

The role of local and regional processes in structuring larval dragonfly distributions across habitat gradients

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Despite the importance of community-structuring processes operating at both local and regional scales, there is relatively little work examining both forces within a single system. I used a combination of observational and experimental approaches to examine the processes structuring larval dragonfly distributions in lentic habitats that encompass a gradient of both permanence and top predator type. I compared the relative vulnerability of species to predators from different portions of this gradient to assess the role of predation as a local force structuring communities. I also assessed the role of regional processes on species' distributions by examining species' propensity to disperse to and colonize artificial ponds distributed across a landscape. In both studies I contrasted habitat specialist species, which had larvae restricted to permanent lakes, with habitat generalist species, which had larvae that occur broadly across the habitat permanence and top predator transition. Results from this work suggest that dispersal and colonization behavior were critical mechanisms restricting the distributions of habitat specialist species, but that predation may act to reinforce this pattern. The habitat specialists dispersed less frequently, colonized artificial ponds less often when they did reach them, and most moved shorter distances than the habitat generalist species. Habitat specialists were also more vulnerable than habitat generalists to an invertebrate top predator with which they do not co-exist. Results from these studies suggest that species distributions can be shaped by processes operating at both regional and local spatial scales. The role of dispersal and recruitment limitation may be generally underestimated as a force shaping species distributions and community structure across habitat gradients in which there is a transition in both the biotic interactions and the disturbance interval across that gradient.

The processes that structure communities can be categorized as local or regional based on the spatial scale at which they operate (Ricklefs 1987). Local processes, including biotic interactions and abiotic tolerances, determine whether species can establish and persist in the habitats to which they have dispersed. In contrast, regional processes act prior to the arrival of species at local sites and determine the number and identity of species reaching a habitat. The relative importance of these processes may shift depending on the spatial and temporal scale examined, and understanding these processes in a synthetic fashion has been the subject of considerable theoretical interest by ecologists (Holt 1993, Loreau and Mouquet 1999, Holyoak et al. 2005a). Historically in community ecology there has been greater emphasis on the effects of local processes. However, the growth of both metapopulation biology (Hanski and Gilpin 1997, Hanski 1999) and metacommunity ecology (Leibold et al. 2004, Holyoak et al. 2005b) have focused attention on the role of dispersal limitation as a potential structuring force in ecological communities and the need for a synthesis of both local and regional perspectives.

Despite interest in how processes operating at different spatial scales affect community structure, relatively few studies explicitly test the contributions of

processes at both levels within a single system. Results from studies that have explicitly considered both local and regional factors vary in their conclusions about the relative importance of these processes, but most indicate that processes at both scales have some degree of effect on community structure (Tilman 1994, Shurin 2000, Kneitel and Miller 2003, Cottenie and De Meester 2004). Additionally, a central approach in understanding the processes affecting community composition has been to analyze species' distributions across habitat gradients, and this approach has generated considerable insight into the local processes structuring communities and the relationship between species' traits that affect local performance and species' distributions across gradients (Wellborn et al. 1996, Holyoak et al. 2005b). The potential role of dispersal limitation in shaping species distributions has been less extensively explored, and relatively few studies have related dispersal limitation to species distributions across habitat gradients (but see Tilman 1994, Bonte et al. 2003, Gilbert and Lechowicz 2004, Ozinga et al. 2005).

A lack of data on the role of both local and regional processes in determining species distributions across habitat gradients is a critical gap in understanding lentic freshwater systems where the structure of the habitat gradients that characterize these systems implicates both local and regional processes in structuring communities. Lentic habitats vary in habitat duration (hydroperiod), and include ephemeral ponds that dry every year, semipermanent ponds that dry in some but not all years, and highly permanent lakes that may hold water reliably for hundreds to thousands of years. For species that experience local extinctions as a result of pond drying, dispersal and recolonization rate following disturbance may act as a critical filter on their presence in habitats that dry periodically.

Associated with the hydroperiod gradient, however, is a transition in the types of top predators that dominate in sites. Vulnerability to drying, limited abilities to handle low oxygen conditions, and low dispersal rates typically restrict large-bodied fish (e.g. Centrarchidae) to permanent habitats deep enough to prevent winter anoxia. Small-bodied fish (e.g. Cyprinidae and Umbridae) also experience local extinctions when ponds dry but many species have greater capacities to withstand low oxygen conditions (Klinger et al. 1982) and rapidly recolonize previously dried sites connected to source habitats through intermittent waterways (McCauley 2005). Therefore, small-bodied fish are common top predators in shallow, permanent and semi-permanent habitats. In contrast, most invertebrate top predators do not require aquatic connections between habitats to facilitate their recolonization of previously dried sites and they dominate in temporary and more isolated permanent habitats, where fish are excluded by their abiotic tolerances and by dispersal limitation (Wellborn et al. 1996). Consequently, the sorting of top predator groups along the hydroperiod gradient results in transitions in local predator—prey interactions, and there is evidence that differential vulnerability to alternative top predator types can shape species distributions in many aquatic taxa (Blois-Heulin et al. 1990, McPeck 1990a, Werner and McPeck 1994, Wellborn et al. 1996, Stoks and McPeck 2003).

The hydroperiod—predator type gradient in which both predator—prey interactions and recolonization rate have the potential to affect community structure provides a useful context to examine the relative impact of both local and regional factors on species distributions and consequent community structure. To examine the effects of these processes, I contrasted species of dragonfly (Odonata: Anisoptera) that differed in the distributional breadth of their larvae across this gradient. To assess whether predation excluded species from a portion of the habitat gradient, I compared the relative vulnerability of larval dragonfly species to alternative top predators. I also used an array of artificial ponds and observations at natural habitats to assess the role of dispersal limitation in structuring species distributions, comparing the dispersal and recruitment behavior of species that differed in their distributional breadths. Combining data from these studies allowed me to assess the relative potential contributions of local and regional processes operating in this system and how these processes may act to reinforce each other in shaping species' distributions.

Methods

Study system

Characterization of the habitat distributions of species used in this study were based on independent data from multi-year surveys of 57 natural lakes and ponds in southeast Michigan. These surveys used a combination of dipnetting and pipe sampling (Skelly 1996, Skelly et al. 1999) during 2-4 time points in each year sampled to generate both presence—absence and abundance data for 45 dragonfly species in these lakes and ponds (details in McCauley 2005). Dragonfly species in this system varied in the breadth of their habitat distributions. Species distributions included habitat specialists, species confined to habitats with a narrow range of hydroperiods and a single top predator type, and habitat generalists that occurred broadly across habitats with varying hydroperiods and alternative top predator types. In these studies, I contrasted predator vulnerabilities and dispersal behavior in a subset of habitat specialist and habitat generalist species. I examined only one type of habitat specialist, species with larvae found exclusively in permanent lakes with large-bodied fish predators. These specialists were compared to habitat generalist species that had larvae found in habitats across the permanence gradient and top predator transition. Although some species in this system have traits that facilitate their use of non-permanent habitats by buffering them from local extinctions (typically a desiccation-resistant egg stage), the species examined in this study all over-winter in the larval stage, are uni- or semi-voltine, and are vulnerable to local extinction from drying events (one possible exception is *Libellula pulchella* which appears to have some resistance to drying through aestivating as larvae in sediments, S. A. Wissinger, pers. comm., Werner et al. unpubl.). These criteria excluded habitat specialist species restricted to temporary, non-fish ponds which over-winter in an egg diapause stage and consequently have more rapid larval development than the

habitat specialists and generalists considered in this study.

Predation experiments

I conducted two experiments with dragonfly larvae having varying distributional breadths to determine their relative vulnerability to important predators that dominate in different portions of the hydroperiod gradient. These experiments involved two major functional groups of dragonfly larvae, non-benthic (species typically associated with vegetation in the water column) and benthic (species typically associated with habitat-bottom substrates). All experiments were conducted in aquaria (25 x 50 x 27cm) in the laboratory and each aquarium held a single predator. Aquaria were kept oxygenated with air bubblers. Structure was provided by gravel covering the bottom portion of the aquarium and a combination of natural materials and polypropylene rope. These structural elements provided cover for larvae, slowing the rate of predation and mimicking natural substrate and vegetation conditions. Prior to beginning each trial, larvae were exposed to non-lethal cues of the presence of the predator they were subject to during the trial. This allowed larvae to respond to the presence of predators and adopt any anti-predator behaviors they would exhibit under natural conditions prior to their exposure to direct predation risk. Details of each experiment varied because of differences in the biology of the benthic and non-benthic larvae.

Experiment I: non-benthic larvae

I compared the vulnerabilities of three species of nonbenthic dragonfly larvae to three top predator types (all predator body size measurements are mean \pm SE): a large-bodied fish species (bluegill, *Lepomis macrochirus*, standard length: 65.07 \pm 1.32 mm), a small-bodied fish species (mudminnows, *Umbra limi*, standard length: 60.08 \pm 1.05 mm), and an invertebrate top predator (*Anax junius*, hereafter: *Anax*, head-width: 6.9 \pm 0.15 mm). The dragonfly species compared included one habitat specialist (*Celithemis fasciata*) and two species of habitat generalists (*Leucorrhinia intacta* and *Erythemis simplicollis*). Structure in each aquarium was provided by 30 g of gravel, 6 g of dried oak leaves, and 6 strands of natural macrophytes (~ 13 cm each) that had been rinsed sequentially in CO₂-infused and normal water drawn from an underground well to remove predator chemical cues and any attached small invertebrates. Each predator treatment had seven replicates. Two aquaria were used as controls with no predators to quantify any intra-guild predation. Predators were caged in clear, screen-topped containers 17 h before being released into the aquarium. A total of 18 larvae, six from each of the three species, were placed in every aquarium. All larvae were matched for size. I removed predators 20 h after they were released into aquaria and then thoroughly searched aquaria and removed all remaining larvae. Surviving larvae were identified to species under a dissecting microscope.

I compared species' survival rates in the presence of all three predators. The proportional survival of species in replicates was arcsine transformed and entered as a continuous dependent variable while species and predator were categorical

fixed explanatory factors. One replicate of the Anax treatment was dropped because the predator never fed and molted soon after the completion of the trial. All larvae were collected from the control replicates, which were consequently dropped from the analyses. A two-way, linear mixed model ANOVA was used to compare species' survival rates in the predator treatments. Bonferroni post-hoc tests were used to make specific treatment and species comparisons. All analyses were done in SPSS 11.5.

Experiment II: benthic larvae

I contrasted the vulnerability of three species of benthic dragonfly larvae to bluegill (standard length: 77.58 ± 1.48 mm) and Anax (head-width: 7.3890.21 mm) predators. All prey species were in the genus *Libellula* and included a habitat specialist (*Libellula incesta*) and two habitat generalists (*Libellula luctuosa* and *Libellula pulchella*). To create structure in each aquarium, I used 170 g of gravel, 30 g dried oak leaves, and 2 strands of polypropylene rope each ~ 30 cm long weighted to the bottom in the middle of the strand. Strands were frayed into 15-20 sections that extended to the water's surface and simulated aquatic macrophytes. Larvae used in the experiment were matched for size. Species could not be combined in predator treatments as was done with non-benthic larvae because positive identification of *Libellula* species requires an examination of intra-labial mouthparts, a process that can damage live larvae. If species were combined, errors in pre-trial identifications could obscure differences in species' vulnerabilities. Consequently, the vulnerability of each species of *Libellula* was examined independently. Fourteen larvae of a single *Libellula* species were used in each replicate. Each species had five replicates for each predator treatment.

To account for errors in identification and for possible cannibalism, I established two control replicates for each species in similar conditions using rectangular plastic containers rather than glass aquaria but otherwise keeping the physical set-up the same. Fourteen larvae of a putative *Libellula* species were used in each control replicate without predators. Larvae from controls were collected, preserved, and identified to species at the end of the trial. Only two of 84 individuals in the control replicates had been misidentified (-2%) and all larvae collected from the predation treatments were from the putative species. Consequently, I made no adjustments to measured predation rates.

Eighteen hours before the trial started, 120 ml of water from tanks where predators had been feeding on *Libellula* larvae was mixed into experimental aquaria, with water from each predator type going into the appropriate predator treatment in the experiment. Predators were placed in screen cages inside aquaria 1.5 h before being released into the experiment to intensify cues indicating the presence of predators. In these trials, survivorships were measured at two time periods: after 23 h and after 46 h. After 23 h, survivorships in the bluegill treatment were at or below 50% and these treatments were taken down, larval survivorship recorded, and survivors preserved in ethanol. After another 23 h

replicates in the *Anax* treatment were taken down, survivorships recorded, and survivors preserved in ethanol. I used a two-way ANOVA to compare species survivorships with both predators on day one. A one-way ANOVA was used to compare species' survivorships with *Anax* on day two of the trial. Tukey's post-hoc tests were used to make specific treatment and species comparisons.

Dispersal to and colonization of artificial ponds

I conducted a study to examine differences between habitat specialists, from permanent lakes with large-bodied fish top predators, and habitat generalists in their propensity to disperse to and to colonize newly created artificial pond habitats. This behavior is expected to affect their probability of reaching and colonizing ponds that have previously dried. Sixteen artificial ponds (cattle tanks) were established in May 2002 and the adult and larval dragonflies arriving at these artificial ponds were monitored through October 2003. This study was conducted on two Univ. of Michigan research properties, the E. S. George Reserve (hereafter: ESGR) and the Fresh Air Camp, both located in southeastern Michigan, USA. Artificial ponds were filled with 1300 liters of water drawn from a common source (an underground well) that had no dragonfly larvae or eggs to prevent contamination during filling. I stocked cattle tanks with initial resource conditions to support larval dragonflies. These included 300 g of oak leaves collected from a common terrestrial habitat, 60 ml of rabbit chow (Purina™), *Daphnia* from a culture, and standard amounts of rope and fiberglass screening material to provide structure within the tank. Perches for adult dragonflies were also provided at each cattle tank. I placed pairs of tanks directly adjacent to three water-bodies that represented different points along the permanence—predator type gradient: a permanent lake with large-bodied fish as top predators, a permanent lake with small-bodied fish as top predators, and a semi-permanent pond which dried in 2001 and 2002 and had invertebrates as top predators. These artificial ponds were placed in open canopy sites adjacent to water-bodies. The remaining ten cattle tanks were placed as pairs in open fields at varying distances from these water-bodies. The positioning of cattle tanks was designed to situate these artificial ponds at a range of distances away from potential source environments moving from each habitat type into the most isolated portion of this landscape, a large old field at the center of the ESGR (Fig. 1). This study allowed me to look at the arrival of species at newly available aquatic habitats standardized for size and other features in a natural landscape. Placement of these artificial ponds was constrained by the availability and arrangement of open field habitats that occur at a range of distances away from the focal habitats in this landscape. Consequently, the design represents a tradeoff between control and working at a realistic spatial scale. Data from this study provide a means of examining how species differ in their propensity to move away from source environments and to colonize new habitats in a natural landscape while controlling for the conditions of those habitats.

Larval dragonfly communities in potential source water-bodies were sampled

prior to beginning this study (McCauley 2005 E. Werner et al., unpubl.). This allowed me to identify the source environments species observed in this study could be coming from. Dispersers were defined as adults observed in the immediate vicinity of artificial ponds while colonists were those larvae collected from artificial ponds. Dispersal to and colonization of these artificial ponds was monitored for two years.

To measure dispersal, I conducted observations of the adult dragonflies visiting artificial ponds in both years. Passive observation rather than capture was used because capturing and handling adult dragonflies may increase their probability of moving away from the site of capture (Koenig and Albano 1987). Four sets of observations were made in 2002 and five in 2003. Observations were spread throughout the adult flying season (2002: 24-26 June, 8-11 July, 22-26 July, 8-9 August; 2003: 20-23 June, 2-3 July, 21-24 July, 4-5 August, 18-19 August). Observations were conducted by sitting 1-2 m away from the cattle tank and scanning for adult dragonflies at the tank and surrounding area (~ 2 m from tank edge) using binoculars. The observer scanned a minimum of 4 times per minute and watched the artificial pond directly between scans. Each observation period lasted 10 min, for a total of 180 min per pair of artificial ponds. Observers were trained in adult dragonfly identifications. Individuals observed were identified to species (based on: Walker and Corbet 1978, Dunkle 2000) and their abundance recorded. Individuals that could not be identified to species were identified to the lowest level possible (typically genus). All observations were conducted on sunny days with low wind between 12:00 pm and 5:00 pm (US Eastern Daylight Savings Time).

To measure colonization, I sampled artificial ponds for larvae three times in 2002 (9-12 July, 23-29 August, 4-11 October) and 2003 (30 April — 2 May, 11-15 August, 6-10 October). One artificial pond was not sampled in May 2003 because winter mortality was substantial and no insects were detected in extensive dipnetting of this pond. All other sample periods involved fully sampling all artificial ponds. To sample artificial ponds, I used a solid divider to split a tank in half and form a seal with the edges to prevent movement of invertebrates between the two halves. A dipnet was used to collect all invertebrates and leaf litter from one half of the artificial pond. Dipnetting continued until all leaf litter had been collected and several dips (a minimum of 8) were made without collecting additional invertebrates. Leaf litter and invertebrates were placed in a large plastic bin and mixed with water from the cattle 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 artificial ponds to prevent cross contamination. Preserved dragonfly larvae were identified to species (Walker and Corbet 1978, Bright and O'Brien 1999) and counted. Individuals that were too small to be identified to

species were identified to genus or family.

Data from this study allowed me to estimate how frequently species dispersed to these newly created pond environments. In conjunction with data on the distributions of species in the natural ponds in this landscape I was also able to estimate how far an individual had traveled to reach a given artificial pond. I estimated dispersal rates, dispersal distances, and colonization distances. I contrasted habitat generalists and those habitat specialists with larval distributions restricted to permanent lakes with large-bodied fish predators. I excluded non-territorial and migratory species without local populations from the analysis. Non-territorial species mate in fields, sometimes far from water-bodies (Corbet 1999, McCauley, pers. obs.). This behavior can produce very different dispersal patterns than those observed in territorial species where mating occurs at aquatic habitats. Dispersal distances could not be estimated for migratory species without local populations and these species are unlikely to be affected by dispersal limitation.

I estimated dispersal and colonization distances for each species using the linear distance to the nearest source habitat for that species (minimum distance to source). Source habitats were defined as a natural habitat where a species had been collected as larvae in the previous year or in spring of that year prior to the breeding season (McCauley 2005, E. Werner et al., unpubl.). Both mean and maximum distances were estimated using observations in both years of the study. Independent sample t-tests were used to compare the mean and maximum dispersal distances for all habitat specialists and habitat generalists observed in the study. I also present dispersal and colonization distances for the six species examined in the predation rate trials. An independent samples t-test was used to compare the ratio of the proportion of tanks a species arrived at to the proportion colonized by that species in habitat specialists and generalists.

Observations of adults at natural lakes

In order to assess whether the habitat specialists are commonly dispersing to all habitat types in the region, I observed dragonfly adults at six natural water-bodies and recorded abundances of the species used in the predation rate trials at each site. Observations were made at sites representing different portions of the permanence-predator gradient: two permanent lakes with large-bodied fish, two permanent lakes where small-bodied fish were the top predators, and two semi-permanent lakes where invertebrates were the top predators. Observations were made during four time periods in 2002 (31 May — 7 June, 27 June — 3 July, 26 July, 8-12 August). These observation periods encompass the phenology of species in this study. At each site observations were made by one or two observers positioned in the littoral zone of the water-body so that they had a clear view of both the emergent vegetation at the edge of the pond and of the area over the open water. Observers used binoculars to scan for adult dragonflies in both sections of the pond. When two observers were at a single site they were positioned in different portions of the water-body. In each sampling period across

the season, observations were made for 20 person-minutes, a total of 80 person-minutes of observation at each site. All observations were made between 1:00 pm and 5:00 pm (Eastern Daylight Savings Time) on sunny days with low wind. Although these observations were not extensive enough to assess whether dispersal limitation is the sole factor restricting the distributions of habitat specialists because observations may have missed rare dispersal events, they did allow me to test the hypothesis of global dispersal and species-sorting after arrival. I used a χ^2 test to compare the relative frequency with which habitat specialists and habitat generalists from the predation rate trials were observed as adults at the three lake types.

Results

Experiment I: non-benthic larvae

There was a significant main effect for predator type on larval survivorship ($F_{2,51} = 9.93$, $p < 0.001$). Larvae of all species had lower survivorships with bluegill than with Anax ($p < 0.001$). Larval survivorships with mudminnows did not differ from survivorships with either Anax ($p = 0.092$) or bluegill ($p = 0.073$). Species did not differ in their overall survivorships ($F_{2,51} = 2.49$, $p = 0.093$) (Fig. 2a). There was, however, a significant species x predator interaction effect ($F_{4,51} = 3.43$, $p = 0.015$). Therefore, to assess how predators differentially affected species' survivorships, one-way ANOVAs were conducted for each predator treatment using the arcsin transformed proportional survivorships as a dependent variable and species as a fixed factor. Species had different survival rates with Anax ($F_{2,15} = 7.22$, $p = 0.006$) but not with mudminnows or bluegill. Tukey's post-hoc tests found that with Anax, the habitat specialist (*C. fasciata*) had significantly lower survivorship rates than *L. intacta* ($p = 0.006$) and marginally lower survivorship rates than *E. simplicollis* ($p = 0.072$) (Fig. 2a).

Experiment II: benthic larvae

A comparison of species' survivorships after 23hrs found no significant species ($F_{2,24} = 0.374$, $p = 0.692$), or species x predator ($F_{2,24} = 0.076$, $p = 0.927$) effects. There was an effect of predator type ($F_{1,24} = 8.46$, $p = 0.008$) with all species having lower survivorships with bluegill than Anax (Fig. 2b). A comparison of species' survivorships in the Anax treatment during the second sampling period, 46h after predators were released, found that species differed in their survival rates ($F_{2,12} = 5.61$, $p = 0.019$). *Libellula incesta* had lower survivorships with Anax after 46 h than *L. luctuosa* (Tukey's HSD, $p = 0.044$) and *L. pulchella* (Tukey's HSD, $p = 0.026$) (Fig. 2c).

Dispersal to and colonization of artificial ponds

Across the two years of this study 499 adult dragonflies representing 21 species were observed at artificial ponds while 10 405 dragonfly larvae from 14 species were collected from these ponds. Adult habitat specialists were observed as

dispersers at a lower proportion of cattle tanks than habitat generalists in both years (2002: $t = -3.12$, $DF = 9$, $p = 0.012$; 2003: $t = -4.35$, $DF = 9.58$, $p = 0.002$) (Fig. 3). In 2002 adult habitat specialists and generalists did not differ in either maximum (unequal variances, $t = -1.45$, $DF = 3.12$, $p = 0.228$) (Fig. 4a) or mean ($t = -1.74$, $DF = 9$, $p = 0.116$) (Fig. 4b) dispersal distance. However, there was a high level of variation in the dispersal distances of habitat specialists that was driven by one species of habitat specialist, *Celithemis eponina*. This species was observed at artificial ponds in fields far from any source lake. In analyses excluding *C. eponina*, habitat specialists dispersed shorter maximum ($t = -10.74$, $DF = 8$, $p = 0.001$) (Fig. 4c) and mean ($t = -2.48$, $DF = 8$, 2002, $t = -1.94$, $DF = 9$, $p = 0.084$; 2003, $t = -0.659$, $DF = 13$, $p = 0.521$).

Habitat specialists colonized tanks to which they had dispersed less frequently than habitat generalists ($t = -2.65$, $DF = 14$, $p = 0.019$). In the two years of this study, eight species of habitat generalists colonized tanks, with the number of species colonizing tanks being proportional to the number of species observed as dispersers at tanks. Only one species of habitat specialist, *Libellula incesta*, colonized artificial ponds, and the tanks colonized were those directly adjacent to the permanent lake with large-bodied fish where this species is a common resident.

Adults of the two habitat specialists used in the predation rate trials were observed at tanks directly adjacent to their source habitat in both years, but their presence at artificial ponds not directly adjacent to these source habitats was limited (*L. incesta*, maximum observed dispersal distance was 218 m; *C. fasciata*, maximum observed dispersal distance was 0 m). In contrast, adults of the four habitat generalists in the predation trials were all found further from their source ponds (range of maximum observed dispersal distances for the four habitat generalist species: 1000-1177 m). All four species of habitat generalist from the predation rate experiments colonized the artificial ponds, at varying distances from their source habitats, while of the habitat specialists only *L. incesta* colonized artificial ponds and only those directly adjacent to a source habitat (Table 1).

Observations of adults at natural lakes

$p = 0.038$) (Fig. 4d) dispersal distances than habitat generalists. In 2003 adult habitat specialists dispersed shorter maximum ($t = -3.77$, $DF = 9.10$, $p = 0.004$) (Fig. 4e) and mean ($t = -3.44$, $DF = 10.38$, $p = 0.006$) (Fig. 4d) dispersal distances than habitat generalists. These estimates of dispersal rate and distance do not appear to result from consistent differences in the regional abundance of habitat specialist and generalist species in natural habitats (McCauley et al., unpubl.). There were also no differences in the abundance of habitat specialists and generalists at tanks where species were observed (i.e. for all tanks where a species' abundance was > 0) (independent samples t-tests:

In observations at six focal lakes, adults of the two habitat specialist species used in the predation trials were commonly seen at permanent lakes where large-

bodied fish were predators but were never observed at other lake types. In contrast, the four species of habitat generalist from the predation trials were observed at focal lakes representing all three habitat types, including one focal site with invertebrate top predators that dried in 2001, resulting in the local extinction of their larvae (Werner et al., unpubl. data). These habitat specialists and generalists differed in the frequency with which they were observed at the three habitat types (Pearson's $\chi^2=49.03$, $DF =2$, $p < 0.001$) (Fig. 5).

Discussion

Results from this work indicate that habitat specialists and habitat generalists differ in dispersal behavior in ways that may generate or reinforce the differences in distributional breadth observed in these two groups. Differences were also found in the relative vulnerabilities of habitat specialists and generalists to alternative predator types. These differences suggest that predation may act to reinforce the distributional limits of habitat specialists across the permanence gradient and top-predator transition. Specialists which do not normally co-exist with invertebrate top predators were more vulnerable to these predators than habitat generalists.

Examined collectively, these results suggest that both regional (dispersal) and local (predation) processes act and interact to shape the distributions of species in this system and consequently community structure.

Habitat specialists and generalists differed strongly in their dispersal behavior. Compared to habitat generalists, the habitat specialists from permanent lakes were less likely to either visit or colonize newly created artificial habitats, and as adults appeared to typically move shorter distances from their source habitats. The habitat specialist species used in the predation rate trials were also not observed as adults at habitats with alternative top predator types, indicating that they rarely reach these sites. In contrast, habitat generalists move broadly across the landscape and readily visit and colonize new habitats that mimic small ponds. The differences between habitat specialist and generalist dispersal behavior were consistent across both years

for most of the species observed. The dispersal behavior of habitat specialists suggests that their limited dispersal acts as the first filter on their presence at non-permanent habitats.

An exception to the observation of limited dispersal in specialists was a single species, *C. eponina*. It was observed in one year (2002) at artificial ponds far from a source environment, indicating that certain species of habitat specialist may disperse far from their source environments with some frequency. McPeck (1989) observed similar dispersal behavior in a species of habitat specialist damselfly, *Enallagma ebrium*. *Celithemis eponina* and *E. ebrium* are habitat specialists found with large-bodied fish but both species are most common in shallow lakes that periodically have fish winter-kills (McPeck 1989, McCauley, unpubl.). These lakes are the most temporally variable part of this generally stable portion of the

habitat permanence gradient. The association between temporal variability and dispersal therefore appears to be robust in these species which are otherwise an exception to the differences between habitat specialists and generalists in dispersal behavior.

Given the strong flight capacity of some dragonfly species (Wikelski et al. 2006), the effects of dispersal limitation are expected to be principally mediated by behavioral dispersal limitation rather than an inability to move across the distances between these habitats. The dispersal behavior observed in this study parallels results from other odonate groups in which relatively limited dispersal has been described (McPeck 1989, Conrad et al. 1999, Angelibert and Giani 2003) and the maximum dispersal distances observed in this study (~ 1.2 km) are similar to other studies of odonate dispersal (zygopterans: Conrad et al. 1999, Purse et al. 2003, zygopterans and anisopterans: Angelibert and Giani 2003). Given the large difference between potential dispersal capacity and observed dispersal behavior, behavioral dispersal limitation is a potentially important force in limiting the distributions of odonates and other dispersers where movement between habitats is an active behavioral choice.

Habitat selection behavior may reinforce the effects of limited dispersal on the distributions of habitat specialists. Habitat specialists were less likely to colonize artificial ponds at which they did arrive, a difference that suggests habitat specialists may have more restrictive habitat selection criteria. Some groups such as amphibians and beetles have been demonstrated to be able to distinguish habitats based on the presence of fish (Resetarits 2001, 2005, Binckley and Resetarits 2005). It is unknown how habitat selection behavior in odonates might affect their distributions across habitats with alternative predator types. However, in a couple of tests, odonates have not demonstrated an ability to distinguish habitats with and without fish (McPeck 1989, McCauley, unpubl.). Odonates may use alternative cues, and greater habitat selectivity by habitat specialists could act as a filter on their presence at low-quality habitats for their offspring and decrease the risks of dispersal for individuals that do move away from the natal environment. Research on habitat selection behavior will provide further insights into the role of this mechanism in structuring odonate species' distributions.

Habitat selection behavior could also have played a role in the detection of adults at tanks. However, a couple of observations suggest that this effect is minor. The lower frequency of specialists observed at artificial ponds reflected an effect of distance rather than differences in absolute abundance at tanks. Adults of habitat specialist and generalist species were equally abundant at those tanks where they were observed to occur. For specialists these were only those tanks close to their source habitats, suggesting that the level of attraction is similar for adults of both groups when they are in the vicinity of artificial ponds. Additionally, surveys of adult dragonflies in natural fields without cattle tanks found that the composition of adults in these fields was very similar to the composition of adults observed in fields with cattle tanks (McCauley, 2006). Therefore, the absence of adult habitat specialists from more isolated artificial

ponds appears to be due to their absence from the surrounding terrestrial environment and not from a differential attraction to artificial ponds. Consequently dispersal, the first filter on a species' presence in a site, also appears to be an important mechanism reducing the probability that they will arrive at non-permanent habitats while the effects of habitat selection may act secondarily to reinforce these effects.

Vulnerability to invertebrate predators may also reinforce the effects of limited dispersal rates and distances in habitat specialists. In the invertebrate predator treatments of both predation rate trials, habitat specialists had lower survivorships than habitat generalists. These results parallel findings about the factors structuring zygopteran odonate communities. McPeck (1990b) found that in lab settings, *Enallagma* damselflies from lakes where fish were the dominant predators were more vulnerable to invertebrate predators than *Enallagma* that co-existed with invertebrates, and that these differential vulnerabilities were important factors in structuring species distributions in the *Enallagma* system. Absolute differences in predator vulnerability are difficult to assess on the basis of lab predation trials because context dependence may affect our ability to extrapolate from mesocosm studies to the effects of processes at more natural scales (Skelly 2002). Therefore, the lower survivorship of all species with bluegill predators needs to be interpreted cautiously. It may suggest that predation by invertebrate predators is not a hard barrier to the use of these sites by habitat specialists and that instead, dispersal and colonization limitation are the principal factors restricting the habitat breadth of these species. More probably, the greater vulnerability of habitat specialists than habitat generalists to invertebrate predators plays a role in decreasing the local performance of habitat specialists in these sites, and local performance and regional dispersal act together to limit the distributions of habitat specialists in this system.

Although limited dispersal may act ecologically as a constraint on the distributional breadth of habitat specialists, the dispersal behavior of both habitat specialists and generalists are likely to be adaptive. The evolution of niche-breadth and dispersal rates are expected to be positively related (Holt 1997, Holt and Gomulkiewicz 1997). There is limited empirical evidence contrasting these characters in multiple species. However, Bonte et al. (2003) found evidence of this in ballooning spiders in which there was a negative relationship between dispersal propensity and degree of habitat specialization. Additionally, several theoretical studies predict a branch point in the evolution of dispersal behavior and local performance that leads to stably co-existing alternative strategies. These strategies parallel those observed across species in this system, including a low-dispersal habitat specialist strategy that utilizes the more temporally stable, higher quality habitat, and a high dispersal habitat generalist that engages in risk-spreading across multiple habitat types (McPeck and Holt 1992, Doebeli and Ruxton 1997, Mathias et al. 2001, Kisdi 2002). Given the long term stability of the lakes utilized by habitat specialists in this study, high levels of philopatry may be adaptive. This strategy reduces the probability that offspring will be deposited

in unfavorable habitats, such as those with invertebrate predators, while the temporal stability of the natal habitats facilitates local recruitment. In contrast, greater dispersal by habitat generalists spreads the risk across multiple sites, and in periods where nonpermanent habitats hold water long enough for one or more generations to complete development, lower levels of competition and predation may make these sites important sources, maintaining selection for movement into these ponds.

Local effects shaping species distributions across the permanence—predator gradient have been studied extensively in freshwater ecology (Wellborn et al. 1996, Schneider and Frost 1996, Wissinger et al. 1999, 2003, Stoks and McPeck 2003). There are fewer examples of direct contrasts of local and regional processes as mechanisms shaping species distributions across this gradient (but see McPeck 1989, 1990a,b). In this system, dispersal behavior is related to species distributional breadths across the predator-permanence gradient and my results indicate that dispersal limitation acts as the first filter on species distributions in this system. The effects of local performance were less clearly established but the data suggest that local and regional processes may reinforce each other to affect species' distributions. This study provides further insight into the roles of local and regional processes in shaping species distributions and resultant community structure across a critical habitat gradient in freshwater systems.

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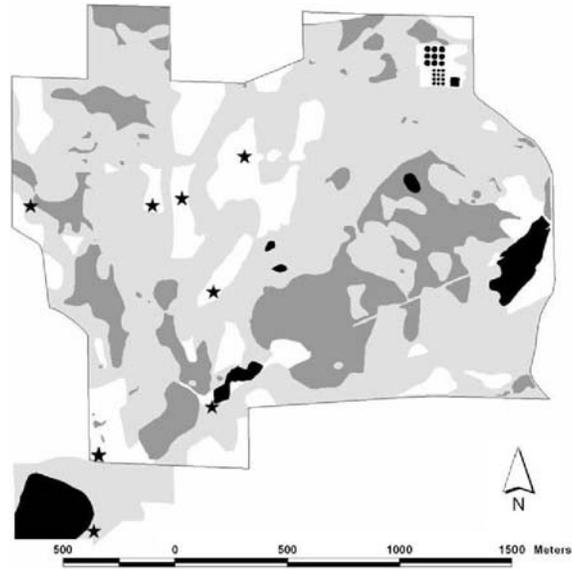


Fig. 1. Map of study sites (E.S. George Reserve inside outline). Stars indicate midpoints between pairs of cattle tanks established in 2002 as artificial ponds. Open field areas are white, areas with forest are indicated in light grey, non-permanent wetlands are indicated in dark grey while permanent natural ponds (sites that have not dried since 1998) are indicated in black. The multiple small permanent ponds located in the northeast corner of the E.S.G.R. are artificial, experimental ponds.

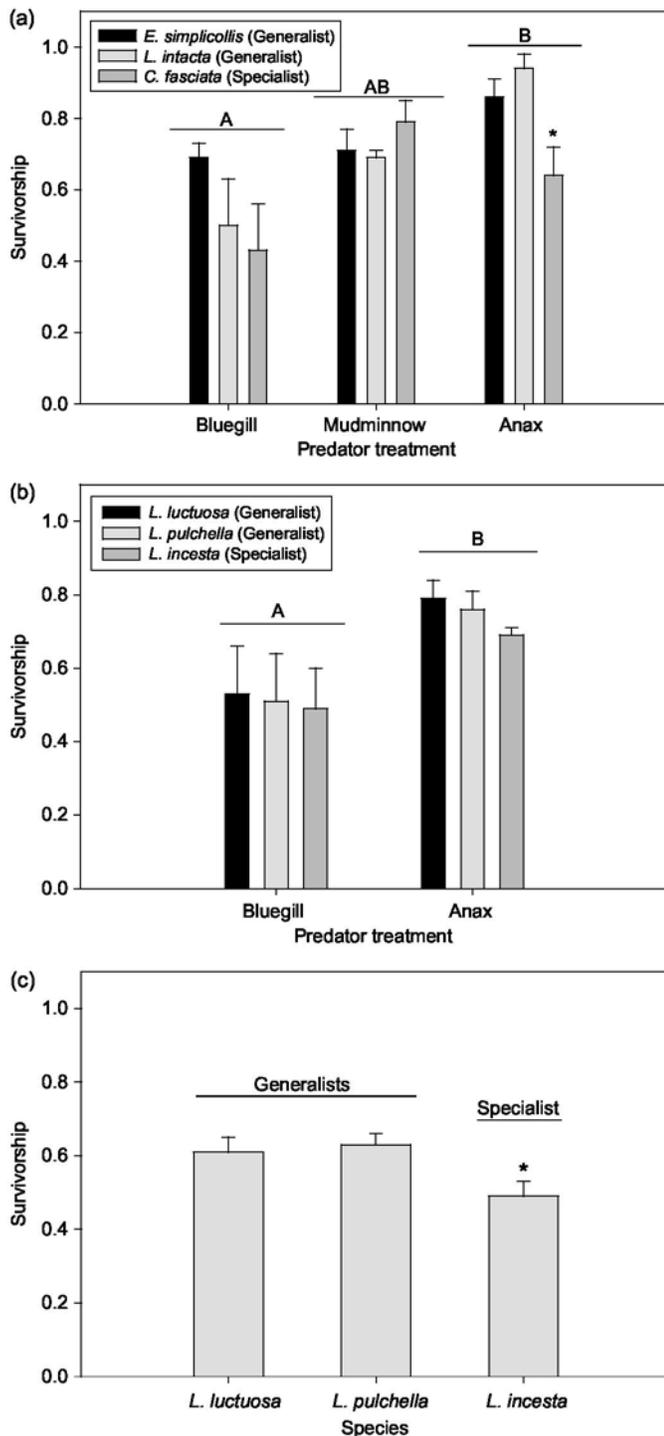


Fig. 2. Survivorship of larval dragonfly species in predator treatments.

Survivorships identified with the same letter do not significantly differ. Asterisks indicate significant or marginal species' differences within a predator treatment. (a)

Survivorships of non-benthic larvae in the presence of three alternative top predators after 20 h.

(b) Survivorships of benthic larvae in the presence of two alternative top predators after 23 h.

(c) Survivorships of benthic larvae in the presence of Anax predators after 46 h.

All data are means ± 1 SE.

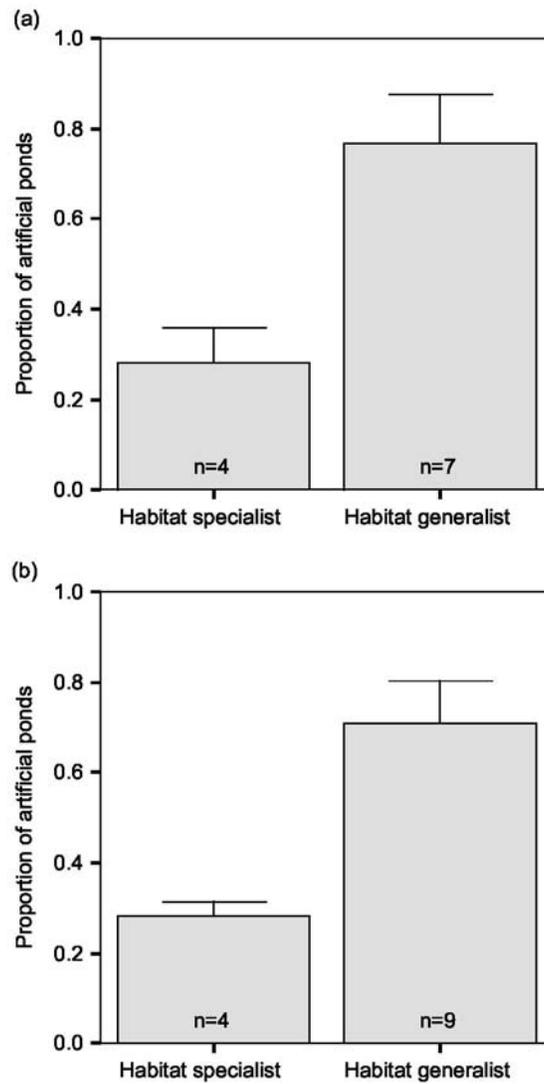


Fig. 3. Proportion of artificial pond pairs at which species were observed in (a) 2002 and (b) 2003. All data are means \pm 1 SE. Sample sizes (n) represent the number of species in each distributional category.

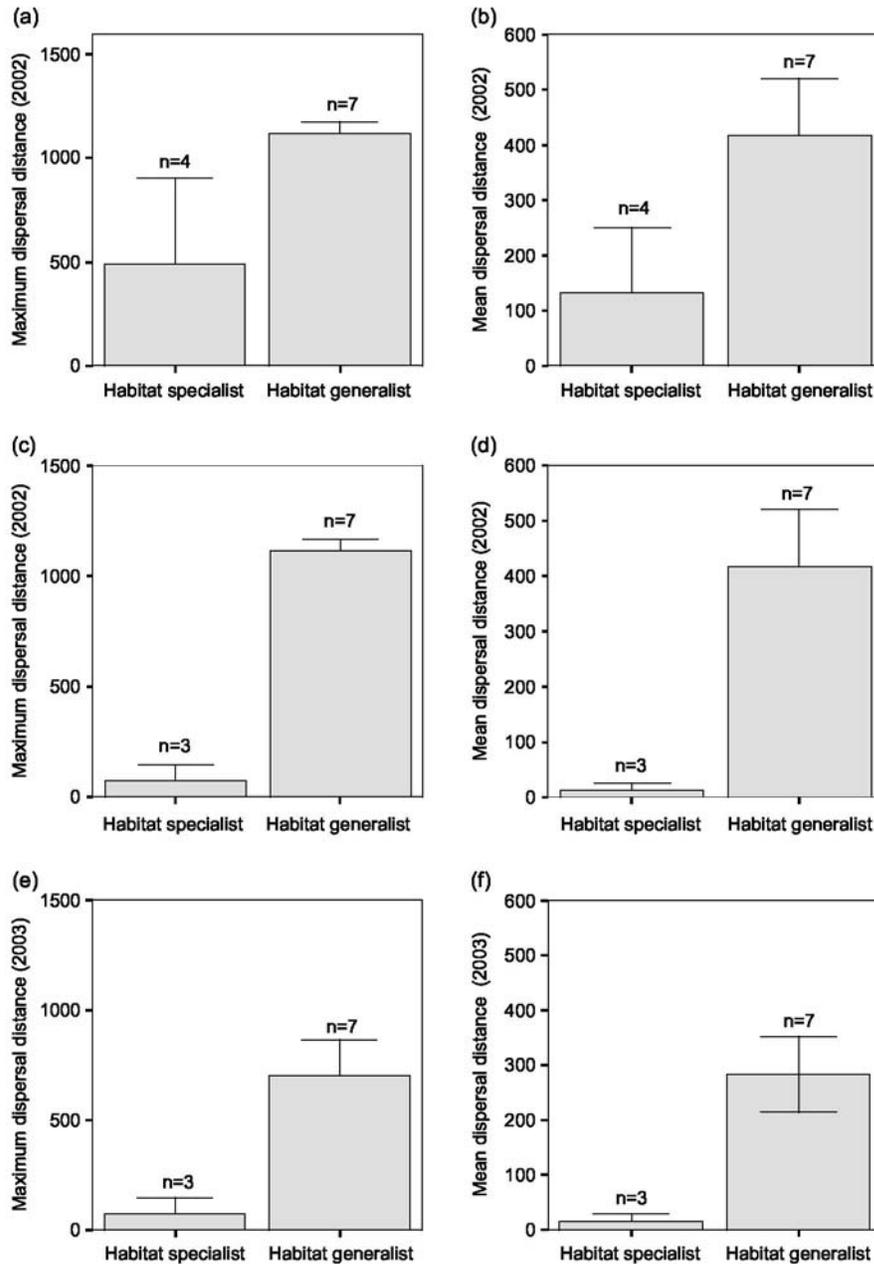


Fig. 4. Dispersal distances of habitat specialists and generalists. Plots are of (a) maximum dispersal distance in 2002 for all species, (b) mean dispersal distances in 2002 for all species, (c) maximum dispersal distance in 2002 excluding *C. eponina*, (d) mean dispersal distances in 2002 excluding *C. eponina*, (e) maximum dispersal distances in 2003, and (f) mean dispersal distances in 2003. All data are means ± 1 SE. Sample sizes (n) represent the number of species in each distributional category.

Table 1. Colonization patterns of the six species examined in the predation rate trials, n/a indicates no colonization by that species in the given year.

Species	Habitat distribution	Maximum distance from source habitat for larval colonization (m)	
		2002	2003
<i>C. fasciata</i>	specialist	n/a	n/a
<i>E. simplicollis</i>	generalist	19	n/a
<i>L. intacta</i>	generalist	0	245
<i>L. incesta</i>	specialist	0	n/a
<i>L. pulchella</i>	generalist	1000	800
<i>L. luctuosa</i>	generalist	982	1105

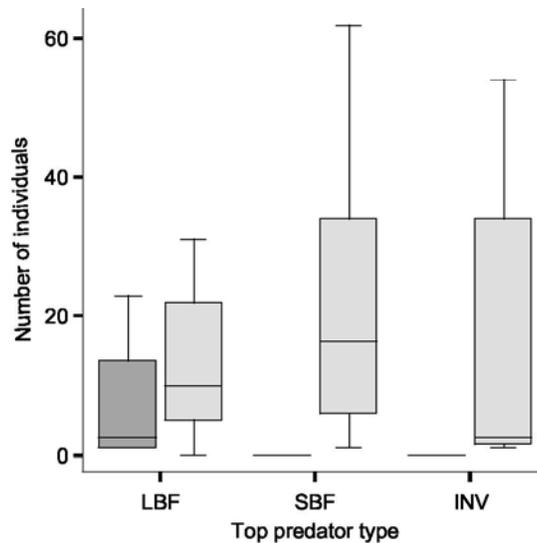


Fig. 5. Box plots of abundance of adult habitat specialists (dark grey) and habitat generalists (light grey) from the predation rate experiment at lakes and ponds representing different points along the predator-permanence gradient. There are two lakes of each habitat type, LBF habitats are permanent lakes with large-bodied fish top predators, SBF habitats are permanent lakes with small-bodied fish predators, and INV are semipermanent ponds with invertebrate top predators. Boxes encompass 50% of the data from the 25th to the 75th percentile. The horizontal line indicates the sample median, and bars encompass 90% of data from the 10th to 90th percentiles.