Groups constrain the use of risky habitat by individuals: a new cost to sociality?

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Predation risk can strongly constrain how individuals use time and space. Grouping is known to reduce an individual's time investment in costly antipredator behaviours. Whether grouping might similarly provide a spatial release from antipredator behaviour and allow individuals to use risky habitat more and, thus, improve their access to resources is poorly known. We used mosquito larvae, *Aedes aegypti*, to test the hypothesis that grouping facilitates the use of high-risk habitat. We provided two habitats, one darker, low-risk and one lighter, high-risk, and measured the relative time spent in the latter by solitary larvae versus larvae in small groups. We tested larvae reared under different resource levels, and thus presumed to vary in body condition, because condition is known to influence risk taking. We also varied the degree of contrast in habitat structure. We predicted that individuals in groups should use high-risk habitat more than solitary individuals allowing for influences of body condition and contrast in habitat structure. Grouping strongly influenced the time spent in the high-risk habitat, but, contrary to our expectation, individuals in groups spent less time in the high-risk habitat than solitary individuals. Furthermore, solitary individuals considerably increased the proportion of time spent in the high-risk habitat over time, whereas individuals in groups did not. Both solitary individuals and those in groups showed a small increase over time in their use of riskier locations within each habitat. The differences between solitary individuals and those in groups held across all resource and contrast conditions. Grouping may, thus, carry a poorly understood cost of constraining habitat use. This cost may arise because movement traits important for maintaining group cohesion (a result of strong selection on grouping) can act to exaggerate an individual preference for low-risk habitat. Further research is needed to examine the interplay between grouping, individual movement and habitat use traits in environments heterogeneous in risk and resources.

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In group-living animals, individuals in groups frequently differ from solitary individuals in their behaviour (Krause & Ruxton, 2002). Many of these differences are thought to result from the benefits conferred by group living. For example, individuals in groups allocate less time to vigilance and more time to foraging, consequently experiencing greater rates of energy gain, than do solitary individuals. Such a temporal release from costly antipredation activities is well documented in diverse taxa (Blumstein & Daniel, 2005; Elgar, 1989; Treves, 2000). However, group living could also increase foraging opportunities and the rate of energy gain by facilitating a spatial release from costly decisions. For example, grouping could promote the use of high-risk habitat

(avoided by solitary individuals), which may have high food availability, by reducing individual risk through processes such as dilution and confusion effects, such that per capita risk is sufficiently low even in high-risk habitat. Surprisingly little is known about such a spatial release.

The use of space by animals is known to be strongly affected by predation risk (Lima & Dill, 1990). In a wide range of taxa, animals appear to avoid habitats with high predation risk, often at the cost of reduced energy gain or decreased access to high-quality resources (Creel, Winnie, Maxwell, Hamlin, & Creel, 2005; Heithaus & Dill, 2006; Nonacs & Dill, 1990; Shrader, Kerley, Kotler, & Brown, 2006; Sih, 1982; Verdolin, 2006). How animals trade off the gains from resources against the costs from exposure to predation appears to be dynamic with an animal's body condition strongly influencing these decisions (Brown & Kotler, 2004; Dill & Fraser, 1984). Individuals closer to starvation are more likely to risk exposure to predation, for example by foraging in high-risk areas

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with high resource availability (Dill & Fraser, 1984; Sih, 1992), than well-fed animals, possibly because the risk of death by starvation outweighs that from predation.

Animals perceive risk not only through direct encounters with predators but also through habitat attributes that influence an animal's chance of encountering and escaping from predators (Heithaus & Dill, 2006; Thaker et al., 2011; Verdolin, 2006). For example, several species appear to perceive vegetation as protective and open habitat as risky because their predators are able to detect and attack them more easily in the open (reviewed in Brown & Kotler, 2004; Verdolin, 2006). Furthermore, animals are reported to show preferences for habitats with particular structural features depending on their antipredator strategies (Heithaus & Wirsing, 2009). For example, antelope that rely on detection and flight to avoid predators appear to prefer open habitats, whereas those that rely on camouflage and avoiding detection by predators appear to prefer habitats with greater structural complexity (Jarman, 1974). How strongly animals discriminate between habitats is likely to depend on how large the difference is between the habitats in structure and the associated payoffs. As the risk differential between two habitats decreases, animals may be less likely to pay the opportunity costs associated with avoiding the riskier habitat (Brown & Kotler, 2004; Sih, 1982).

These influences of different aspects of predation risk on space use and the factors influencing decisions regarding the use of high-risk habitats have largely been studied assuming that individuals act independently. However, in group-living animals, individual behaviour is likely to be influenced by social interactions. Group living in many taxa appears to be an antipredator tactic. Grouping appears to reduce individual predation risk in many ways (reviewed in Krause & Ruxton, 2002). Additionally, grouping appears to be sensitive to predation intensity: group size may increase with increasing predator density across populations; and even within a population, individuals may increase their grouping and/or group cohesion in response to direct and indirect predator cues and to habitat indicators of predation intensity (Banks, 2001; Dupuch, Magnan, & Dill, 2004; Heithaus & Dill, 2002; Magurran & Seghers, 1994; Rangeley & Kramer, 1998; Thaker, Vanak, Owen, Ogden, & Slotow, 2010). How grouping might influence the use by individuals of habitats varying in risk is not well understood. An experiment with sticklebacks, *Gasterosteus aculeatus*, showed that group size affected the use of refuges by large (but not small) individuals (Krause, Longworth, & Ruxton, 2000); and a study of bison, *Bison bison*, reported differences in the movement and habitat selection of small and large groups (Fortin, Fortin, Beyer, & Duchesne, 2009). Overall, we have detailed information on the influence of predation risk on grouping and, separately, on the influence of predation risk on individual space use decisions, but surprisingly little is known about how group living affects individual space use decisions in an environment varying in predation risk.

We experimentally examined how grouping influences the use of high-risk habitat in an insect, larvae of the mosquito *Aedes aegypti*, and tested the hypothesis that grouping provides spatial release such that individuals can increase their use of high-risk habitats which often have high food availability. Risk taking is reported to be closely influenced by body condition with individuals closer to starvation taking greater risks (Dill & Fraser, 1984). Therefore, to allow for any effect of body condition on individual responses, we tested individuals reared under different resource abundances. In addition, the degree of difference in habitat attributes between two habitat patches might influence habitat use patterns because the associated degree of difference in risk will affect the payoffs to reducing the use of the riskier habitat. Hence, we conducted these experiments under two environments, one

with stark and one with mild differences in structure between habitats. We predicted that individuals in groups should show greater use of high-risk habitat than solitary individuals allowing for influences of body condition and degree of difference in structure between habitats. We also predicted that individuals should show greater use of high-risk habitat when they are from resource-poor rather than resource-rich rearing environments; and when the difference in habitat structure between the two habitats is small than when the difference is large.

METHODS

Aedes aegypti, an important vector of dengue, chikungunya and yellow fever viruses, is found throughout tropical and subtropical regions. It undergoes complete metamorphosis with aquatic egg, larval and pupal stages. Larvae feed on organic, particulate matter, can move vigorously, occur in relatively high densities in the small aquatic pools in which adult females prefer to oviposit and group in response to several disturbance cues (Clements, 1999; Merritt, Dadd, & Walker, 1992). Information from several mosquito species indicates that, overall, predation is an important ecological factor influencing mosquito populations, larvae respond behaviourally to predator cues and they prefer shaded areas within aquatic bodies to open water (Fincke, Yanoviak, & Hanschu, 1997; Foley, Torres, & Mueller, 2002; Kesavaraju & Juliano, 2008).

We obtained eggs from a colony of *A. aegypti* maintained in our laboratory and conducted the study from January to May 2013. Eggs were soaked in water and freshly hatched first-instar larvae were randomly assigned to one of four rearing environments varying in the amount of food (finely powdered dried fish food) provisioned: 0.02, 0.04, 0.1 and 0.2 mg/40 ml. This range in food provisioned represented a resource-poor to resource-rich range in food availability and was finalized based on preliminary experiments which monitored larval development and survival under a wide range of food concentration conditions (Sharma, 2012; additional details in Appendix). Larvae were reared together, 30 to a petri plate (90 mm in diameter) with the assigned food treatment. After 48 h in the rearing environment, larvae were removed, run through clean water and tested in habitat use assays.

Two types of assay environments were created. To represent habitats differing in risk, we used mosaic patterns on paper placed on the bottom of a container as a simple index of the typical heterogeneity in background patterns found in natural populations. Petri plates (90 mm in diameter) were divided in half, one half representing a lighter and the other a darker background. The lighter background was presumed to represent a habitat of higher risk than the darker background because mosquito larvae are detected more easily by predators against a lighter background and some studies have shown that mosquito larvae avoid lighter, more open habitats (Foley et al., 2002). Our two assay environments differed in the level of contrast between the two halves. In the stark-contrast assay environment, representing a large difference in risk between the two habitats, the high-risk half of the plate had only 50 (1.57 per cm^2) randomly placed dots (each 0.18 mm in diameter) and the low-risk half had a very dark background with 10 000 randomly placed points (314.25 per cm^2). In the mild-contrast assay environment, on the other hand, the lighter, high-risk habitat had 500 points (15.71 per cm^2) and the darker, low-risk one 5000 points (157.13 per cm^2; Fig. 1). Thus, there was a 200-fold difference in dot density between the two habitats in the stark-contrast and only a 10-fold difference in the mild-contrast environment.

An individual larva was tested only once, either as a solitary individual or in a group, and in either the stark- or the mild-contrast assay environment. In each trial, an individual or one