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# Patch size influences perceived patch quality for colonising *Culex* mosquitoes

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## Abstract

1. Colonisation is a critical process driving the abundances and diversity of species in spatially discrete communities. Although patch size and patch quality are well known as determinants of post-colonisation species richness and abundance, less is known about how patch size affects colonisation.
2. Patch size and quality may not be independent, so assessment of potential interactions is necessary for understanding patterns of species abundance in natural systems. In freshwater systems, presence and identity of predators is a dominant determinant of patch quality, with larger habitat patches often supporting larger and more diverse predator assemblages.
3. To examine potential interactions, we manipulated patch size and quality (fish presence/absence) using naturally colonised experimental landscapes and assayed oviposition by *Culex* mosquitoes.
4. *Culex restuans* selected patches that were smaller, did not contain fish, and had higher temperatures. We demonstrate that patch size, along with patch quality, can generate patterns of abundance at the colonisation stage that are contradictory to traditional patch size-based models of species distributions.

KEYWORDS
colonisation, community assembly, immigration, metapopulation, oviposition

## 1 | INTRODUCTION

Patch size and patch quality are important characteristics that influence species persistence, coexistence, colonisation and dispersal (Fretwell & Lucas, 1970; MacArthur & Wilson, 1967). However, despite their importance, there has been little investigation into patch size and how patch size and quality interact to affect these dynamics. Early studies considered only size and isolation of habitat patches, as they have a long history in ecology as determinants of species richness and abundance (Arrhenius, 1921; Cain, 1938; Gleason, 1922; MacArthur & Wilson, 1963). Much of the current theory surrounding patch size and isolation is derived from the Equilibrium Theory of Island Biogeography (ETIB) (MacArthur & Wilson, 1967), which hypothesises that larger islands with less isolation (i.e. more connectivity to source populations) will have greater species richness due to higher immigration and lower extinction rates compared to small, isolated islands. This theory gave rise to metapopulation (Hanski & Gilpin, 1991) and metacommunity ecology (Leibold et al., 2004; Wilson, 1992), with the recognition of the importance of patch size and isolation in determining species distributions in spatially connected systems. These theories are not limited to islands as islands are merely a type of patch, which exist in a variety of forms ranging from agricultural landscapes (Fahrig & Jonsen, 1998) and fragmented forests (Debinski & Holt, 2000; van Dorp & Opdam, 1987) to freshwater systems (Binckley & Resetarits, 2005; Laan & Verboom, 1990) and disease hosts (Burdon, Jarosz, & Kirby, 1989; Jennersten, Nilsson, Wästljung, & Wastljung, 1983). The wide applicability of these concepts cemented patch size and isolation as fundamental ecological factors affecting species distributions.

The effects of patch characteristics on population sustainability (extinction risk) and species diversity begin with their effects on immigration rates. Higher immigration in less isolated patches is axiomatic, and in larger patches is generally attributed to their associated larger capture areas (target area hypothesis) (Connor & McCoy, 1979; Hanski, 1999; MacArthur & Wilson, 1967). While these capture effects should be true under random colonisation, many organisms actively choose habitat patches based upon their perceived quality (expected fitness) (Rausher, 1983; Resetarits & Wilbur, 1989; Singer, 1984). As outlined by the ideal free distribution (IFD), the expected fitness of patches is thought to be the ultimate driver of habitat selection (Fretwell & Lucas, 1970). Patch selection is "ideal" when information on patch characteristics is available and cost-free, whereas patch selection is "free" when movement between patches is cost-free. Under this framework, we expect optimal patch selection for fitness maximisation; however, information on patch quality (or even size) is rarely complete or cost-free, thus organisms rely on estimations or indirect information on patch quality (Orians & Wittenberger, 1991). Thus, optimal patch selection will be more frequent with easier patch detection and assessment, along with greater dispersal capabilities of colonists.

Patches vary in their attractiveness to active colonists. Though patch size surely plays a role in detection, and larger patches have a greater probability of encounter, patch quality is the primary factor in habitat selection (Fretwell & Lucas, 1970; Wiens, 1976). Resource density (Binckley & Resetarits, 2008; Blaustein & Kotler, 1993), disease (Robertson & Hamilton, 2012), predator presence/absence (Resetarits & Wilbur, 1989; Vonesh & Blaustein, 2010; Vonesh, Kraus, Rosenberg, & Chase, 2009), canopy cover (Binckley & Resetarits, 2007, 2009), productivity (Binckley & Resetarits, 2007) and pesticides (Bentley & Day, 1989; Kibuthu et al., 2016; Takahashi, 2007; Vonesh & Buck, 2007) may all influence perceived patch quality. However, patch quality and patch size are seldom independent, and changes in patch size often affect patch quality, confounding the two, especially when limiting resources are correlated with habitat area (see reviews in Haynes & Cronin, 2004; Krauss, Steffan-Dewenter, Müller, & Tscharntke, 2005; Rabasa, Gutiérrez, & Escudero, 2008). Thus, effects of patch characteristics on immigration rates may be misattributed to either size or quality, whereas both are important.

There is considerable experimental evidence demonstrating that patch quality has powerful effects on colonisation rates (Binckley & Resetarits, 2005; Franzén & Nilsson, 2010; Mortelliti et al., 2014; Oertli et al., 2002; Rausher, 1983; Resetarits, 2001; Resetarits & Wilbur, 1989; Singer, 1984). In particular, predator presence is one aspect of patch quality that has been repeatedly demonstrated to have profound effects on colonisation rates (Chesson, 1984; Eitam & Blaustein, 2004; Hanski & Gilpin, 1997; Kneitel & Miller, 2003; Petranka & Fakhoury, 1991; Resetarits & Silberbush, 2016; Resetarits & Wilbur, 1989). In aquatic systems, the presence or absence of fish has dramatic effects on species distributions, creating a strict dichotomy for colonists (Resetarits & Wilbur, 1989; Schilling, Loftin, & Huryn, 2009; Wellborn, Skelly, & Werner, 1996) and a useful model system for researchers.

Mosquitoes are useful models to study colonisation dynamics because they disperse and colonise discrete habitat patches through female oviposition behaviour, where females select a patch for their aquatic larval offspring. Female mosquitoes utilise multiple sensory capabilities and are highly sensitive to numerous aspects of patch quality, which are assessed as they select habitats to maximise larval performance (Bentley & Day, 1989; Day, 2016; Kiflawi, Blaustein, & Mangel, 2003). Those of the genus *Culex* (Culicidae) have few (often one) lifetime reproductive events, making oviposition site choice a crucial fitness decision (Blaustein, 1999; Resetarits, 1996). Larval mosquitoes are highly susceptible to predation (DuRant & Hopkins, 2008), and adults avoid predators through selective oviposition (Chesson, 1984; Vonesh & Blaustein, 2010). Since mosquitoes are capable of directly detecting and identifying predators via kairomones (Eveland, Bohenek, Silberbush, & Resetarits, 2016; Silberbush et al., 2010), we should expect clear avoidance of patches containing predators and higher colonisation rates of predator-free patches. When it comes to size, females must choose between smaller ephemeral habitats and larger more permanent habitats (Juliano, 2009). Smaller patches are susceptible to desiccation (Juliano, O'Meara, Morrill, & Cutwa, 2002) and strong density-dependent effects (Fish & Carpenter, 1982; Reiskind & Lounibos, 2009), but they are protected from predators that are more common in larger patches (Chase & Knight, 2003; Pearman, 1995; Schneider & Frost, 1996). However, in the absence of predators, larger habitats should offer clear advantages.

We conducted a field experiment manipulating both patch size and patch quality to determine the influence of each factor and their interaction on mosquito colonisation. Our experimental design directly and independently manipulated both size and quality, holding other factors constant, allowing examination of relative effects. To do this, we utilised mesocosms (cattle tanks) of three different sizes (patch size) crossed with the presence and absence of fish predators (patch quality). We then assayed oviposition habitat preferences of natural mosquito populations by quantifying egg rafts deposited in each patch.

## 2 | METHODS

### 2.1 | Study site

The study was conducted at the University of Mississippi Field Station (UMFS) in Abbeville, MS (34.427452° N, 89.388107° W). UMFS is a 787-acre complex situated in the Eocene hills of the interior Gulf Coastal Plain that contains over 200 ponds along with multiple small streams, wetlands, fields and mixed forests. At the time of the experiment, day length was *c.* 14 h.

### 2.2 | Study species

Our focal species, *Culex restuans*, is a very abundant, generalist, freshwater wetland breeding mosquito (Carpenter & Lacasse, 1955), which provides a contrast with "container breeding" mosquitoes (Laird, 1988). *Culex restuans* is an important vector of West Nile virus (Andreadis, Anderson, & Vossbrinck, 2001). Adults are capable of dispersing over 1 km (Ciota et al., 2012), but only *c.* 100 m after a bloodmeal (Greenberg, Dimenna, Hanelt, & Hofkin, 2012). Peak activity for *C. restuans* occurs at dusk, when females seek bloodmeals and then search for an oviposition site (Macdonald, Madder, & Surgeoner, 1981; Stough & Wallace, 2016). They deposit egg rafts, as opposed to single eggs. Females readily use artificial pools for oviposition sites, but avoid pools with aged water (Brust, 1990) and predators (Blaustein, Blaustein, & Chase, 2005; Eveland et al., 2016). Females prefer localities with fewer patches (Reiskind & Wilson, 2004), but nothing is known about how females respond to patch size or related variables like patch temperature, though it has been suggested that temperature and nutrients may interact to affect pool attractiveness (Jackson, Paulson, Youngman, Scheffel, & Hawkins, 2005). Larval development in *C. restuans* is temperature (Ciota, Matacchiero, Kilpatrick, & Kramer, 2014; Madder, Surgeoner, & Helson, 1983; Muturi, Lampman, Costanzo, & Alto, 2011), density (Madder et al., 1983) and nutrient dependent (Reiskind, Walton, & Wilson, 2004), suggesting that these habitat attributes may be important to ovipositing females.

## 2.3 | Experimental design

Our experiment was conducted in a large, old field at UMFS situated 20 m north and west of the nearest ponds, which contained fish. We established six rectangular mesocosm arrays (blocks) of six pools each (*N* = 36), crossing three pool sizes (1.2, 1.8 and 2.7 m diameter) with the presence/absence of fish, specifically green sunfish (*Lepomis cyanellus*: Centrarchidae) and golden shiners (*Notemigonus crysoleucas*: Cyprinidae) (Figure 1). These two species were selected because of their extensive distributions, generalist diets and general applicability. Pools (=patch) were of the same material, colour and round shape (Ace Roto-Mold, Hospers, IA, U.S.A.), 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); pools held *c.* 593, 1,334 and 3,002 L, respectively. Treatments were randomly assigned to positions within each array. The treatments in arrays were positioned so that an equal number of blocks had more fish and fish-free pools on the forest side. Pools of the same size, but opposite quality, were positioned opposite one another to maintain constant interpatch distances of 5 m (Figure 1), and each array contained alternating fish and fish-free pools. From the perspective of colonising mosquitoes, their abilities should allow them to first assess patch sizes from a distance followed by patch quality as they approach and assess patch-specific semiochemicals. We began filling pools with well water on 9 May 2016, one block at a time, completing two blocks/day, and tight-fitting fiberglass screen lids (1.3 mm$^2$, 1.13 mm openings) were fastened onto each mesocosm. Concurrent with filling, dried leaf litter (mixed hardwoods) was added to 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 pool received fish at an initial density of *c.* 2.3 g/100 L; small (1.2 m) pools received 4 fish total (2 *N. crysoleucas* + 2 *L. cyanellus*), medium (1.8 m) pools received 9 fish total (4–5 *N. crysoleucas* + 4–5 *L. cyanellus*), and large pools (2.7 m) received 20 fish total (10 *N. crysoleucas* + 10 *L. cyanellus*). Because medium pools required an uneven number of fish, each medium pool in blocks 1, 3, and 5 received 1 extra *L. cyanellus*, while those in blocks 2, 4, and 6 received 1 extra *N. crysoleucas*. To equalise biomass within blocks, we created 8 complementary (1 "large," 1 "small") pairs within each of the two species for each block (by eye to minimise stress), and randomly assigned the appropriate number of pairs to each Fish pool within that block, thus maintaining the same fish density and size structure across pool sizes within blocks. Both *N. crysoleucas* and *L. cyanellus* were haphazardly sampled from holding tanks and their

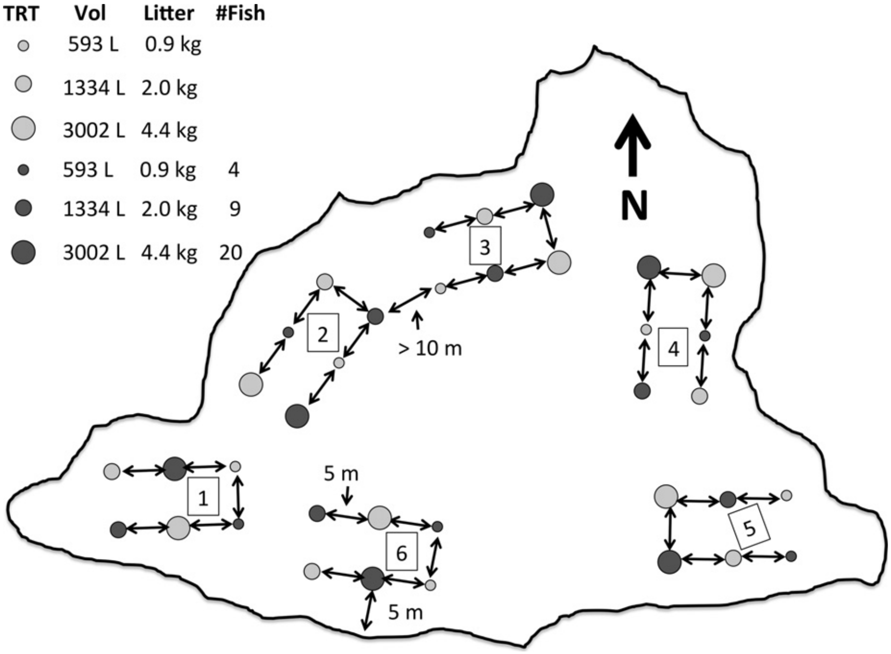

**FIGURE 1** Experimental layout with treatment summary. Circle size indicates patch size while circle colour indicates patch quality (dark grey = fish, light gray = fish-free). Outline corresponds to the tree line surrounding the field. Each block was >10 m from the nearest neighboring blocks and 5 m from the tree line. All pools within a block were 5 m from the nearest neighbouring pools (interpatch distance)

mean masses were estimated at *c*. 3.5 g. Fish subsisted on ambient prey populations that established in the semi-natural mesocosms. On 12 May, the fiberglass lids covering the tanks were sunk below the water surface to “open” the pools for oviposition while preventing fish from consuming any adult mosquitoes or egg rafts. We collected mosquito egg rafts each morning (8–9 a.m.) from 13 May to 26 May. Pool temperatures were spot measured in the centre of the pools, 2 cm below the surface at 11 a.m. on 26 May. On 16 May, all egg rafts collected that day were brought to the lab for rearing and subsequent identification following Darsie and Ward (2005). Out of thousands of *Culex* (Diptera) egg rafts identified at UMFS, *c*. 99% have been identified as *C. restuans* (Bohenek, J R, unpublished data).

## 2.4 | Statistical analyses

The main unit of analysis is relative egg raft counts, which were scaled to patch surface-area to account for passive patch capture probability. Relative counts allow us to explore true oviposition preferences as opposed to proportional increases in egg rafts with surface area, which would indicate no size preference; count data were square root transformed $(\sqrt{X + 0.5})$. To test for differences in the number of egg rafts we utilised a factorial ANOVA. We also compared temperatures between patch sizes with an ANOVA; however, measuring pool temperature was not initially planned, but was considered after observing potential differences between pool sizes during the 2 week sampling period. Thus, our temperature data is limited and a separate experiment would be required to determine the effects of temperature. Finally, we regressed the number of egg rafts against patch temperature and conducted a separate ANOVA excluding large pools to examine the effects of patch size independent of size-related temperature differences. All analyses used R v 3.2.5 (R Core Team, 2016) and the car package v 2.1.2 (Fox & Weisberg, 2011) with Type III sums of squares and $\alpha = .05$. Effect sizes (partial $\eta^2$) were calculated using the heplots package v 1.3.3 (Fox, Friendly, & Monette, 2016).

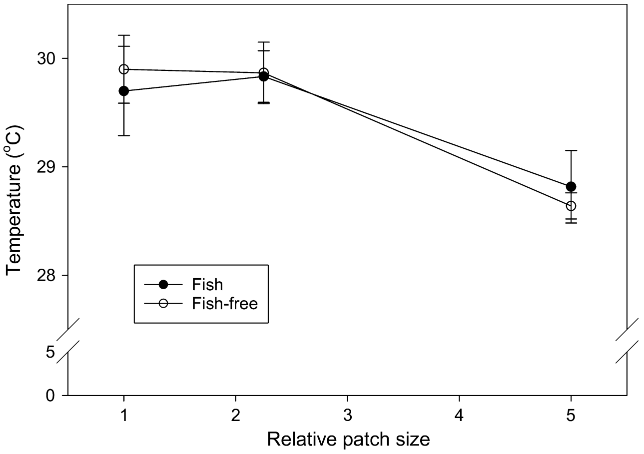

**FIGURE 2** Patch temperature (mean ± *SE*) in relation to patch size. Relative patch size indicates that medium and large patches are factors larger (2.25 × and 5 × respectively) than small patches. At the time of our measurement, large patches were significantly cooler than small and medium patches

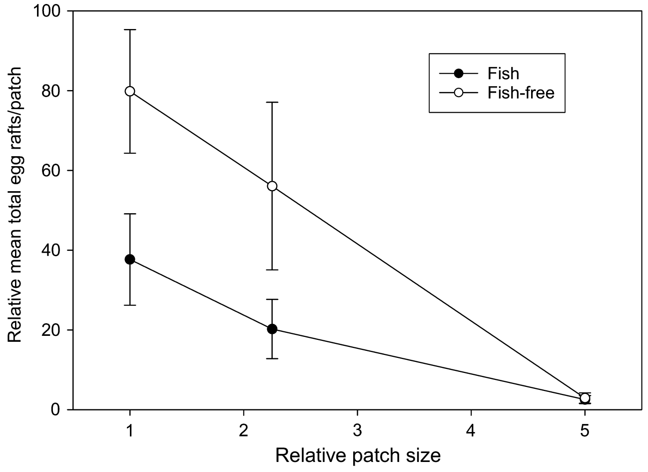

**FIGURE 3** Relative total egg rafts (mean ± *SE*) in relation to relative patch size. Relative patch size indicates that medium and large patches are factors larger (2.25 × and 5 × respectively) than small patches. Smaller and fish-free patches consistently received more egg rafts

## 3 | RESULTS

Female mosquitoes laid 1,968 egg rafts in our pools over a 2 week period. Fitting with previous findings at UMFS, 100% of the 264 identified egg rafts were *C. restuans*. We removed a single large, fish-free pool from the analysis because it was partially shaded, 3.58°C cooler than the experiment average and 2.94°C cooler than the average of the other five pools in its block. This lone pool’s low temperature was an outlier that highly influenced the effect of temperature and was excluded from all analyses. At the time of our measurement, patch size significantly affected patch temperature ($F_{2,24} = 15.61$, $p < .001$; Figure 2). Small and medium patches, which did not differ from each other ($F_{1,17} = 0.04$, $p < .846$), were warmer than large patches (Figure 2), potentially confounding the effect of patch size with patch temperature in large patches. However, since we only measured temperature at the end of the experiment, we do not know if these temperatures represent consistent differences during the course of the experiment. Patch size (partial $\eta^2 = .6262$, $F_{2,24} = 20.10$, $p < .001$) and patch quality (partial $\eta^2 = .2985$, $F_{1,24} = 10.21$, $p = .004$) had significant effects on relative total egg rafts, indicating clear oviposition preference for fish-free and smaller patches (Figure 3). There was no effect of the patch size × patch quality interaction on relative total egg rafts (partial $\eta^2 = .0616$, $F_{2,24} = 0.79$, $p = .467$), but the block effect was marginally significant (partial $\eta^2 = .3347$, $F_{5,24} = 2.42$, $p = .066$). Mean relative total egg rafts in blocks ranged from 11.54 to 53.50 (34.66 ± 6.20) (mean ± *SE*), which reflects spatial variation in mosquito activity across the landscape at UMFS. When excluding large patches and comparing only small and medium patches, which did not

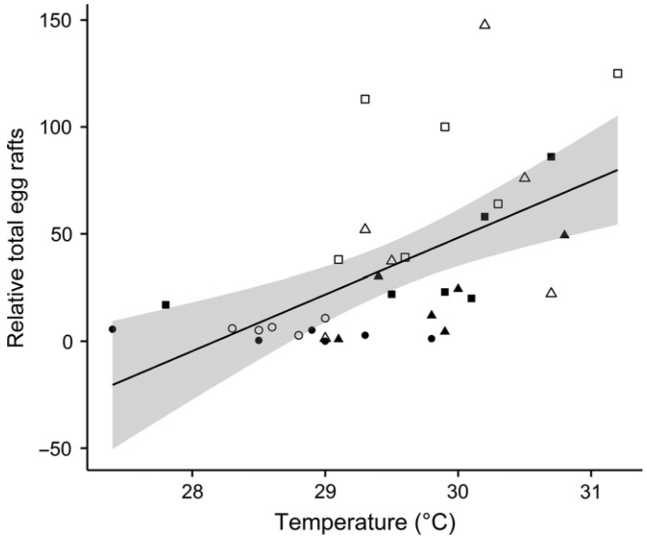

**FIGURE 4** Linear regression depicting relative total egg rafts as predicted by patch temperature. There was a positive linear relationship between patch temperature and relative total egg rafts ($R^2 = .33$, $F_{1,33} = 16.26$, $p < .001$). Symbols represent different treatments: large fish (closed circles), medium fish (closed triangles), small fish (closed squares), large fish-free (open circles), medium fish-free (open triangles) and small fish-free (open squares)

significantly differ in temperature, patch size ($F_{1,16} = 4.57$, $p = .048$) and patch quality ($F_{1,16} = 9.69$, $p = .007$) significantly affected relative total egg rafts, while the block effect was again marginal ($F_{5,16} = 2.65$, $p = .063$). For this latter analysis, the patch size × patch quality interaction was highly non-significant ($p > .90$) and excluded from the model. Though the regression analysis suggests that some component of the preference for smaller patches could be related to patch temperature (Figure 4), the latter analysis calls into question whether temperature is a potential driver of the size effect, as there was a significant egg raft difference between small and medium patches, but no temperature difference. Because we did not manipulate temperature, and size and temperature are confounded, we cannot resolve this issue here.

## 4 | DISCUSSION

We simultaneously manipulated both patch size and patch quality to experimentally test how each factor and their interaction affects mosquito oviposition rates. Large, high quality (fish-free) patches should support the greatest resource diversity, be easiest to detect and have lowest mortality risk, thus, in accordance with ETIB and IFD, we expected highest oviposition rates in the largest patches of the highest quality (fish-free). Though mosquito oviposition rates across the predator gradient (patch quality) were in accordance with past findings (Eveland et al., 2016; Resetarits & Silberbush, 2016), oviposition across the size gradient conflicted with our original prediction. Many mosquitoes species utilise small habitat types (i.e. container breeding mosquitoes) (Day, 2016; Juliano, 2009; Laird, 1988), but many of those studies assayed larval abundance as opposed to oviposition behaviour (Bradshaw & Holzapfel, 1983; Lester & Pike, 2003; Sunahara, Ishizaka, & Mogi, 2002), which are very different given post-colonisation species sorting (Kraus & Vonesh, 2010). Multiple studies have found proportional increases in mosquito oviposition with increasing pool size (Blaustein, Kiflawi, Eitam, Mangel, & Cohen, 2004; Harrington, Ponlawat, Edman, Scott, & Vermeylen, 2008; Saward-Arav, Sadeh, Mangel, Templeton, & Blaustein, 2016) as would be expected under the target area hypothesis (MacArthur & Wilson, 1967). Only Saward-Arav et al. (2016) experimentally identified true preference for larger patches in at least one mosquito species (*Culex laticinctus*). Our results provide evidence of oviposition preference for smaller patches, which contrasts with Saward-Arav et al. (2016) and predictions under ETIB and IFD.

Under the IFD framework, the expected fitness of each patch should decrease for each subsequent ovipositing female in the absence of Allee effects. Therefore, we would expect egg raft densities to remain constant across patch sizes, but we found a preference for smaller patches. However, since we removed egg rafts after each night of oviposition, densities on any particular night may not have reached a required threshold to shift oviposition to alternative patches. Though ovipositing mosquitoes avoid conspecifics (Kiflawi et al., 2003; Reiskind & Wilson, 2004), the observed pattern in our study produced a higher density of egg rafts in small patches, which would lead to greater larval competition and lower expected fitness (Agnew, Haussy, & Michalakis, 2000). Reiskind and Wilson (2004) found conspecific avoidance in *C. restuans*, suggesting that larval competition is an important factor in oviposition, and they also found preference for small patches, but their larger "patches" were comprised of clusters of small patches. Thus, they manipulated patch number, not patch size, which are very different (Allen, 1987; Nicol & Possingham, 2010).

Preference for smaller patches when larger neighbouring patches of identical quality are available is puzzling, but could be due to an association of patch size with predator diversity (Bradshaw & Holzapfel, 1983; Sunahara et al., 2002; Washburn, 1995; Wellborn et al., 1996), though it has recently been suggested that predators do not mediate this pattern in mosquitoes (Westby & Juliano, 2017). In aquatic landscapes, larger patches are more likely to contain fish or predatory insects (Pearman, 1995; Schneider & Frost, 1996), both of which are important mosquito predators (Blaustein, 1998; DuRant & Hopkins, 2008). In fact, predators typically found in large aquatic habitats preferentially prey on mosquito species that are typically found in small, ephemeral habitats (Schneider & Frost, 1996). In single-species experimental systems, ovipositing *C. restuans* have a wide range of responses to an array of predator species, from almost complete avoidance to no response (Bohenek, J R; et al. unpublished data). However, natural systems rarely consist of a single predator species, and accurate assessment of the full predator assemblage of a patch may be difficult. Likewise, predator cue reliability should be better in smaller patches if predator densities are low and/or predators are patchily distributed. Thus, mosquitoes, and potentially many other aquatic insects with high susceptibility to predation, may actively avoid large habitat patches due to a lack of appropriate defences and an association of large habitats with higher predator probability and greater predator diversity. Evolutionary history may have canalized this behaviour since mosquito larvae are air-breathers with fast development times, enabling growth to maturity in small, ephemeral and anoxic habitats that may preclude other predators and competitors, and thus consistently offer optimal conditions. However, when considering that mosquitoes can utilise kairomones to directly assess predator presence (Petranka, Kats, & Sih, 1987; Silberbush et al., 2010), this behaviour seems redundant and can potentially lead to missed offspring growth opportunities in large, high quality habitats. Alternatively, some predators may not be detectable via kairomones, so avoiding large habitats may be a strategy to avoid a different group of predators.

Some of the preference for smaller patches may be explained by variation in temperature, with smaller patches (small and medium) reaching warmer daytime temperatures (Figure 4). Mosquitoes are attracted to chemical cues produced from bacteria decomposing organic matter (Kramer & Mula, 1979; Lindh, Nnaste, Knols, Faye, & Borg-Karlson, 2008; Ponnusamy et al., 2008). Jackson et al. (2005) suggested that this process may be amplified in warmer temperatures and may increase pool attractiveness to *C. restuans*. Though evidence is limited, there may be a potential interaction between patch size and patch quality, where higher temperatures represent higher quality for offspring in the form of additional bacterial food resources (Bentley & Day, 1989; Blaustein & Kotler, 1993; Chaves, Keogh, Vazquez-Prokopec, & Kitron, 2009) and faster development rates (Ciota et al., 2014; Madder et al., 1983; Muturi et al., 2011). Our temperature data is limited and may not be representative of temperature patterns during the entire experiment, especially at night when small and medium patches cool faster compared to large patches. However, peak mosquito activity occurs around dusk (Macdonald et al., 1981; Stough & Wallace, 2016) and accrued daytime temperature differences may still be present before significant cooling occurs, but our data is insufficient to comment further.

Colonisation of freshwater patches embedded in terrestrial matrices by organisms with complex, multistage life cycles offers an ideal model system for investigating patch dynamics in metapopulation and metacommunity ecology. These habitats are indeed “islands” that harbour a disproportionate amount of biodiversity relative to their percent land cover (Dudgeon et al., 2006), illustrating both their complexity and suitability for answering questions concerning community assembly. There has been a growing body of literature suggesting an overriding importance of patch quality in driving colonisation rates (Dennis & Eales, 1997; Fleishman, Ray, Sjögren-Gulve, Boggs, & Murphy, 2002; Mortelliti, Amori, & Boitani, 2010; Resetarits & Binckley, 2013; Summerville & Crist, 2001). Patch quality can be divided into abiotic and biotic components, which are neither spatially nor temporally constant. We have shown here that both biotic (predator presence) and abiotic (size) factors can simultaneously influence active colonists through direct effects or indirectly by interacting with the environment, as in the case of patch size and temperature. There is considerable evidence that predators affect colonisation rates (Bentley & Day, 1989; Blaustein & Kotler, 1993; Chesson, 1984; Resetarits & Wilbur, 1989), but predators are often implanted in experiments as constant properties of habitat quality (as we did here) when they themselves are in fact colonists. The patch-dynamic paradigm (Leibold et al., 2004) and habitat matching perspective (Resetarits & Silberbush, 2016) in metacommunity theory have addressed the persistence of multiple species in patchy landscapes via differences in dispersal (patch-dynamic) and/or colonisation rates (habitat matching). The patch dynamic paradigm applies to our system since fish, which are major components of patch quality, lack the life history traits of vagile insects that allow for dispersal across the terrestrial matrix and rapid colonisation of new habitat patches**.** The habitat matching perspective requires species interactions to occur during colonisation, not post-colonisation, via cues (e.g. predator-released kairomones) that directly impact colonisation rates. Therefore, species interactions can occur without species co-occurrence in the habitat matching perspective. Thus, mosquitoes can avoid patch extinction by choosing predator-free habitats and “staying ahead” of dominant predators (Kraus & Vonesh, 2010). This relationship illustrates the important role that priority effects and early colonisation have on community composition (Alford & Wilbur, 1985; Chase & Leibold, 2003; Vonesh et al., 2009; Wilbur & Alford, 1985).

Patch size and isolation have been considered important factors determining species distributions and abundances for decades (Arrhenius, 1921; Cain, 1938; Gleason, 1922; MacArthur & Wilson, 1963), but not until decades later has experimental work begun to examine the effects of patch quality and their interactions with size and isolation on habitat selection (Bentley & Day, 1989; Blaustein & Kotler, 1993; Fahrig & Jonsen, 1998; Resetarits & Wilbur, 1989). Though our study consisted of a single species, mosquitoes may constitute one taxa that does not support the species–area relationship. Species, or perhaps groups of species, may have specific preferences that can be explained by correlating niche characteristics with patch characteristics. Understanding the importance of patch characteristics to particular species or groups of species will help us understand the influence of both patch quality and patch size on colonisation, and assess their importance for species conservation, or control, in an increasingly fragmented and warming world (Hodgson, Thomas, Wintle, & Moilanen, 2009).

Many organisms actively select habitats based upon their perceived quality and size. We provide evidence that some characteristics of patch quality and size interact to reverse expectations concerning colonisation rates. Despite being a generalist wetland species, *C. restuans* actively chose small, high quality (fish-free) habitats versus larger high quality patches. The actual selective forces driving this preference are unknown, but may include greater tolerance of small, ephemeral habitats relative to predators and competitors, lack of anti-predator defenses, and the association of greater predation risk with larger aquatic habitats. One of the main goals of ecology is to identify the mechanisms that create and maintain species distributions and biodiversity, and understanding the contributions of both pre and post-colonisation community assembly processes within a broadly spatial (metacommunity) context are critical to this understanding (Chesson, 2000; Leibold et al., 2004).

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## AUTHOR CONTRIBUTIONS

JRB, MRP, TMB and WJR designed the experiment, analyzed the data and contributed to the manuscript. JRB, MRP and TMB constructed the experiment and collected the data. All authors agree on the current form on the manuscript.

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