

Notonecta exhibit threat-sensitive, predator-induced dispersal

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Dispersal is a central process determining community structure in heterogeneous landscapes, and species interactions within habitats may be a major determinant of dispersal. Although the effects of species interactions on dispersal within habitats have been well studied, how species interactions affect the movement of individuals between habitats in a landscape has received less attention. We conducted two experiments to assess the extent to which predation risk affects dispersal from an aquatic habitat by a flight-capable semi-aquatic insect (*Notonecta undulata*). Exposure to non-lethal (caged) fish fed conspecifics increased dispersal rates in *N. undulata*. Moreover, dispersal rate was positively correlated with the level of risk imposed by the fish; the greater the number of notonectids consumed by the caged fish, the greater the dispersal rate from the habitat. These results suggest that risk within a habitat can affect dispersal among habitats in a landscape and thus affect community structure on a much greater scale than the direct effect of predation itself.

Keywords: predator–prey; *Notonecta*; dispersal; remote-control effects

1. INTRODUCTION

Individual dispersal behaviour has consequences that extend far beyond the fate of the individual, playing a central role in determining the structure of ecological systems (Hanski 1999; Holyoak *et al.* 2005). By driving prey emigration, predators can influence the population dynamics and community structure of habitats in which they are not present through prey immigration into these patches ('remote-control predator effect'; Orrock *et al.* 2008). Predator-induced movement has been particularly well documented in aquatic systems (Sih & Wooster 1994; Preisser *et al.* 2005). However, studies of predator-induced dispersal have focused on systems where dispersal occurs within defined habitats, rather than between habitats across discontinuous landscapes. For example, in one well-documented case, mayflies tend to disperse downstream by drift in response to predator cues (e.g. McIntosh *et al.* 2002). Although this may result in movement of considerable distance, it is restricted to within, rather than between streams.

Movement within a continuous habitat is unlikely to link distinct populations or communities, whereas dispersal among habitats may well. Theory suggests

that predator-induced dispersal has consequences for the stability of tri-trophic systems (Abrams 2008; Orrock *et al.* 2008), metacommunity structure and the community resilience to perturbations. Only a few studies have found that predators affect movement among habitats across a discontinuous landscape, and none of these is in aquatic habitats. For example, predation risk from ladybirds increases the production of dispersal morphs in pea aphids (*Acyrtosiphon pisum*; Weisser *et al.* 1999), and in a few cases, predator presence in a patch results in emigration from that patch (Hakkarainen *et al.* 2001; Cronin *et al.* 2004). In these cases, risk was considered as a binary effect, predators were either present or absent, rather than a continuous variable, despite evidence that the effect of predators on movement within a habitat can be sensitive to the level of predation risk an individual experiences (e.g. Allan 1978; Sih & Wooster 1994; McIntosh *et al.* 2002).

We investigated the effect of predation risk within a defined habitat (the pool) on dispersal among habitats on a landscape, and thus its potential to affect community structure on a much greater scale than the direct effect of predation itself. The prey species, *Notonecta undulata* (Heteroptera: Notonectidae) occurs in lakes and ponds with and without fish (Bendell & McNicol 1987). As adults, notonectids are flight capable and can disperse long distances (Briers & Warren 2000). However, notonectids can complete their life cycle within a single aquatic habitat and do not use the terrestrial environment for life-history functions other than dispersal, so movement out of an aquatic habitat indicates plastic dispersal to a new site. In the first test, we ask whether notonectid emigration from pools is sensitive to the presence/absence of risk (a caged predator). In the second experiment, we ask whether the rate of dispersal is sensitive to the perceived level of risk.

2. MATERIAL AND METHODS

Experiments were conducted at the Koffler Scientific Reserve (44°01' N, 79°32' W) in Ontario, Canada. For each experiment, adult *N. undulata* were collected from a fishless pond over 2 days and held in two 378 l pools for 3–5 days before being placed into experimental pools. Pools were filled with aged tap water and inoculated with a standard volume of zooplankton as a food resource for notonectids. Habitat structure was provided including fibreglass window-screened predator cages. All tanks received predator cages irrespective of treatment. Cages allowed visual and chemical cues indicating the presence of fish to reach notonectids in the pools, but prevented fish from consuming them.

(a) Experiment 1: predator induction of dispersal

This experiment had two treatments, the fish treatment in which cages held one pumpkinseed sunfish (*Lepomis gibbosus*, standard length: 92.6 ± 7.0 mm), and the control in which cages were empty. Each treatment was replicated five times. *Notonecta* were collected from the holding pools in batches of 20, marked dorsally using permanent marker with a colour code for each treatment, and then placed into experimental pools in the random sequence of treatments assigned to pools. Two *N. undulata* per day were added to the fish cages each day for food.

On each of 5 days, all notonectids within a pool were collected to determine each individual's colour code, the number of individuals from each treatment was counted and then individuals were returned to the pool. Pools were searched for dead notonectids to avoid counting them as dispersers. Dead individuals were then discarded. At the end of the experiment, the number of 'feeder' *Notonecta* remaining in each cage was counted.

(b) Experiment 2: risk sensitivity of dispersal

In this experiment, we assessed whether notonectid dispersal rates were sensitive to the level of risk posed by predators in the

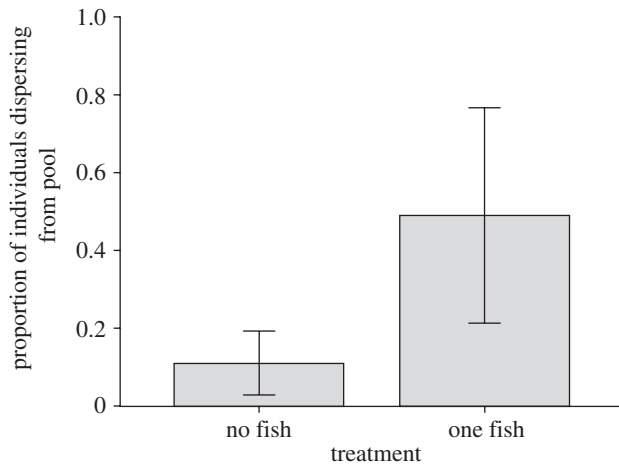


Figure 1. The proportion of individuals dispersing from the experimental pool was greater when *Notonecta* were exposed to one caged fish in experiment 1 (means \pm 2 s.e.).

environment. This experiment had three treatments: empty cages with no fish, one caged fish (*L. gibbosus*) and two caged fish (*L. gibbosus*), each replicated four times (fish standard length: 73.4 ± 6.0 mm). Each fish was fed two notonectids per day. Dispersal rates were monitored daily for 5 days in the same manner as in experiment 1. Treatment effects on dispersal rates were tested using ANOVA. Analyses were conducted in SPSS v. 17.

3. RESULTS

In experiment 1, notonectids dispersed from both fish and no-fish treatments, but dispersal was 4.5 times higher in the presence of a caged fish, and this effect was significant ($t(8) = -2.64$, $p = 0.03$; figure 1).

In experiment 2, notonectids also had higher rates of dispersal in the presence of fish ($F_{2,9} = 11.28$, $p = 0.004$; Tukey's *post hoc* no-fish versus one fish $p = 0.017$, no-fish versus two fish $p = 0.004$, figure 2a). Although mean dispersal from the two-fish treatment was higher than the one-fish treatment, fish density did not significantly affect dispersal rate (Tukey's *post hoc* one-fish versus two-fish $p = 0.56$). Previous research suggests that risk may be assessed by the scent of predators consuming prey, rather than predators themselves (Crowl & Covich 1990; Schoepner & Relyea 2009). Therefore, we analysed these data using number of prey consumed in cages as a covariate in an analysis of covariance (ANCOVA) comparing one-fish and two-fish treatments. Dispersal rate was unrelated to fish density but was strongly related to the number of conspecific notonectids consumed by fish (ANCOVA: treatment effect: $F_{1,7} = 1.71$, $p = 0.248$, effect of number eaten: $F_{1,7} = 8.1$, $p = 0.036$, model $R^2 = 0.662$, figure 2b). This indicates that the dispersal response was related to the level of threat that fish posed, signalled by their predation rate. In light of this, we reanalysed the data from experiment 1 to assess the relationship between the number of prey consumed and dispersal rate within the fish treatment. Although not significant, and despite a small sample size, there was a trend towards a positive correlation between these variables ($r = 0.86$, $p = 0.061$, $n = 5$).

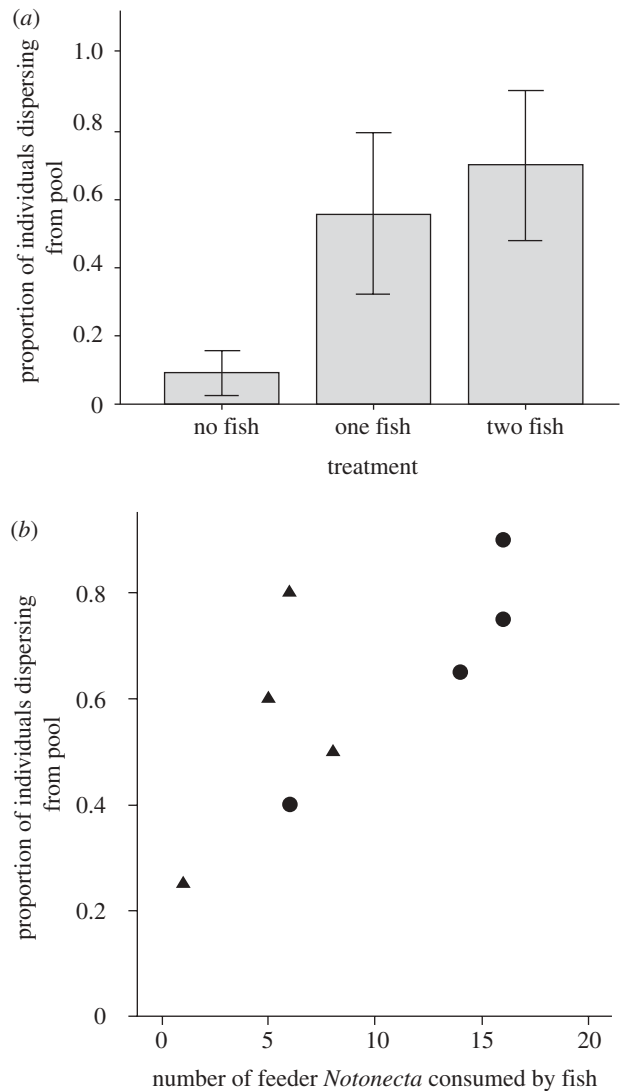


Figure 2. In experiment 2, (a) *Notonecta* dispersed at higher rates from pools containing caged fish but there was no difference between tanks with one or two caged fish. (b) There was a positive relationship between the number of *Notonecta* consumed by caged fish (triangles, one-fish treatment; circles, two-fish treatment) and the proportion of individuals dispersing from that pool.

In both experiments, most dispersers left the area of experimental pools and mortality was low. In experiment 1, three of 61 dispersing individuals were recaptured in pools differing from their starting pool, and in experiment 2, the corresponding numbers were three of 91. One notonectid died (no-fish treatment) in experiment 1. Two *Notonecta* died in experiment 2, one each in the no-fish and the two-fish treatments.

4. DISCUSSION

Our results demonstrate that *N. undulata* responds to predation risk by increasing its dispersal rate out of risky habitats and the rate at which *Notonecta* dispersed from pools containing fish was positively correlated with the number of conspecifics fish consumed. These results provide evidence for predator-induced dispersal that can introduce linkages among habitats

on a discontinuous landscape. Our results also demonstrate a dose-dependent effect of risk, where dispersal propensity is adjusted to changes in perceived risk. Our findings emphasize the connections between consumptive and non-consumptive effects on metacommunity structure (Holyoak *et al.* 2005; Orrock *et al.* 2008).

It is well documented that fish can have strong effects on community structure (Wellborn *et al.* 1996). These include both the direct effects of mortality within habitats, and the effects of predator-induced dispersal within continuous habitats. Our results extend these findings to predator-induced movements among disconnected habitats. Thus, fish may also influence the structure of communities in which they are not present by driving prey immigration/colonization across a metacommunity.

These results may provide an empirical example of the prey behaviour necessary for predators to exert 'remote control' effects on prey populations (Orrock *et al.* 2008), where predators at one location affect prey dynamics in another, through their effects upon migration between locations. This in turn may have cascading effects upon competition among prey species and resource depletion in habitats where predators are not present (e.g. Holyoak *et al.* 2005; Abrams 2008; Orrock *et al.* 2008). In metapopulation models that include predator-induced dispersal (e.g. Abrams 2008; Orrock *et al.* 2008), it is often assumed that the distribution and abundance of predators is independent of the distribution and abundance of prey. This assumption fits our study community because the semi-aquatic notonectid prey can move among aquatic habitats across a terrestrial matrix, whereas the fish predator cannot, thus severing a tight linkage between the two.

Our results also demonstrate that risk-sensitive dispersal by notonectids is dose-dependent, suggesting that they do not perceive habitats with and without fish as a binary state across the landscape. This aspect of predator-induced dispersal is also an assumption of metapopulation models exploring the impacts of predator-induced dispersal on prey populations. Despite this, our study is one of the few to demonstrate such dose dependence in a metapopulation context. Surprisingly, we could not detect an effect of predator density on dispersal that was independent of the number of prey consumed by predators. These data suggest that the notonectid perception of risk does not result from signals given off by the predators alone, but by their consumption of prey (cf. Crowl & Covich 1990; Schoeppner & Relyea 2009). Nevertheless, in general predation rate and thus perceived levels of threat will often scale with fish density and population size structure, factors that in turn may influence *Notonecta* dispersal rates from these sites. Predator-induced dispersal in *Notonecta* can affect the population dynamics and community structure of habitats receiving these colonists. Notonectids are predators on a broad range of prey including both aquatic vertebrates and invertebrates and *N. undulata* have, for example, been demonstrated to affect zooplankton community structure (Shurin 2001).

Evidence that predators have indirect effects that operate at the regional scale through prey habitat selection (Resetarits & Binckley 2009) and by driving prey dispersal (Weisser *et al.* 1999; Hakkarainen *et al.* 2001; Cronin *et al.* 2004; this study) is accumulating. Evidence of indirect effects operating at a metacommunity scale suggest that understanding community structure requires a broader view of species interactions that encompasses interactions operating across habitats, even when one member of the interacting pair is restricted to only one habitat. Dispersal behaviour including threat-sensitive, predator-induced dispersal provides one example of how conditions at the local level may scale up to affect species distributions and community structure at regional scales.

This study complies with the laws of Canada and the necessary permits were obtained from the University of Toronto (Animal Use Protocol 7765) and Ontario Ministry of Natural Resources (permit no. 1050756).

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