

## A hump-shaped relationship between isolation and abundance of *Notonecta irrorata* colonists in aquatic mesocosms

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**Abstract.** We examined the relationship between the isolation of experimental aquatic mesocosms and the abundance of an aquatic insect colonist, *Notonecta irrorata*, over two years. We used a curve-fitting approach to assess whether linear or quadratic models better describe the relationship between isolation and abundance. For two measures of mesocosm isolation, distance to nearest source and distance to the largest source population, there was a significant quadratic relationship between isolation and abundance. Abundance of colonizing *N. irrorata* was not found to be significantly related to a third measure of isolation, mesocosm connectivity. These results indicate that the relationship between habitat isolation and colonist abundance may not be a monotonic decline across all spatial scales, a finding that contradicts the usual assumption incorporated in measures of habitat connectivity. Our results suggest that under some circumstances individuals that have undertaken dispersal may bypass patches they encounter early in this process and preferentially settle in patches encountered later. This behavioral preference in conjunction with decreased numbers of potential colonists at sites far from the source environment could lead to the “hump-shaped” colonist abundance by habitat isolation relationship we observed in this study. We suggest that simple assumptions about the relationship between habitat isolation and the probability a site is colonized need to be reexamined and alternative possible forms of this relationship tested.

**Key words:** *colonist abundance; colonization; dispersal; habitat isolation; inter-pond distance; Notonecta irrorata; patch connectivity.*

### INTRODUCTION

The movement of organisms between habitat patches affects the composition and diversity of communities within local patches as well as the population dynamics of both dispersing species and the species with which they interact in the new patch (MacArthur and Wilson 1967, Hanski 1999, Holyoak et al. 2005). However, the difficulties of quantifying dispersal movements often make it necessary to incorporate a number of assumptions about movement behavior which have been insufficiently tested. For example, while mortality and prior settlement necessarily result in a decrease in the number of potential colonists arriving at increasingly

isolated sites, the assumption that the abundance of colonists will monotonically decrease as isolation increases also implicitly incorporates the assumption that colonization rate is directly proportional to the number of individuals that reach a patch. Many animals, however, exhibit distinct habitat selection preferences and exert considerable control over where they take up residence or leave behind their offspring (Binckley and Resetarits 2005, Blaustein et al. 2005, Resetarits 2005, Brodin et al. 2006, Vonesh and Buck 2007). Therefore, habitat selection choices made by dispersers can change our assumptions about how colonization patterns will develop across a range of distances from the source environment.

Within-patch conditions have been the principal focus of most studies of habitat selection behavior. However, distance itself may affect the relative, or perceived, value of a patch to a disperser. Dispersers may be more likely to settle in available habitats as they travel for longer periods from their source and the costs of dispersal accumulate (Kennedy and Booth 1963, Ward 1987, Stamps et al. 2007) but in the absence of variation in

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patch quality does distance itself influence the colonization decision? For active dispersers one hypothesis is that having made the decision to disperse, individuals will have a “refractory period” during which they will be less inclined to settle in suitable habitats which they encounter. This strategy could be favored under several conditions including when individuals disperse to avoid poor or deteriorating conditions, a common trigger for dispersal (Dingle 1996), and habitat conditions are spatially autocorrelated. This behavior may also be favored when dispersal is a means of reducing kin competition and inbreeding avoidance (Hamilton and May 1977). Under these conditions settling close to the source will do little to alleviate kin competition or the probability of mating with relatives.

Refractory periods have been documented in a number of animal groups including insects (reviewed in Stamps et al. 2007). The behavioral propensity of individuals to bypass habitat patches close to the source they are dispersing away from may alter how we understand and quantify patch connectivity. Unfortunately, to date there have been few tests for this pattern from free-ranging individuals moving through natural landscapes to assess how this behavior affects colonization of habitat patches (Stamps et al. 2007). A variety of metrics have been used to calculate patch connectivity which all assume, directly or implicitly, that distance from the source and probability of colonization are negatively related across all distances (for reviews of these metrics, see Moilanen and Nieminen 2002, Winfree et al. 2005). At sufficiently large spatial scales this assumption is undoubtedly true but at smaller spatial scales (with both scales being determined by the organisms’ movement capacity) habitat selection behavior may produce alternative forms of this relationship. Given the often poor fit of these connectivity metrics to empirical data (Moilanen and Nieminen 2002, Winfree et al. 2005) testing for alternative shapes in the distance-colonization curve may provide new insights into how habitat connectivity is assessed. In order to bridge the divide between the behavioral ecology of habitat selection and landscape-centered measures of patch connectivity, these data need to come from studies done at the appropriate spatial scales. Additionally, most studies have focused on the relationship between patch connectivity and occupancy and there has been notably less work on the relationship between connectivity and colonist abundance. Colonist abundance, however, is a critical parameter and can positively affect the probability that colonization will result in a population’s successful establishment (Ahlroth et al. 2003).

In this study, we examined the relationship between colonization and distance to source environments in a common pond insect, *Notonecta irrorata* (Hemiptera: Notonectidae). Notonectids are capable of dispersal by flight in the adult stage and can be strong fliers (Briers

and Warren 2000) but are aquatic throughout the life cycle. We used mesocosms (cattle watering tanks) that had identical initial conditions to eliminate inter-patch variation in habitat quality. These mesocosms were arranged across a natural landscape at varying distances from known source environments. Data from surveys of *N. irrorata* colonists in the tanks across two years were used to examine the relationship between the abundance of colonists and mesocosm isolation using three metrics of patch isolation, distance to nearest source, distance to the largest source population, and Hanski’s connectivity index which is an inverse of isolation (Hanski 1999). If individual habitat settlement decisions are not influenced by distance from the source environment we would expect to find a monotonically negative relationship between isolation and the abundance of colonists within a mesocosm. In contrast, if habitat selection is affected by distance to the source and dispersers preferentially bypass the first habitats they encounter we expect to find a “humped-shaped” (or inverse U) curve relating colonist abundance and connectivity of the mesocosm to sources. Our goal in this study was to examine whether in the absence of environmental variation in habitat condition of the sites colonized, dispersers would differentially colonize habitats based on their proximity to sources.

#### METHODS

Eighteen cattle tanks were established on the Edwin S. George Reserve (Michigan, USA; hereafter ESGR) (42°28′ N, 84°00′ W; Appendix) in 2002 and sampled in 2002 and 2003. Tanks (1.9 m in diameter and ~0.5 m deep) were filled with 1300 L of well water, stocked with a nutrient source (oak leaves and rabbit chow), and given an initial inoculum of zooplankton to support invertebrate colonists (further details in McCauley 2006). Water was added to tanks when necessary to maintain them near to the starting volume. Tanks were placed in similar sites in open field environments where there was minimal canopy cover from surrounding trees. By controlling for pond conditions and the local environment around these ponds, spatial autocorrelation among ponds was not a problem. The need for open-canopy habitats constrained us to using old-field habitats that are not uniformly distributed across the ESGR. As a result tank placement could not occur at precise intervals of distance from the ponds of interest. Nonetheless tanks were placed at a range of distances away from source ponds that reflects the natural landscape pattern of inter-pond distances in this region. In the first year of the study, four of these tanks contained caged fish, part of a test for habitat selection based on the presence or absence of fish. These tanks were dropped from the analysis. All tanks were included in analyses in 2003 when fish were no longer a treatment

in the experiment. Insect colonists were eliminated from these tanks by freezing during the winter of 2002–2003.

Tanks were sampled for invertebrates three times per year. Sampling was conducted by dividing tanks using a solid barrier that split each tank in half and formed a seal with the tank edges to prevent the movement of invertebrates between the two halves. Invertebrates and leaf litter were then collected from one half using a dip net. Dip netting continued until all leaf litter from the sampled half of the tank had been collected and several dips (a minimum of eight) were made without collecting additional invertebrates. Leaf litter and invertebrates were placed in a large plastic bin and mixed with water from the tank. Leaves were rinsed and thoroughly searched for invertebrates, which were collected and placed in 70% ethanol for later identification. After searching leaves, the remaining water was filtered through successively smaller sieves. Invertebrates caught in the filters were collected and preserved in 70% ethanol. All equipment was thoroughly rinsed with well water before moving between tanks to prevent cross contamination. In a 2003 April/May sampling (see McCauley 2006 for details on sampling times) one tank was not sampled in this way because extensive dip netting without dividing the tank detected no invertebrates. This tank and all others were sampled using the tank division approach in the other five sampling periods. All notonectids collected from cattle tanks were identified to species.

Among the other groups of invertebrates collected one group, dragonfly larvae, were enumerated and identified to species. Other colonists were identified to the level of order or family and presence and absence in each tank was noted. Observations during the identifications of the notonectids and dragonflies suggest that most taxonomic groups were represented by multiple species. Within the other taxa identified to species, dragonflies, the high abundance (over 10 000 dragonfly larvae were collected from these tanks) and diversity (14 species) of larvae collected from these tanks (McCauley 2006) suggests that at least some invertebrate groups perceived these tanks as attractive habitat and their presence in these is comparable to abundance and diversity levels in natural small ponds in the region (McCauley et al. 2008). To assess the similarity of the communities forming in these pools to small ponds across a wider set of taxa we compared the presence–absence data we had at the order level (McCauley 2005) to data from Urban (2004) on the presence or absence of invertebrate orders in 14 northeastern ponds which have a similar regional species pool. We found no difference in the number of orders observed in our tanks and Urban's ponds ( $t_{14,18} = 1.02$ ,  $P = 0.33$ ). This is a relatively coarse level of identification but our observations suggest that these orders are represented by multiple species and that the level of invertebrate

abundance and diversity are comparable to those of small ponds in the region.

Source environments for *N. irrorata* were identified using data from surveys of the aquatic habitats on the ESGR. These surveys collect amphibians and aquatic invertebrates including notonectids. Sources were defined as those habitats in which *N. irrorata* were present for a given study year. The size of a source population was estimated using the catch per unit effort (CPUE) multiplied by the pond area. Sources were also monitored for drying and drying dates estimated as the mid-point between a census period in which the pond had water and when it was observed to be dry (details of sampling and habitat monitoring in Werner et al. 2007). We characterized the isolation of each tank using three measures: (1) distance to nearest source, (2) distance to the largest source population in a given year, and (3) connectivity (Hanski 1999). Distance to nearest source and distance to the largest source do not weight habitats but connectivity incorporates both distance to source habitats and population size in the source. Connectivity is an inverse measure of isolation and  $S_i$  increases as mesocosms are more connected to potential sources. Hanski's index of connectivity (1999) was used:

$$S_i = \sum_{j \neq i} \exp(-\alpha d_{ij}) N_j$$

where  $\alpha$  is a measure of the effect of distance on migration (inverse of mean dispersal distance),  $d_{ij}$  is the mean distance (edge to edge) between a source pond and the tanks in a pair, and  $N_j$  is the estimated population size of *N. irrorata* in the source pond. Population size was estimated based on surveys of source ponds in 2002 and 2003 (Werner et al. 2007). We used  $\alpha = 1$ . Connectivity is not especially sensitive to the estimation of the parameter  $\alpha$  and alternative values would not change the rank order of mesocosm connectivities (Hanski 1999). Because the isolation of a mesocosm increases with increasing distance to a source, the relationship between distance to source (nearest or largest) and colonist abundance is expected to be negative. In contrast because connectivity,  $S_i$ , is an inverse of isolation the relationship between colonist abundance and mesocosm connectivity is expected to be positive.

#### Data analysis

We combined data from the two years in our analysis, treating the data from a tank in a given year as independent from the data for that tank in the other year. Tank-years were considered independent for two reasons. First, water in these tanks froze thoroughly during the winter eliminating notonectids, so there was no population carryover between years. Second, source ponds differed between the two years resulting in large differences in how isolated a given tank was in the two

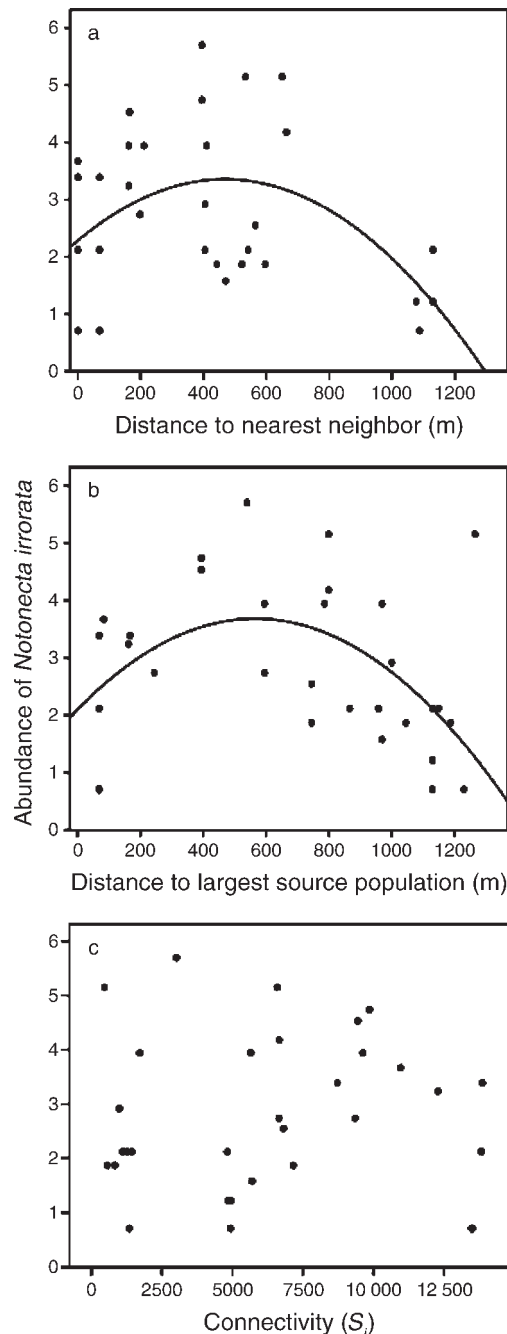


FIG. 1. Relationship between the abundance of the aquatic insect *Notonecta irrorata* (square-root transformed) and tank isolation measured (a) as distance to nearest neighbor, (b) as distance to the source pond with the largest population in a given year, or (c) connectivity. Solid lines indicate a significant best-fit quadratic relationship, and points are the observed data. No significant relationship was found between abundance and connectivity (c).

years. The count of *N. irrorata* collected from each tank was square-root transformed ( $\sqrt{(N+1)}$ ) which improved the normality of the data. We examined the relationship between the abundance of *N. irrorata* colonists and the three measures of tank isolation using a curve-estimation analysis, examining how well a linear or a quadratic model explained the abundance data for each isolation metric. These two models were chosen a priori because based on the study scale they were expected to be the most likely to fit these data. We used a goodness of fit *F* ratio test to compare the ability of the linear and quadratic models to explain the data.

To assess whether the distributions of potential predators and competitors affected the patterns of abundance in *N. irrorata* we conducted two tests focusing on hemipterans that feed at the water surface boundary. A Pearson's correlation was used to assess whether the abundance of other *Notonecta* species, which can be both competitors and predators, was related to abundance patterns in *N. irrorata*. Species in the family Gerridae (Hemiptera) were not enumerated but 12 of the 32 tanks were not colonized by this group. We used a *t* test to determine whether the abundance of *N. irrorata* differed based on the presence or absence of this group of potential competitors. We also used a Pearson's correlation to test for a correlation between *N. irrorata* abundances and the abundance (square-root transformed) of another group of potential competitors enumerated in this experiment, dragonfly larvae. All analyses were conducted using SPSS 15.0 (SPSS, Chicago, Illinois, USA).

## RESULTS

A total of 356 *N. irrorata* were collected in the two years. This species comprised 98% and 78% of total notonectid abundance in these tanks during 2002 and 2003, respectively. In both years, the majority of our artificial ponds were colonized by *N. irrorata*, 97% of tanks were colonized in 2002 and 70% in 2003. There were eight source ponds in 2002 and seven in 2003 with four of these ponds being sources in both years (Appendix). The source pond with the largest *N. irrorata* population differed between the two years. The largest source population in both years was a minimum of four times larger than the population in any other habitat on the ESGR.

There was a significant quadratic, but not linear, relationship between distance to nearest source and *N. irrorata* abundance (quadratic,  $R^2 = 0.216$ ,  $F_{2,29} = 3.99$ ,  $P = 0.03$ ; linear,  $R^2 = 0.028$ ,  $F_{1,30} = 0.86$ ,  $P = 0.363$ ; Fig. 1a). A goodness-of-fit *F* ratio test found that the quadratic model provided a better fit to the data than the linear model ( $P < 0.025$ ). A similar relationship was found for distance to largest source and *N. irrorata* abundance (quadratic,  $R^2 = 0.226$ ,  $F_{2,29} = 4.24$ ,  $P = 0.024$ ; linear,  $R^2 = 0.034$ ,  $F_{1,30} = 1.05$ ,  $P = 0.314$ ; Fig. 1b)



and again a goodness-of-fit test found that the quadratic model provided a better fit to the data than the linear model ( $P < 0.025$ ). The abundance of this species in tanks was not significantly related to tank connectivity (quadratic,  $R^2 = 0.048$ ,  $F_{2,29} = 0.74$ ,  $P = 0.488$ ; linear,  $R^2 = 0.032$ ,  $F_{1,30} = 1.0$ ,  $P = 0.325$ ; Fig. 1c).

There was no relationship between the abundance of *N. irrorata* and the abundance of other *Notonecta* species in these tanks (Pearson's correlation = 0.238,  $N = 32$ ,  $P = 0.189$ ). The abundance of *N. irrorata* did not differ between tanks with and without gerrids ( $t = 1.57$ ,  $df = 30$ ,  $P = 0.127$ ). There was no evidence for competitive or predatory suppression of *N. irrorata* abundances by dragonfly larvae. Indeed there was a positive correlation between the abundances of larval dragonflies and *N. irrorata* (Pearson's correlation = 0.418,  $N = 32$ ,  $P = 0.017$ ). This pattern was, however, driven by the abundance of one dragonfly species, *Libellula pulchella*, which reaches peak abundances nearly 1 km from its source habitats (McCauley 2005). When this species is removed there is no relationship between the abundance of *N. irrorata* and larval dragonflies (Pearson's correlation = 0.005,  $N = 32$ ,  $P = 0.979$ ).

#### DISCUSSION

For two measures of mesocosm isolation, nearest neighbor distance and distance to the largest source population, the abundance of *N. irrorata* colonists peaked at intermediate levels of isolation. For these measures of isolation a quadratic function best fit the data and explained approximately 20% of the variation in abundance. For the third measure of isolation, connectivity, there was no significant relationship between colonist abundance and mesocosm isolation. The connectivity metric may be inappropriate to fit to these data as it incorporates an assumption of a negative exponential relationship between distance and colonization probability that appears to be an inappropriate assumption for this species at this scale of movement. The connectivity measure did not, however, find a monotonically negative relationship between mesocosm isolation and colonist abundance which is the typical assumption for this relationship. Taken together the patterns observed in our experiment indicate that the assumption that colonist abundance will decrease monotonically across all spatial scales may not hold true for some species moving at realistic landscape scales. The hump-shaped relationship found between colonist abundance and two measures of habitat isolation, nearest neighbor and distance to largest source, further suggest that highly connected habitats may receive fewer colonists than habitats at intermediate levels of isolation under some conditions.

Our results are striking in part because with the possible exception of microbes (Finlay 2002; but see

Telford et al. 2006), the most commonly observed pattern is that the probability or abundance of dispersers decreases with distance (Levin et al. 2003, Nathan et al. 2003, Bowler and Benton 2005). The only other example of a hump-shaped distance by abundance curve that we are aware of is in a ballistically dispersed tree where this dispersal kernel was inferred from patterns of recruitment and mortality (Boudreau and Lawes 2008). However, this pattern may be more common than reports so far indicate but may not have been commonly tested for. Theoretical work found that a peak in dispersal probabilities at intermediate distances can be favored under conditions of kin competition and when the cost of dispersal is an increasing function of distance (Rousset and Gandon 2002) and the existence of refractory periods in a variety of taxa (reviewed in Stamps et al. 2007) suggests that behaviors that decrease the probability of settling in the first habitats encountered can evolve. Because measuring dispersal at a relatively fine scale is critical to detecting this pattern, this effect may be missed if close and intermediate sites are lumped in analysis. However, the scale across which we detect this hump-shaped association between colonist abundance and patch isolation can be important for population and community processes at the landscape scale. Although notonectids can be strong fliers, for example Briers and Warren (2000) found that *Notonecta* in dewponds could disperse as far as 1.6 km, these maximum dispersal distances are likely to be achieved relatively infrequently with most dispersal occurring at smaller scales. Our experimental ponds were placed up to 1.23 km from sources (nearest neighbor or major source) and therefore are likely to capture a large fraction of the population dispersal. The natural ponds in this region are highly dynamic and experience regular disturbances from drying (Werner et al. 2007). In this study, we saw a number of shifts in the source habitats including local extinctions across just two years, suggesting movement at this scale is important in the persistence of these populations in this landscape. Mortality and prior settlement would necessarily result in a continued decline in the abundance of colonists if we moved further from source habitats and this larger scale is likely to be the more relevant one for large-scale regional processes such as range expansions. However, based on the frequent colonization and extinction events observed in these ponds even in highly mobile taxa such as dragonflies (McCauley et al. 2008) and the distances between natural ponds (Appendix) the scale at which we detected this hump-shaped relationship between distance and colonist abundance is capable of affecting processes at the population and metacommunity scale. Our results indicate that a negative relationship does not hold across all scales that are likely to be of ecological importance and suggests that models of dispersal should explore the impact of

alternative dispersal kernels including hump-shaped curves that have a long tail of decline.

The function of dispersal to these tanks (i.e., how dispersers are utilizing these cattle tank habitats) is currently unknown and would affect how we interpret the behavioral mechanisms that drive the observed pattern. The majority of dispersal we observed occurred in the fall, well after the breeding period, and was most likely recently matured individuals that were dispersing from their natal site (*N. irrorata* is typically univoltine in Michigan). Consequently, we found little evidence of notonectid reproduction in these tanks (tanks froze in the winter eliminating populations). Thus, there are several nonexclusive mechanisms that might explain the pattern we observed in this study. If individuals are leaving their natal habitat and dispersing to sites (tanks) to potentially overwinter and reproduce, two mechanisms are likely to be important. First, once they have undertaken the decision to disperse individuals may not respond to stimuli that indicate the presence of suitable habitat for some refractory period. This is similar to the behavior of individuals engaged in true migration (Dingle 1996). Second, if dispersers are leaving low-quality habitats (e.g., a drying pond) their perception of the quality of new sites they encounter may be influenced by the distance traveled from their original patch, what Resetarits (2005) called "contagion." Alternatively, individuals may be using the tanks as stepping stones in searching for overwintering sites (breeding habitats are often unsuitable overwintering sites), and the higher abundance of individuals at distances of 400–500 m from a source may reflect how far they typically travel in a given flight. Based on current data we cannot determine which of these mechanisms is responsible for the hump-shaped isolation by abundance curve observed in this study. However, for notonectids and other taxa in which dispersal by incidental displacement is unlikely because the matrix environment does not form an important component of their daily operational environment (i.e., the matrix habitat is not used for maintenance activities and may only be entered during the dispersal process) and they experience a distinct transition at the habitat boundary, refractory periods appear likely to be an important mechanism. In these organisms, the behavioral decision to disperse may have a great deal in common with migratory behavior despite operating on a more local scale.

Behavioral ecologists have long recognized that the searching behavior of dispersers can affect their probability of selecting certain habitats and that dispersers can have refractory periods during which they are less likely to settle in suitable habitats (Kennedy and Booth 1963, Stamps et al. 2007). Ecologists have not, however, sufficiently integrated this behavior into predicting patch occupancy or colonist abundance in

patches that differ in spatial isolation. The pattern we observed in this study suggests two things for future studies of how habitat isolation affects population and community processes. First, negative relationships between habitat isolation and colonist abundance should not be assumed at small to moderate spatial scales. Behavioral decisions made by dispersers can generate non-monotonic relationships between distance and settlement choice. When this occurs the effects of isolation on population processes, including the extent to which the population is buffered from extinctions by the rescue effect, can differ significantly from predictions based on standard models of connectivity. Highly connected habitats may receive fewer immigrants, and intermediate distance habitats more, than expected based on strictly structural measures of patch isolation. This pattern also suggests that in metacommunities where species composition is affected in part by the differential dispersal limitation of member species understanding differences in habitat selection behavior, as well as dispersal capacity, will improve predictions about the effects of habitat isolation on community structure. A second conclusion that emerges from our results is that abundance should be explicitly incorporated into studies of patch colonization as it may show patterns that are not detected by occupancy alone. In our study most patches were colonized by *N. irrorata* but differed widely in the abundance of colonists, a factor that can critically affect population establishment and persistence (Ahlroth et al. 2003).

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#### APPENDIX

Map of the study sites, E. S. George Reserve, Michigan, USA (*Ecological Archives* E090-183-A1).