Notonecta exhibit threat-sensitive, predator-induced dispersal

Shannon J. McCauley* and Locke Rowe

Ecology & Evolutionary Biology, University of Toronto, 25 Willcocks Street, Toronto, Ontario, Canada M5S 3B2

*Author for correspondence (shannon.mccauley@utoronto.ca).

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 feeding 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 (Acrthosiphon 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 fiberglass 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 the number of individuals in each 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
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; Schoepfner & 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).

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 habits 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.
Evidence that predators have indirect effects that operate at the regional scale through prey habitat selection (Reshetaritis & Binkley 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).

We thank Celina Baines and Stephan Schneider for help in the field. This study was funded by a Natural Sciences and Engineering Research Council grant to L.R.


Preisser, E. L., Bolmick, D. I. & Benard, M. F. 2005 Scared to death? The effects of intimidation and consumption in


