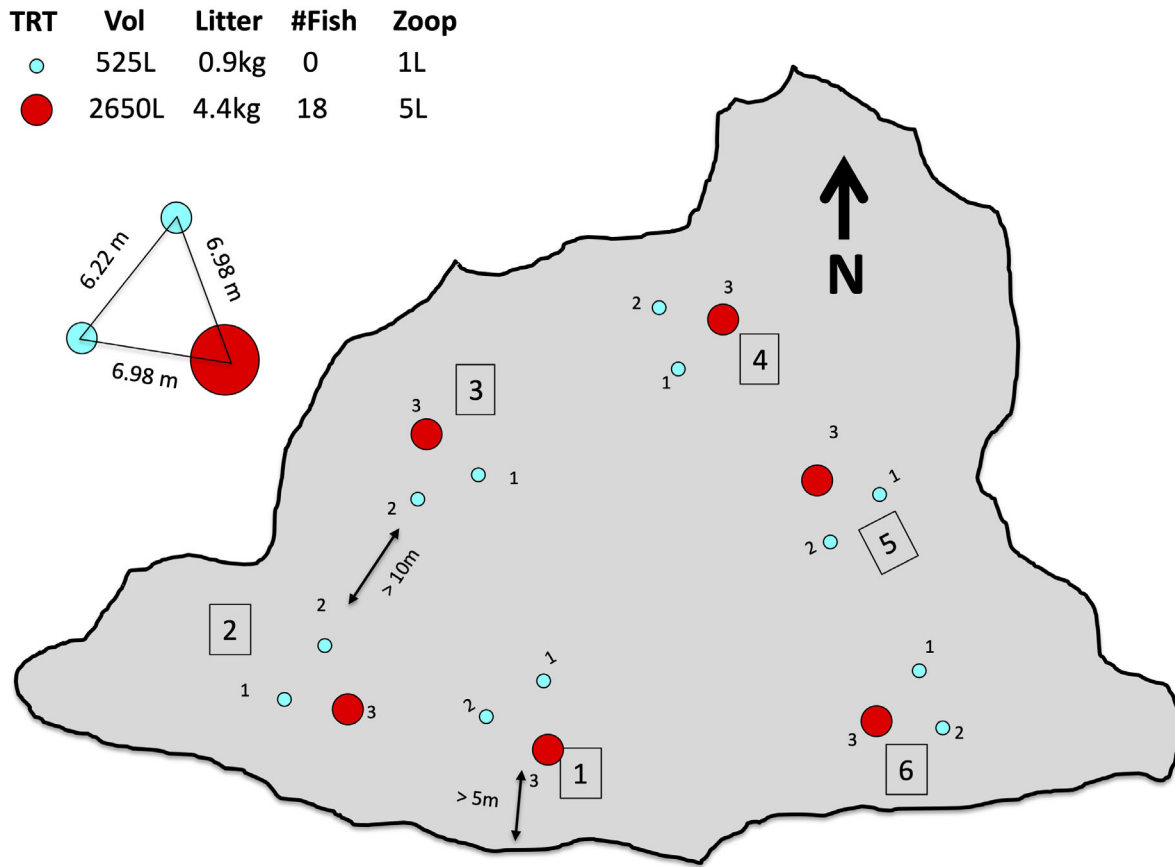


Fig. 1. Physical layout of the experiment, not precisely to scale. Red = fish, cyan = fishless. Oldfield is surrounded by mixed forest. Block six was virtually unused and not included in analyses.

$P = 0.694$), which means that within a block, and across the experiment, approximately twice as many eggs were laid in small fishless patches (55,889 eggs in 44 oviposition events over 24 nights, 67%) vs. large patches with fish (27,883 eggs in 22 events over 14 nights, 33%; Fig. 2a). If we decompose number of eggs laid into mean oviposition events (eggs in a patch on a night = hits) and mean deposition (eggs/hit), the numbers are almost identical; large patches with fish had a mean of 4.4 hits/patch and 1267 ± 928 eggs/hit (range 29–3342), while small fishless patches had a mean 4.4 hits/patch and 1270 ± 904 eggs/hit (range 317–5859). This even distribution resulted large differences in egg density between the two patch types. The only noteworthy difference was that large patches with fish had 3/22 hits that contained less than 100

eggs, while small fishless had 0/44; these three hits are clearly far less than the smallest clutch size (~300), and thus represent attempts that were either begun or ended in another patch. The 2016 experiment (Resetarits et al. 2018), which had six treatments, shows a very different pattern; when large patches with fish were available, the vast majority of eggs were in those patches (63,076/76,925 total eggs, in 71 oviposition events over 35 nights) with many fewer in medium fishless (11,126 in 15 events over 14 nights), and a scattering of eggs in large patches with fish (1876 in three events on three nights), and medium fish (1018 in events on three nights), with no eggs in either small fishless or small fish patches (Fig. 2a). The large patches with fish in 2016 had a much higher mean (vs. 2019) of 14.2 hits/patch and much more even distribution with

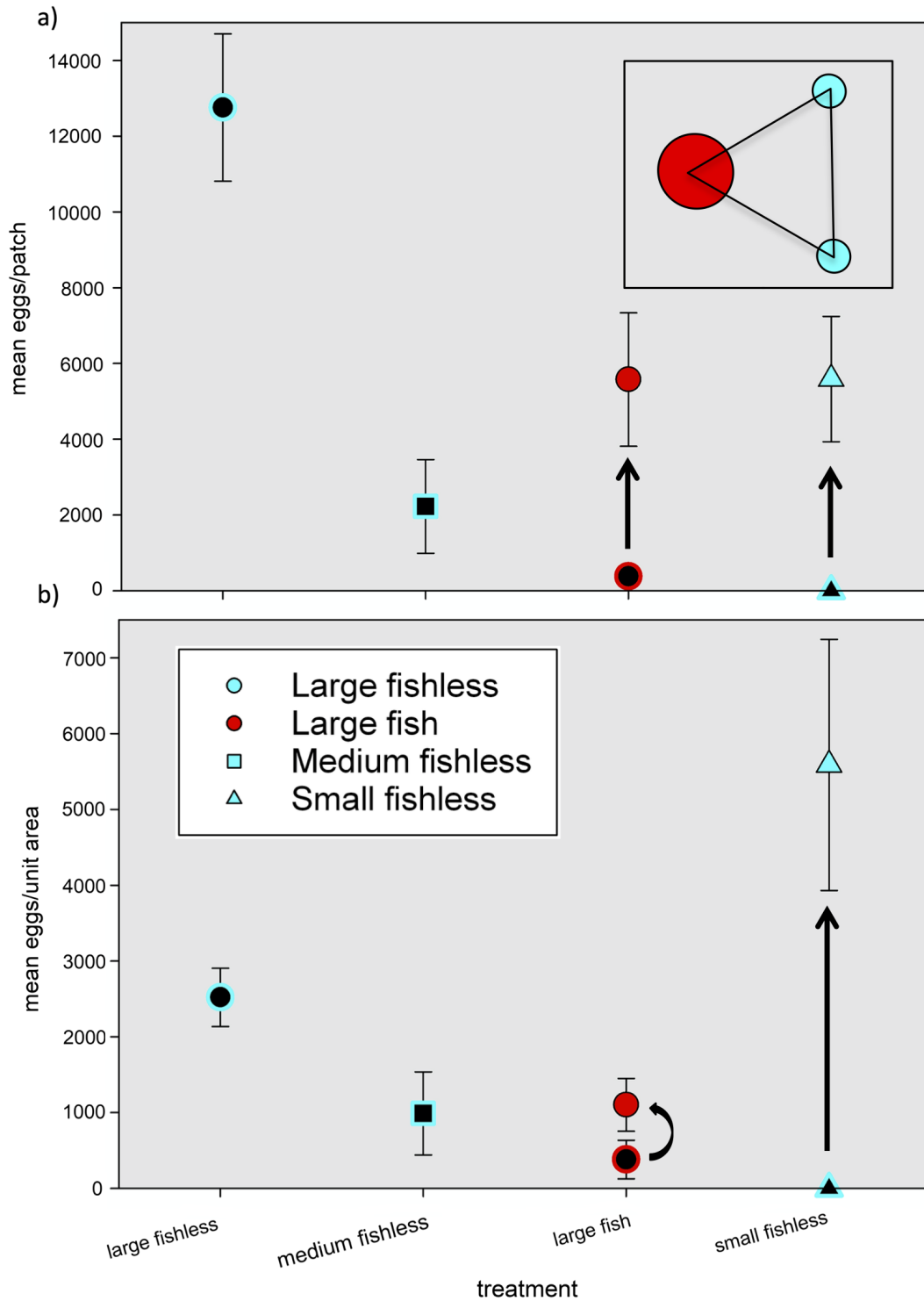


Fig. 2. (a) Mean eggs/patch and (b) scaled eggs/patch for 2016 (open symbols; data, Resetarits et al. 2018) and 2019 (closed symbols) experiments. Red = fish, cyan = fishless. Inset illustrates layout of a single block. Arrows indicate boost for large patches with fish and small fishless patches when preferred patch types (medium and, especially, large fishless) are unavailable.

889 ± 400 eggs/hit (range 43–2080). Only 3/71 hits had fewer than the estimated minimum clutch size.

The number of eggs scaled to the size of tanks was significantly different between large patches with fish and small fishless patches ($F_{1,9} = 7.84$, $P = 0.0207$; Fig. 2b), with egg density much higher in the smaller patches (Cohen's $d = 7.78$). In the 2016 experiment, by way of contrast, egg density was significantly higher in the large fishless patches, though not as dramatically different (Cohen's $d = 1.74$), emphasizing the dominance of large fishless patches, when available, as favored oviposition sites (Resetarits et al. 2018).

It is instructive to look at the cumulative number of eggs/time, across the duration of both experiments. In 2019, eggs were roughly evenly distributed between large patches with fish and small fishless patches for the first week of the experiment, then diverged to favor large patches with fish during the second week, after which almost all eggs were laid in small fishless patches (Fig. 3a). Repeated-measures ANOVA on scaled eggs showed a significant treatment × time interaction ($F_{2, 373} = 3.28$, $P = 0.0385$), as is clearly evident in the cumulative egg plot (Fig. 3a). The pattern for the 2016 experiment was very different, with large fishless patches dominating from the beginning (Fig. 3b). We also looked at whether density dependence, in terms of breeding activity on a given night, might explain the number of eggs in less preferred habitat. Data from both 2016 (Fig. 4) and 2019 (Fig. 5) show a significant positive relationship between total eggs on a given night and eggs in the less preferred patch type (s) (2016 $n = 37$, $r^2 = 0.467$, $P < 0.0001$, 2019 $n = 26$, $r^2 = 0.509$, $P < 0.0001$). Though the relative proportion of eggs/night in non-preferred treatment(s) does not increase with total oviposition activity, the frequency of a substantial number of eggs (>100) in non-preferred treatment(s) changes markedly. In 2019, the frequency of eggs in non-preferred treatment(s) increased from 35% (6/17) below 3500 eggs/night to 67% above (6/9), and in 2016, it increased from 26% below 3500 to 100% above (6/6). Thus, time plays a significant role in the pattern from 2019, while oviposition activity/night plays a significant role in the pattern of oviposition in both 2016 and 2019.

DISCUSSION

Patch size and predation risk are two factors that vary universally across habitats, but are especially variable in aquatic systems because of the relatively discrete nature of many small aquatic habitat patches (Wellborn et al. 1996, Wilbur 1997, Semlitsch and Bodie 1998). Many species of ovipositing treefrogs strongly favor fishless patches when they are available (Resetarits and Wilbur 1989, Resetarits 2005, Resetarits et al. 2005, Vonesh et al. 2009, Kraus and Vonesh 2010), and work has recently established the strong preference of ovipositing female *H. chrysoscelis* for larger patches ($1.13 \text{ m}^2 \ll 2.54 \text{ m}^2 \ll 5.73 \text{ m}^2$; Resetarits et al. 2018). Here, we address the relative importance of predation risk and patch size in the oviposition decisions of female treefrogs using a very specific design presenting ovipositing treefrogs two suboptimal choices: large patches of the optimal relative size, but with fish present, and small patches of suboptimal relative size, but optimal fish-free conditions (Fig. 1). We compared these results to a previous experiment (Resetarits et al. 2018) that provided the expectations for our habitat manipulations.

The attractiveness of both large patches with fish and small fishless patches was enhanced when neither the optimal patch type—large fishless patches, or the second favored treatment (by a large margin), medium fishless patches, was not available (Fig. 2). Large and medium fishless patches received 81% and 14%, respectively, of the 76,925 eggs laid in the previous experiment (Resetarits et al. 2018), with none laid in small fishless or small fish patches. Here, in the absence of the preferred alternatives, egg numbers were basically split evenly between the three patches within each block, producing a per area egg density in small fishless patches ~5× greater than in large patches with fish. Large patches with fish received far more eggs (27,883 vs. 1876) and a greater proportion of eggs (33% vs. 2.4%) in the absence of large and medium fishless patches as alternatives, while small fish patches went from zero eggs when the larger fishless patches were available to getting the bulk of the eggs laid (55,889), 67% of the total vs. 0% (Fig. 2). Clearly, patch size remains a factor in the decision process, even given the presence of a fishless

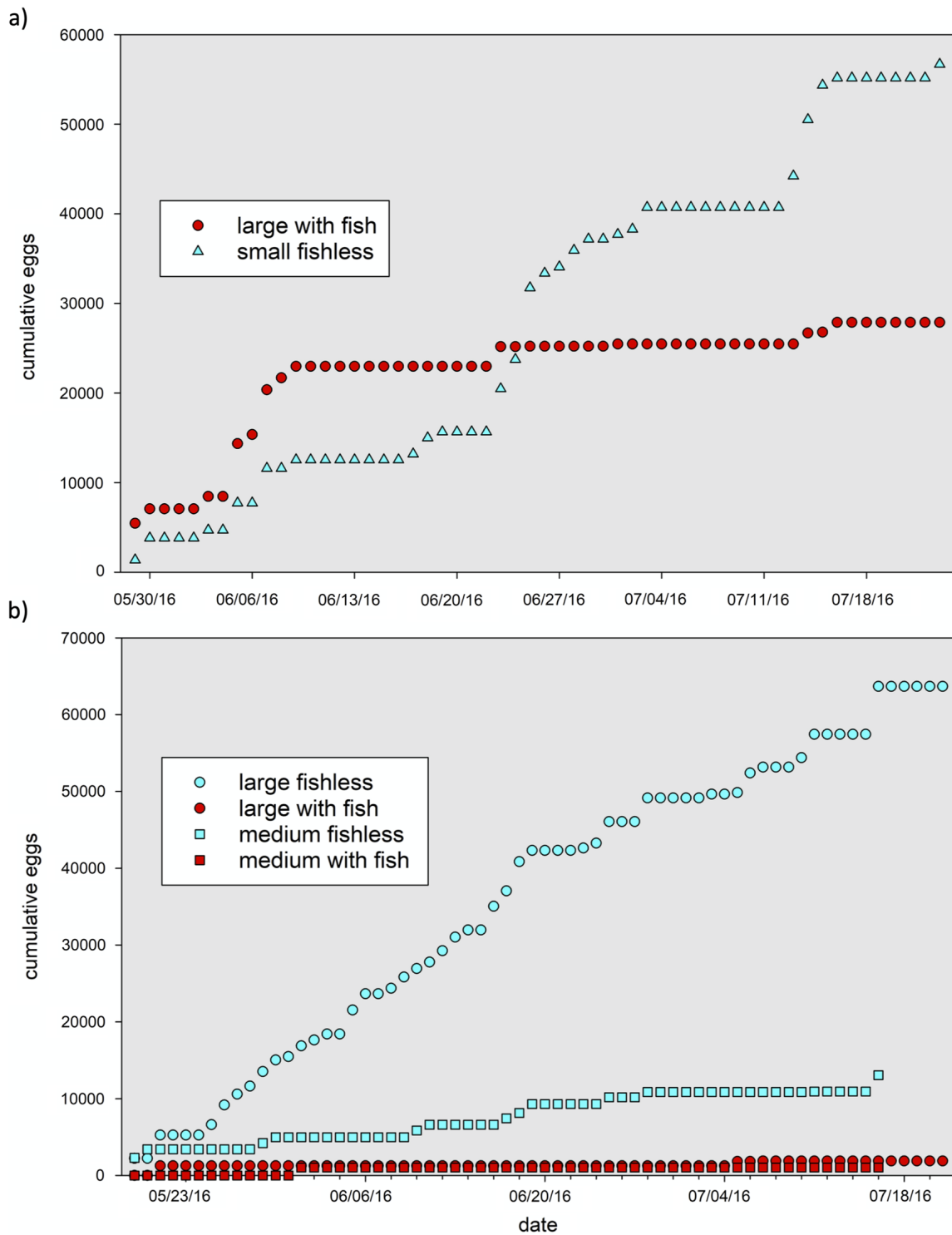


Fig. 3. Cumulative eggs per patch type across the 2019 experiment (a) and 2016 experiment (b). Red = fish, cyan = fishless. Each experiment had ~80,000 eggs divided largely between the only two treatments in 2019 and two of the six treatments in 2019. Small patches received no eggs in 2016 and are not shown.

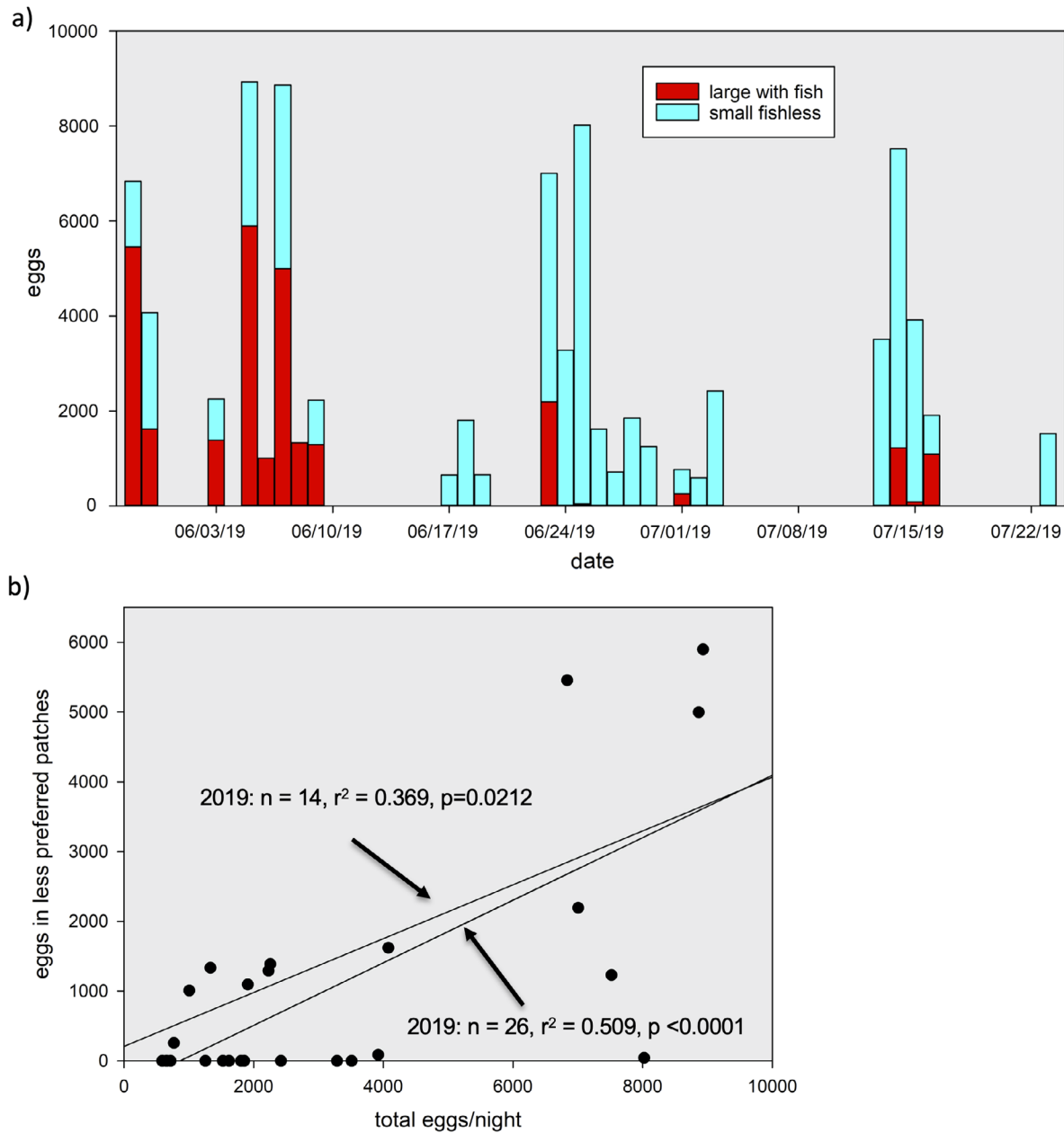


Fig. 4. (a) Nightly egg totals by treatment across the 2019 experiment, and (b) the relationship between total eggs/night and eggs in the less preferred treatment (large with fish). Lower line is regression of all points; upper line is regression of non-zero points.

alternative (and given that density dependence was obviated, at least over time). But it remains clear that, as has been shown in numerous prior experiments, when patch size is held constant fish have primacy over all other factors that have been examined.

The most puzzling aspect of our data is the shift from a relative preference for large patches with fish at the start of the experiment, to the almost total dominance of small fishless patches from 17 June to the end of the experiment. Again, eggs were removed daily, so larval density is not

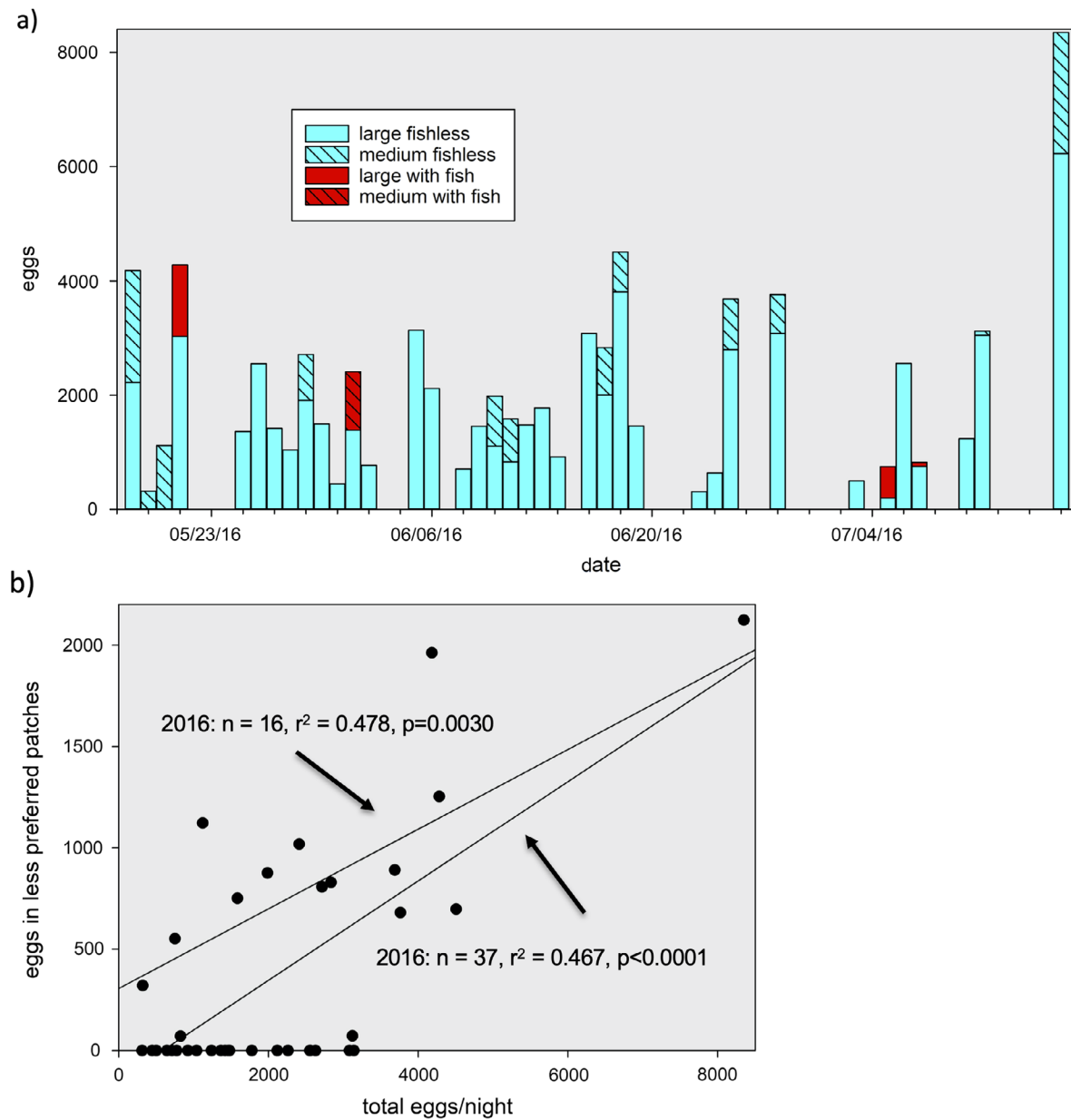


Fig. 5. (a) Nightly egg totals by treatment across the 2016 experiment, (b) the relationship between total eggs/night and eggs in the less preferred treatments (all except large fishless). Lower line is regression of all points; upper line is regression of non-zero points.

a factor, and nightly density of females/eggs does not explain the shift. Fish chemical cues are volatile and short-lived, degrading in a few days and so should not build up over time (Van Buskirk et al. 2014). It is unclear whether females at UMFS are capable of breeding twice in a given

season, or whether they can breed a second time in the time frame of our experiment, but our assumption is that we are primarily seeing one clutch per female. Thus, different segments of the population are breeding at different times across the season. It seems likely that early breeders are

females that were mature the previous year, and later breeders those that matured late the previous year or in early spring/summer. However, this really does not get us any further in understanding why. Fish do grow over time, so that biomass density increases, but only incrementally over so short a time frame. It is possible that biomass density reached a point where perceived risk changed the relative valuation of the two patch types or that the sensitivity threshold for a greater proportion of females was reached at some point. But in contrast, fish patches were completely avoided from the very beginning in the 2016 experiment, which had the same starting biomass density; however, it did provide the optimal combination of patch size and lack of fish. Algae and phytoplankton would tend to increase over time as fish remove grazers, but the 2019 temporal pattern runs counter to that argument. Nothing else differentially changes over time between large patches with fish and small fishless patches. Presumably the value of larger patch size may be lower desiccation risk (but see below), which should be more highly valued later in the summer when temperatures are higher and rainfall is reduced, but we see the opposite pattern.

What is also unknown is how intraspecific density would alter the attractiveness of the two patch types, *sensu* the ideal free distribution (Fretwell and Lucas 1970), since survival, growth, and time to metamorphosis are strongly negatively density-dependent in larval anurans (Wilbur and Collins 1973, Werner 1986). We remove eggs every morning in order to provide the same choice scenario each night, so negative density dependence is not in play over time—patches do not accumulate larvae, and we have never observed positive density dependence in oviposition. However, we have previously observed density-dependent responses, where eggs are laid in non-preferred (fish) pools only on very active oviposition nights, presumably in response to either female density or egg density (Binckley and Resetarits 2003, Rieger et al. 2004). Density dependence of this type partly explains the distribution of eggs in both experiments considered here (Figs. 4, 5). There is a positive relationship between the number of eggs/night and the number of eggs in the less preferred treatment(s), but the slopes are relatively constant, so

the proportion in non-preferred treatments/night does not increase with total oviposition activity. What does change dramatically is the frequency of eggs in non-preferred treatment(s), which approaches 100% at higher activity levels, above a threshold of ~3500 eggs for both experiments (Figs. 4b, 5b). This is somewhat surprising both because it is so abrupt, and thus is not a random probability issue, and because 3500 eggs on a night are not very high activity even if we just consider the preferred patch types. Experiments at the same location have had up to >17,000 eggs laid on a single night (W. J. Resetarits, *unpublished data*), but the pattern across two different years is quite strong.

Under natural conditions, one can envision a scenario where the preference for the two patch types would shift back and forth as densities change. On one of the more active nights in 2019 (6/25), with 8025 eggs laid, 5859 of those were laid in one small fishless patch. How would that density effect the attractiveness of that patch, and subsequent choices, going forward? Under natural conditions, densities would increase more slowly, if at all, in patches containing fish (due to consumption), so that the perceived quality of the large patches with fishless patches would remain relatively constant, while that of small fishless patches would decline, perhaps precipitously, with density. This assumes that treefrogs only respond to fish cues, and not fish diet cues. Under this scenario, large patches with fish might eventually serve as population sinks, or even ecological traps (Delibes et al. 2001). Or conversely, the small fishless patches might serve as sinks if their attractiveness does not decline with density, since survival, growth, and time to metamorphosis are strongly negatively density-dependent (Wilbur and Collins 1973, Werner 1986).

It is abundantly clear why fishless patches are preferred, but why is larger better for larval treefrogs? The 2016 experiment established that it was a strong preference for larger patch size, not simply greater detectability, and while preferring larger patches seems straightforward and intuitive, the actual advantage is unclear. What immediately comes to mind for treefrogs is avoiding desiccation, which is always viewed as the primary trade-off for most fish intolerant anurans—permanent habitats are generally less

productive and more frequently contain fish, while temporary habitats are usually quite productive, fishless, but are of highly variable duration (Wellborn et al. 1996, Wilbur 1997); ovipositing females must balance the competing risks. While fish can be detected and avoided using chemical cues, some surrogate would need to be used to predict desiccation risk. Patch size would seem a likely candidate, but surface area is a poor predictor of hydroperiod in smaller ponds (Eason and Fauth 2001). Ovipositing *H. chrysoscelis* do prefer ponds of greater depth, which does correlate with hydroperiod (Pintar and Resetarits 2017), but our large and small patches had the same water depth. The probability of encountering fish increases with pond size, but if you are already determining the presence of fish directly that seems an unnecessary redundancy. Perhaps it is simple as density—females can react to existing density, or assess expected density based on current activity, but they cannot predict what happens after they lay their eggs, so larger patches may be a reliable indicator of lower density and provide a form of bet-hedging against future density changes (Resetarits 1996). So, it remains unclear what specific attributes of pond size generate the strong preference, which, in this case, partly overrides the typically dominant effect of fish.

What is also not clear is how the partitioning of choice between patch size and predation risk is achieved. Given the choice between two sub-optimal conditions, in which each patch has a characteristic that is strongly favored all else being equal, is the distribution of eggs between patch types a result of variation in the decision algorithm among females, variation in the ability to assess variation in patch characteristics, or bet-hedging by dividing clutches between both patch types (Resetarits et al. 2005)? Here, much of it is a temporal effect. Given the fact that we assay the outcome of habitat selection in naturally colonizing populations in relative long duration experiments in which oviposition is highly sporadic and unpredictable, it is difficult to sort out the different mechanisms—we do not have information on individual females.

Nature rarely presents colonizing organisms with unequivocal choices or unlimited habitable patches. More typically, organisms are forced to choose among habitat patches that provide a

mosaic of characteristics that must, somehow, be identified, evaluated, and integrated in terms of expected fitness relative to one another. Our results vividly illustrate both the strong spatial context dependence of habitat selection behavior and the ability of ovipositing gray treefrogs to integrate across multiple axes of patch quality. In an earlier paper, a specific outcome of decision making was described as compromise (Resetarits et al. 2005), where changes in patch characteristics force the use of otherwise unused habitats. But in truth all habitat choices are compromise, and between the hypothetical, optimal habitat, whose quality may begin to decline as soon as the first colonists arrive, and truly untenable habitats that are only used when nothing else is available, there is huge range of variation that must be navigated by colonizing/ovipositing organisms.

ACKNOWLEDGMENTS

The authors thank M. Pintar, J. Bohenek, R. Scott, S. McNamara, and K. Potts for fieldwork and thoughtful discussion. Support was provided by the Henry L. and Grace Doherty Foundation, the University of Mississippi, and the UM Field Station. This is publication #022 from the Center for Biodiversity and Conservation Research at the University of Mississippi.

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