Effects of size structure and habitat complexity on predator–prey interactions

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Abstract. 1. A predator’s ability to suppress its prey depends on the level of interference among predators. While interference typically decreases with increasing habitat complexity, it often increases with increasing size differences among individuals. However, little is known about how variation in intrinsic factors such as population size structure alters predator–prey interactions and how this intrinsic variation interacts with extrinsic variation.

2. By experimentally varying the level of vegetation cover and the size structure of the predatory damselfly Ischnura posita Hagen, we examined the individual and interactive effects of variation in habitat complexity and predator size structure on prey mortality.

3. Copepod prey survival linearly increased as the I. posita size ratio decreased and differed by up to 31% among different predator size structures. Size classes had an additive effect on prey survival, most likely because intraspecific aggression appeared size-independent and size classes differed in microhabitat preference: large I. posita spent 14% more time foraging on the floor than small larvae and spent more time in the vegetation with increasing habitat complexity. Despite this difference in microhabitat use among size classes, habitat structure did not influence predation rates or interference among size classes.

4. In general, results suggest that seasonal and spatial variation in the size structure of populations could drive some of the discrepancies in predator-mediated prey suppression observed in nature, and this variation could exceed the effects of variation in habitat structure.

Key words. Behavioural interference, cannibalism, damselfly, habitat complexity, prey suppression, size structure.

Introduction

Even within simple communities, the impact of a predator on its prey can vary substantially across time and space, and it has been a central challenge in community ecology to understand the mechanisms driving this variation. Habitat structure can vary substantially across space and time, and is known to influence the strength of predator–prey interactions by altering interference among predators and providing prey with refuges (e.g. Crowder & Cooper, 1982; Johnson, 2006; Janssen et al., 2007; Schmitt et al., 2009). While this source of ‘external’ heterogeneity could explain some of the variation in predator–prey interactions (Janssen et al., 2007), there is also increasing evidence that ‘intrinsic’ heterogeneity (i.e. variation within a population) can alter predator–prey interactions. For example, the size structure of predator populations is known to vary across time (e.g. during the course of a season) and space (e.g. Wissinger, 1989a, 1992; Woodward et al., 2005; Urban, 2007), and recent evidence suggests that a change in the size structure of populations alters predator–prey interactions (Crumrine, 2005, 2010; Griffen & Byers, 2006; Rudolf, 2006, 2007, 2008a,b). However, the relative importance of such extrinsic and intrinsic factors and their interaction is largely unknown.

Changes in predator size structure could influence predator–prey interactions in several ways. First, different-sized predators often vary in their foraging rate for a given prey size (e.g. Thompson, 1978; Bence & Murdoch, 1986; Wahlstrom et al., 2000; Aljetlawi et al., 2004; Rudolf, 2008a). Thus, changes in the size structure of a predator population are also likely to alter the net effect of the predator on the prey.
population. Second, recent studies indicate that the presence of different-sized cohorts within a predator population often result in lower prey mortality than expected based on their individual effects (Crumrine, 2005, 2010; Griffen & Byers, 2006; Rudolf, 2006). In most cases the reason for this reduction is that increasing the size difference among individuals also increases the potential for lethal (cannibalism) and non-lethal interactions among individuals that indirectly alter prey survival. For example, in the presence of large cannibalistic conspecifics, small individuals often alter their activity rate or habitat use, which also reduces their foraging rates (e.g. Persson & Eklov, 1995; Claus-Walker et al., 1997; Biro et al., 2003; Rudolf, 2006, 2007; Crumrine, 2010). Thus, because of size-specific differences in foraging rates and indirect interactions among size classes, changes in the size structure of predator populations across different habitats or within a season could drive some of the variation in predator–prey interactions observed in nature. However, previous studies simply manipulated the presence and absence of size classes but not how the net effect of a predator changes across a range of size structures.

Several studies suggest that structural complexity, like predator size-class variation, can alter predator efficiency and prey survival, although the predictions and results seem to differ dramatically. Some studies found greater prey survival with increasing habitat complexity (e.g. in amphibians (Babitt & Tanner, 1998; Suutari et al., 2004), crustaceans (Moksnes, 1997), and fish (Crowder & Cooper, 1982), although the specific underlying mechanisms are often unclear and could either result from a reduction in the predator’s capture rate due to structural complexity and/or an increase in the number of refuges for the prey. However, in some cases, habitat complexity had little effect on predator-mediated prey suppression (Anholt, 1990; Alto et al., 2005), or prey suppression increased with an increase in structural complexity (Finke & Denno, 2006; Johnson, 2006). In the latter studies, habitat complexity increased prey suppression because it reduced predator interference (Finke & Denno, 2006; Janssen et al., 2007). If this is true among intraguild predators, we may expect this to be true among intraspecific predators of varying sizes. Thus, habitat complexity could alter interference among individuals within a predator population, although this effect may be weak or unimportant in ambush or sit-and-wait predators (Alto et al., 2005). In addition, different-sized predators often use different micro-habitats (e.g. Werner & Hall, 1988; Persson & Eklov, 1995; Biro et al., 2003; Rudolf, 2006; Rudolf & Armstrong, 2008) and might thus be differentially affected by changes in habitat heterogeneity. Thus, the effect of changes in predator population size structure could vary with habitat complexity, but this has not been tested.

Here we use an experimental approach in a damselfly larvae (Ischnura posita)–copepod system to test how intrinsic (size structure) and extrinsic (habitat structure) sources of variation interact to affect predator–prey interactions. In particular, we evaluate the individual and combined effects of habitat complexity and size structure on predator efficiency, predator interference, and spatial distribution of I. posita.

Materials and methods

Study organisms

Larval Ischnura posita Hagen are most commonly found in fishless lentic habitats especially in shallow areas on vegetation. Ischnura posita primarily consume zooplankton and small invertebrates, but other odonates (including conspecifics) are part of their diet as well. We chose this species for two reasons. First, this species is known to mainly forage by perching on aquatic vegetation. Secondly, preliminary studies indicate that large individuals readily attack smaller conspecifics, and failed attacks often result in loss of caudal lamella (P. Del-clos and V.H.W. Rudolf, unpublished data). Two replicates of damselflies were collected on 15 May 2010, and a third was collected on 28 July 2010 from Davey Crockett National Forest near Groveton, Texas. Copepod prey was collected on 16 May 2010 and 30 July 2010 from the Center for Environmental Studies at Sam Houston State University in Huntsville, Texas. All larvae were kept individually in a climate-controlled environmental room at 25 °C and natural 10 : 14 h dark : light cycle. To standardise hunger levels, larvae were fed copepods ad libitum and subsequently starved for the 24 h before the start of a trial.

Experimental design

All experiments were performed in small aquaria (30.5 cm × 17.8 cm × 10.2 cm) in 11 : 13 h dark : light conditions filled with reconditioned reverse osmosis water. Each aquarium received 100 copepods that served as prey. We used a 3 × 6 full factorial design with three replicates per treatment to assess the individual and combined effects of habitat structure and size structure on predator–prey interactions and cannibalism: three levels of habitat complexity [one, two, and three plastic artificial plants (three-stemmed 15.3 cm tall Ambulalia) per aquarium] were crossed with a no-predator control treatment and five different size-class pairings of the predator (10 small damselflies, seven small and three large, five small and five large, three small and seven large, and 10 large per container). Two sets of replicates were run on 19 May 2010. For logistical reasons, the third set of replicates could not be run on the same day as the first two and was run on 2 August 2010. The size classification of larvae was determined by instar. Small corresponded to F-4 and F-5 instars, and large were F-1 and F-2 instars. Note that this was a substitutable design where the total predator density was kept constant and only the size structure was varied to avoid confounding density effects with size-structure changes.

At the end of the experiment, all surviving copepods and damselflies were counted and the lamella loss per damselfly was determined. All trials were concluded after 36 h. Aquaria were checked every 6 h during the day and 12 h overnight. During these check-ups, dead damselflies without any signs of cannibalism and emerged damselflies were replaced. Missing specimens or specimens with signs of cannibalism (dead with missing body parts) were considered cannibalised. To gain additional insight into treatment effects on predator behaviour including interactions among different size classes, we also
recorded microhabitat use of individual size classes during these check-ups following Murdoch and Sih (1978): two positions were noted, (i) perched on an artificial plant within the aquarium and (ii) open, which was considered any position not along an artificial plant. In addition, we recorded loss of caudal lamellae at the end of the experiment. Failed cannibalism attacks commonly led to loss of caudal lamellae, and lamella loss has been used in previous studies to estimate the degree of aggressive behaviour among individuals (Stoks, 1998; Rudolf, 2008a).

Statistical analyses

To assess the effects of habitat structure, size-class variation, and their interaction on the amount of copepod prey consumed and microhabitat preference of predators, a two-way ANOVA was used. To account for differences in starting day among replicates we included replicate as random block factor. However, the block factor was only significant for microhabitat use and not included in the final analysis of prey survival. Because of the non-normal distributions, we used randomisation tests to analyse treatment effects on damselfly survival and lamella loss using a randomisation-test wrapper for SAS (SAS Institute, Inc.) with 1000 runs (Cassell, 2002). Survival rates of copepods in predator treatments were determined by dividing the number of survivors by the average number of survivors in the control that contained the same number of plants. Also, proportion of time predators of a given size class spent on the floor was determined by dividing the number of times damselflies from that size class were seen on the floor by the total number of damselflies per 6-h (or 12-h) period. In addition, we used a null model that assumed a linear, additive effect of different prey size classes to calculate expected prey mortality in the absence of indirect interactions. If \( \mu_o \) is the natural background mortality of the prey, \( \mu_X \) is the size-specific predation rate of size class \( X \) [with \( X = L \) (large) or \( S \) (small)], then the expected mortality rate for a prey in a given treatment (\( m_{exp}^* \)) of the null hypothesis (i.e. no interaction effects between size classes) is: \( m_{exp}^* = N_L \mu_L + N_S \mu_S + \mu_o \), where \( N_X \) is the number of individuals of size class \( X \) present in the respective treatment. The individual mortality rate, \( \mu_X \), was calculated using the survival model \( N_t = N_0 e^{-\mu t} \), with \( N_t = \) final prey density of a cage within the respective treatment, \( N_0 = \) initial prey density, and \( t = \) duration of the experiment, and solving for \( \mu_X = -\ln(N_t/N_0)/t \). For the parameterisation of the model, we calculated the per capita mortality rate \( \mu_X \) of size class \( X \) from the difference between the control and the respective treatment with only that size class present (i.e. large only or small only), and the difference was divided by the number of individuals in the respective size class (i.e. 10). All calculations were based on observations within blocks (Vance-Chalcraft & Soluk, 2005a,b). Thus we had two observations, expected and observed mortality rates per block for treatments with multiple large size classes. Both observations are independent of each other because they are calculated using different treatments. To test whether different size classes had linear, additive effects and this was affected by size structure or habitat complexity we used a two-way ANOVA with the difference between expected (null model predictions) and empirical observation as dependent variable and size ratio and habitat complexity as fixed factors. Note that this formulation is based on the log-transformed proportional mortality rates and thus inherently implies a multiplicative risk model (Soluk & Collins, 1988; Wilbur & Fauth, 1990; Sih et al., 1998) that accounts for prey depletion, i.e. prey individuals consumed by one size class cannot be consumed by another size class (Rudolf, 2008b).

Results

A decrease in the large : small \( I. posita \) ratio led to a significant increase in copepod survival rates (\( F_{4,28} = 8.01, P = 0.0002 \)) (Fig. 1) resulting in up to 31% higher copepod survival in treatments with only small damselfly larvae compared to treatments with only large damselfly larvae (all small = 51.2% ± 4.5, all large = 20.4% ± 3.5). Neither plant abundance (\( F_{2,28} = 0.04, P = 0.9601 \)) nor the interaction of plants and size ratio [(\( F_{4,28} = 1.35, P = 0.2604 \))] affected copepod survival rates. A comparison of observed and expected mortality rates of copepods indicated no significant treatment effects (plants: \( F_{2,18} = 0.20, P = 0.8207 \), size ratio: \( F_{2,18} = 0.20, P = 0.8233 \), plants × size ratio: \( F_{4,18} = 1.77, P = 0.1785 \)), indicating that different size classes had linear, additive effects on prey mortality.

While there was some indication that survival of small damselflies might decrease with an increasing large : small \( I. posita \) ratio (Fig. 2), cannibalism rates were generally low and no treatment effect was significant (size ratio: \( P = 0.383 \), plant density: \( P = 0.590 \), interaction of size structure and plant density: \( P = 0.991 \)). Survival of large damselflies was on average 100% and did not vary across treatments. Similarly, while there was significant caudal lamella loss in both small and large predator stages across all habitat structures (small: 26.6% ± 3.4, large: 26.6% ± 2.7 t-test, \( P < 0.05 \)), indicating some level of interference among individuals.

Fig. 1. Mean (±1 SE) survival rate of copepods according to size class ratio of \( Ischnura posita \) and amount of vegetation per container. Circles indicate one plant per container, triangles indicate two, and squares three.
average proportional caudal lamella loss of small or large damselfly larvae did not differ across size ratio, plant density or the interaction of both (for small lamella loss, size ratio \( P = 0.444 \), plant density \( P = 0.992 \), plant \( \times \) size \( P = 0.956 \); for large lamella loss, size ratio \( P = 0.558 \), plant density \( P = 0.748 \), plant \( \times \) size \( P = 0.493 \)) (Fig. 3).

Large damselflies spent twice as much time on the floor, and half as much time perching on plants, than small damselflies (large on floor = 26.9% ± 2.7, small on floor = 12.8% ± 1.6, \( t = 4.54 \), d.f. = 22, \( P < 0.001 \)) (Fig. 4). Size ratio (\( F_{2,22} = 0.03 \), \( P = 0.9928 \)) and the interaction of plant abundance and ratio (\( F_{6,22} = 1.54 \), \( P = 0.2109 \)) had no impact on microhabitat use by large I. posita. However, plant abundance significantly altered large damselflies’ microhabitat use (\( F_{2,24} = 7.25 \), \( P = 0.0038 \)); the proportion of time large damselflies spent on the floor was highest in low vegetation containers (33.6% ± 10.5), and lowest in intermediate vegetation containers (17.4% ± 10.9). The proportion of time small I. posita spent on the floor significantly increased by 12.4% as the large : small damselfly ratio decreased (7/3 small on floor = 6.48% ± 6.94, 0/10 small on floor = 18.9% ± 9.8, \( F_{3,22} = 3.225 \), \( P = 0.040 \)). Plant abundance (\( F_{2,22} = 0.25 \), \( P = 0.7837 \)) and its interaction with the size ratio (\( F_{6,22} = 0.62 \), \( P = 0.7118 \)) had no significant effect on microhabitat use by small I. posita.

Discussion

It is well known that extrinsic factors such as habitat heterogeneity can alter the impact of a predator on its prey (e.g. Crowder & Cooper, 1982; Johnson, 2006; Janssen et al., 2007; Schmitt et al., 2009). However, little is known about how intrinsic variation, such as changes in the size structure of a population, influences predator–prey systems and how this variation interacts with extrinsic variation. Here, we show that prey suppression varied along a size-structure gradient (i.e. change in size ratio) of the predator while habitat structure did not affect prey suppression or how size structure influences prey survival.

We found that both consumption rates and overall behaviour of the predator population changed as the population’s size ratio changed. Copepod prey survival rates increased with a decrease in the ratio of large : small damselfly predators. Survival was nearly 31% higher in the absence of large I. posita than when only large damselflies were present. These data suggest that larger I. posita larvae are more voracious than smaller conspecifics and that prey populations would decrease as larval populations increase in size, which is in accordance to previous studies that relate foraging rates to body size (e.g. Thompson, 1978; Bence & Murdoch, 1986; Wahlstrom et al., 2000; Aljetlawi et al., 2004; Rudolf, 2008a). Given that many systems show substantial variation in size structure of natural populations across time (e.g. across seasons) or space (Wissinger, 1989b, 1992; Woodward et al., 2005; Urban, 2007), this intrinsic variation within a population could be an important factor driving the variation in predator–prey interactions observed in natural communities.

Interestingly, we found that size classes had linear, additive effects, i.e. the combined effect of different size classes was not different from a null model assuming no indirect interactions. Previous studies in other systems have found mixed results:

Fig. 2. Mean (±1 SE) survival rate of small Ischnura posita according to size class ratio and amount of vegetation per container. Circles indicate one plant per container, triangles indicate two, and squares three.

Fig. 3. Mean (±1 SE) caudal lamella loss rate in (a) large and (b) small Ischnura posita according to size class ratio and amount of vegetation per container. Circles indicate one plant per container, triangles indicate two, and squares three.
they either found a risk reduction when two size classes were present (i.e. higher than expected prey survival) (Crumrine, 2005, 2010; Rudolf, 2006, 2008c) or no significant difference depending on the predator species or prey identity (Crumrine, 2005; Griffen & Byers, 2006). The question is what caused these mixed results. In general, risk reduction in prey survival is expected under strong asymmetrical behavioural interference among different predator size classes. It is possible that the lack of risk reduction in previous studies was either based on absence of asymmetrical interference, or the range of size structures explored was too narrow. We addressed both potential issues by analysing behavioural interference and using a large range of different size structures. Although predator interference was present in the form of cannibalism and lamella loss, this antagonistic behaviour between individuals was not size-specific, and these rates were very low, suggesting a low amount of interference between I. posita. This lack of size-specific difference in aggressive behaviour could explain why changes in the size structure did not lead to non-linear, non-additive effects. In addition, we found that size classes differed on average in their microhabitat use. Such differences are assumed to reduce the potential for non-linear interactions among predators (Schmitz & Sokol-Hessner, 2002; Schmitz, 2007) and could have contributed to the additive effect we observed.

Interestingly, we found that habitat complexity had no effect on prey survival or the effect of changes in predator size structure. This pattern persisted despite the fact that size classes differed in their microhabitat use and how they responded to change in habitat complexity. Alto et al. (2005) suggest that one important determinant of the outcome of predator efficiency in structurally complex habitats is the mechanism by which predators hunt, distinguishing among two types of predators: ‘actively searching predators’ and ‘ambush’ or sit-and-wait predators. While an increase in habitat complexity has been shown to decrease predator efficiency, or increase prey survival, in actively searching predator–prey systems, ambush predators have been shown to be unaltered by or increase in their hunting efficiency as structural complexity was increased (e.g. Heck & Crowder, 1991; James & Heck, 1994; Flynn & Ritz, 1999). This is due, in large part, to the levels of intraspecific predator interference. Actively searching predators are expected to interact more with members of their own species, and this can lead to predator interference. This can be either direct, in the form of attacks or cannibalism, or indirect, inducing a change in behaviour among the predators. According to this hypothesis, ideal sit-and-wait predators would rarely experience intraspecific interference due to the lack of interaction with members of their own species, so predator efficiency would be unaltered by this effect. Ischnura posita generally exhibited a sit-and-wait hunting mode and spent the majority of their time perched (∼80%). This could explain why we did not see an effect of habitat structure on prey survival. However, we set up the low habitat complexity such that individuals would have to share plants thus increasing the potential for interactions.

Large damselflies spent around 14% more time on the floor than small I. posita, and small larvae spent more time foraging as the large : small population ratio decreased. In addition, large damselflies altered habitat use with increasing habitat complexity, spending more time on plants. This difference in microhabitat use and response to habitat complexity among size classes indicates some form of interference among individuals. It is also possible that our plant abundance levels did not cover high enough plant densities or that our statistical power was too low to detect any differences. However, given the large number of replicates within a plant density treatment (five size classes × three replicates), we would have expected to be able to detect some difference given a reasonably strong effect size. In addition, effect sizes (e.g. differences among plant treatments) were very small, and there was no consistent pattern (e.g. increase in survival with plant density) in the effect size as well. Furthermore, large damselflies did show a significant change in habitat use with changes in plant density, indicating that our treatment was effective in altering some aspects of damselfly behaviour. Finally, habitat complexity did not have any effects in other studies as well (Alto et al., 2005), suggesting that the importance of habitat complexity for predator–prey interactions may vary among systems. Although all vegetation levels in this experiment had been observed in natural conditions, more extreme levels should be chosen in the

Fig. 4. Mean (±1 SE) proportion of time spent on floor according to size class ratio and amount of vegetation per container for (a) large and (b) small Ischnura posita. Note the difference in scale between (a) and (b). Circles indicate one plant per container, triangles indicate two, and squares three.
future in order to obtain more discernible results on the effects of vegetation on cannibalism, aggression, prey survival and microhabitat use.

In general, our results suggest that intrinsic variation within predator populations (i.e. variation in the population size structure) can have important consequences and alter the impact of a predator on its prey. Interestingly, our results suggest that this effect was stronger than any change in extrinsic variation (i.e. habitat complexity), although this pattern may change if more extreme levels of extrinsic variation are used. This suggests that spatial or temporal variation in population size structure could explain some of the variation in predator-mediated prey suppression observed in natural systems.

Acknowledgements

We are grateful to N. Rasmussen, C. Dibble, K. Banneyer, and J. Garcia for help in the field and two anonymous reviewers for helpful comments on the manuscript. Funding was provided by NSF DEB-0841686 to VHWR.

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Accepted 13 September 2011