

Seasonal shifts in predator body size diversity and trophic interactions in size-structured predator–prey systems

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Summary

1. Theory suggests that the relationship between predator diversity and prey suppression should depend on variation in predator traits such as body size, which strongly influences the type and strength of species interactions. Prey species often face a range of different sized predators, and the composition of body sizes of predators can vary between communities and within communities across seasons.

2. Here, I test how variation in size structure of predator communities influences prey survival using seasonal changes in the size structure of a cannibalistic population as a model system. Laboratory and field experiments showed that although the per-capita consumption rates increased at higher predator–prey size ratios, mortality rates did not consistently increase with average size of cannibalistic predators. Instead, prey mortality peaked at the highest level of predator body size diversity.

3. Furthermore, observed prey mortality was significantly higher than predictions from the null model that assumed no indirect interactions between predator size classes, indicating that different sized predators were not substitutable but had more than additive effects. Higher predator body size diversity therefore increased prey mortality, despite the increased potential for behavioural interference and predation among predators demonstrated in additional laboratory experiments.

4. Thus, seasonal changes in the distribution of predator body sizes altered the strength of prey suppression not only through changes in mean predator size but also through changes in the size distribution of predators. In general, this indicates that variation (i.e. diversity) within a single trait, body size, can influence the strength of trophic interactions and emphasizes the importance of seasonal shifts in size structure of natural food webs for community dynamics.

Key-words: biodiversity, body size, cannibalism, functional diversity, multi-predator effects, ontogenetic niche shift, risk enhancement, size spectra, size structure

Introduction

Theory suggests that the relationship between predator biodiversity and prey suppression should depend on variation in traits of individuals and types of interactions between them (reviewed in Ives, Cardinale & Snyder 2005; Duffy *et al.* 2007). Body size is arguably one of the most important traits of an individual and, to a large extent, determines the strength and type of species interactions (reviewed in De Roos, Persson & McCauley 2003a; Yang & Rudolf 2010). For example, smaller individuals typically have lower foraging rates and face higher predation risks than larger individuals. Consequently, relative body size is often a better predictor of predator–prey dynamics than species identity

(e.g. Taylor, Trexler & Loftus 2001; Persson *et al.* 2004; Rudolf 2008a; Rudolf & Armstrong 2008). Thus, natural changes in the size structure of predators could alter predator–prey interactions and top-down suppression of prey densities in natural communities.

In natural communities, the size distribution of predators commonly differs between communities and within communities during a season. This may occur either because predator species arrive or leave a community during the course of a season or because of seasonal changes in the size structure within predator populations (Wissinger 1992; Woodward *et al.* 2005; Urban 2007). Recent field studies indicate that seasonal shifts in mean predator size can alter prey survival (Urban 2007), but it remains unclear how prey mortality is influenced by concurrent changes in the size distribution. In cannibalistic populations, changes in size distribution within

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populations could also alter interactions between cohorts and cannibalism rates, leading to seasonal changes in the mortality rates of natural populations.

The distribution of body sizes in a predator community could influence predator–prey interactions simply through changes in mean predator size but also because of changes in ecological interactions and among predators, and what traits are present within the predator community (Fig. 1). A predator's attack rate typically increases with increasing size difference between predator and prey, although too small prey may be less preferred by the predator (e.g. Thompson 1978; Bence & Murdoch 1986; Wahlstrom *et al.* 2000; Aljetlawi, Sparrevik & Leonardsson 2004; Rudolf 2008a). Thus, assuming a constant predator density, increased or decreasing the mean size of predators in the community is also likely to increase or decrease prey survival respectively (note that if instead total biomass stays the same, consumption rates may be similar or even higher (Chalcraft & Resetarits 2004)). However, changes in the predator size distribution could also influence prey survival. Theory suggests that in multi-predator systems, the effect of increasing functional diversity of predators on prey survival depends on prey use patterns (i.e. resource partitioning) and ecological interactions between predators (Ives, Cardinale & Snyder 2005; Casula, Wilby & Thomas 2006). If the prey consists of different sized individuals and predators differ in their preferred prey size, this would decrease predator redundancy. In this scenario, increasing predator body size diversity should strengthen top-down cascades (Ives, Cardinale & Snyder 2005; Casula, Wilby & Thomas 2006). However, increasing the size range of predators is also likely to concurrently alter interactions

between predators. For instance, if the size difference between predators is large enough, small predators become vulnerable to predation by large predators. Thus, increasing the size range of predators can promote predation among predators and thereby reduce predator density. In addition, small predators might alter their foraging behaviour and habitat use in the presence of larger predators to avoid being injured or consumed, which can create non-consumptive indirect interactions that can also alter prey survival (Griffen & Byers 2006; Rudolf 2006; Crumrine 2010). Thus, increasing the size range in predators increases the potential of indirect interactions (consumptive and non-consumptive mediated) that are predicted to decrease the strength of trophic cascades (Ives, Cardinale & Snyder 2005; Casula, Wilby & Thomas 2006) (Fig. 1). Furthermore, the presence of such nonlinear effects (positive and negative) that arise from indirect interactions between different sized predators would indicate that estimating the effects of predators based on their average size would lead to erroneous predictions.

Here, I use seasonal variation in the size structure of a cannibalistic population as a model system to test how changes in the size distribution of predators (cannibals) influence the survival of prey (conspecific victims). In particular, I use a combination of field and laboratory experiments to test (i) how attack rates of cannibalistic predators scale with size, (ii) whether cannibalistic predator size classes are substitutable or whether size differences between cannibals lead to non-consumptive (behavioural)-mediated indirect effects that alter per-capita effect of cannibals on prey survival and (iii) how seasonal changes in average cannibal size and cannibal size distribution influence survival of conspecific prey. Results show that prey mortality was higher than expected in treatments with the highest predator size diversity, indicating that per-capita effect of different size classes of cannibals change with the size distribution of the predator population. In general, this suggests that the strength of top-down cascades depends on both mean body size and size distribution within predator communities.

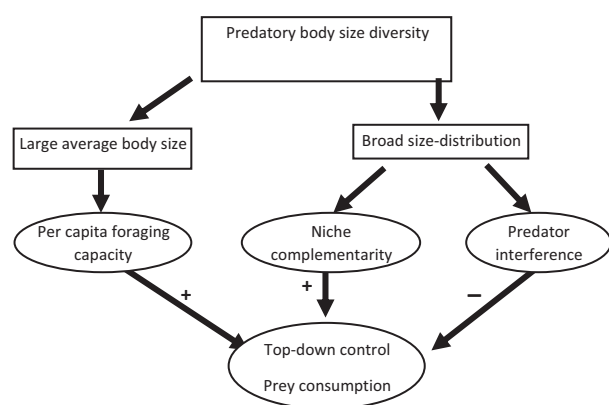


Fig. 1. Hypothetical relationship between changes in predator body size diversity and top-down control. Changes in predator body size diversity can influence prey populations through both changes in the average body size and the size distribution of predators. Increase in body size typically increases per-capita foraging rates of predators, which should increase the strength of top-down control. Increasing the size range of predators has the potential to increase resource partitioning and thus niche complementarity (including indirect positive interactions) of predators, which should strengthen top-down control. However, increasing the size differences between predators can also lead to concurrent changes in interactions between predators (e.g. intraguild predation), leading to interference between predators, which should decrease the strength of top-down control.

Materials and Methods

STUDY SPECIES

The species used in this study is the common whitetail *Platthemis lydia*. Larvae of this dragonfly species can reach very high densities (c. 380 ind m⁻²) during peak summer months (Wissinger 1989). It reproduces nearly all summer and overwinters in pond as larvae. As a consequence, the size structure of a population changes substantially during the course of a season, resulting in a large range of size distributions. Populations can show a narrow unimodal size distribution, a bimodal size distribution (where coexisting cohorts can differ by up to fourfold) or a size distribution where all size classes are present (Wissinger 1989; V. H. W. Rudolf, unpublished data). Cannibalism is uncommon within an instar but becomes more likely with increasing instar differences (Wissinger 1988; V. H. W. Rudolf, unpublished data). Cannibalism can be severe under natural conditions and increase natural mortality rates by 7.4 times (Rudolf 2008b). Small individuals use chemical and visual cues to detect

larger, cannibalistic conspecifics (Ferris & Rudolf 2007) and alter their behaviour in their presence to reduce the risk of cannibalism (Rudolf 2008b). For the purpose of the experiment, I focused on four size classes: small larvae (S) [head width (HW) = 0.16 cm \pm 0.012 SD, body length (BL) = 0.66 cm \pm 0.05 SD, N = 107] served as prey because they are highly abundant and are commonly cannibalized by three larger, cannibalistic size classes that served as predators in the experiments; medium (M) (all F-3 instars, HW = 0.26 cm \pm 0.01 SD, BL = 1.04 \pm 0.06 SD, N = 10); medium-large (ML) (F-2 instars, HW = 0.34 cm \pm 0.02 SD, BL = 1.41 cm \pm 0.10 SD, N = 10); and large (L) (F-1 instars, HW = 0.45 cm \pm 0.02 SD, BL = 1.74 cm \pm 0.07 SD, N = 10). All larvae were collected from one pond close to Mountain Lake Biological Station, Giles Co., VA, USA, in 2007 from August to September.

SIZE-SPECIFIC PER-CAPITA CANNIBALISM RATES

I used a series of laboratory experiments to gain detailed insight into how cannibalism rates and behavioural interactions scale with differences in size. All laboratory experiments were carried out in plastic containers (L \times W \times H: 32 \times 14 \times 8 cm) with a 1-cm-deep sand layer and filled with unfiltered pond water in a climate controlled room at 24 °C with a natural light/dark cycle of 14/10 h. First, I estimated how individual per-capita cannibalism rates scale with differences in predator size by exposing six small *P. lydia* (S) to one medium (M), one ML, or one large (L) predator size class. Each size class was replicated six times and set up in a completely randomized design. Replicates in which cannibals moulted were terminated at the time of moulting. All other replicates ran for 9 days, and survival was checked every 24 h except for day three because of logistic constraints. All cannibals were fed *ad libitum* 24 h before the experiment to standardize hunger levels. I analysed cannibalism rates using a generalized nonlinear mixed model to fit an exponential survival model to the data. The model estimates two parameters: a , the per-capita cannibalism rate, and b , a size-specific change in cannibalism rate (a). If b is significantly different from zero, this indicates that size classes differ in their cannibalism rate (see Appendix S1, Supporting information for analysis details).

SIZE-STRUCTURED BEHAVIOURAL-MEDIATED INDIRECT INTERACTIONS BETWEEN TWO DIFFERENT CANNIBAL SIZE CLASSES

I conducted a laboratory experiment to test whether medium-sized instars alter their cannibalism rates in the presence of larger conspecifics. The experiment consisted of three treatments, each replicated seven times in a completely randomized design. Each treatment received 10 small instars that served as prey for larger cannibalistic instars. The control treatment contained only small instars. In the other two treatments, two individuals of the medium size class (M) were added to the containers and allowed to forage either in the absence (Cann) or in the presence (Cann + Lg) of one non-lethal, large (L) conspecific with glued mouth parts [for details on gluing procedure, see (Rudolf 2008b)]. Previous studies have shown that the gluing procedure completely prevents cannibalism, but glued individuals show normal foraging behaviour, including attempted (but unsuccessful) attacks on other conspecifics (Rudolf 2008b). Any statistical difference in cannibalism rates between the two cannibal treatments (i.e. Cann vs. Cann + Lg) would thus indicate a behaviourally mediated indirect interaction between large and medium-sized cannibals that alters the cannibalism rate of medium-sized *P. lydia*. All cannibals were fed *ad libitum* 24 h before the experiment. All

absolute and relative densities of instars are within the range of observed in natural populations and are similar to previous experiments (Rudolf 2008b; V. H. W. Rudolf, unpublished data; Wissinger 1989, 1992). The experiment was terminated after 4 days, when I counted the number of surviving individuals of each instar. Only instars that were missing or partially consumed were assumed to be cannibalized.

FIELD EXPERIMENT: IMPACT OF PREDATOR SIZE DISTRIBUTION ON PREY POPULATION

In most populations, the size distribution (i.e. relative abundance of size classes) changes during a season. I used a field experiment to test (i) how seasonal changes in size distribution influence the mortality rates of natural populations and (ii) whether the change in mortality can be predicted simply based on per-capita effects of individual size classes or whether indirect interactions between size classes are present (i.e. whether size classes are substitutable).

Experiments were conducted in cylindrical field enclosures (diameter 40 cm, height 60 cm, 1 mm mesh width) that were set up in the Station Pond at MLBS where the species naturally exists. The top remained open to allow colonization by invertebrates until the experiment started. The bottom of each cage was sewn shut and contained a removable plastic dish of 40 cm diameter holding 2 cm of sediment and leaf litter collected from the same pond. One week before the start of the experiment, cages were set up at a water depth of 30 cm in a line along the border of the pond to allow natural colonization by invertebrates. Cages were separated by 70 cm. At the start of the experiment, a variety of species (mostly zooplankton, small mayfly and zygoptera larvae, beetle larvae and adults) had colonized the cages, providing ample alternative prey for small and larger *P. lydia*. Predatory invertebrates that were large enough to consume small *P. lydia*, and juvenile bullfrogs were removed from the cages before and during the experiment.

The experiment manipulated the presence/absence and relative abundance of four size classes of *P. lydia* (S, M, ML and L) to mimic the changes in size distribution over a year (Table 1). Size classes were similar to those used in laboratory experiments. Treatments consisted of seven different combinations of size classes, each replicated six times using a substitutive design that kept the total density constant at 38 larvae per cage (300 individuals m^{-2}) and the predator density constant at six larvae per cage (Table 1). The design served

Table 1. Predator treatments used to test how changes in the size distribution of a predator community affect prey mortality and whether effects of predator size classes are independent. Numbers are individuals per treatment. Season indicates what time of the year is characterized by the respective size structure in the population

	Treatment						
	I	II	III	IV	V	VI	VII
Season	Late spring		Summer–Fall			Early spring	
Size class							
Small (S)	38	32	32	32	32	32	32
Medium (M)	0	6	4	0	2	0	0
Medium–large	0	0	2	6	2	2	0
Large (L)	0	0	0	0	2	4	6
Total	38	38	38	38	38	38	38

multiple purposes: first, treatments I–III and V–VII represent changes in size distribution over the course of a year (Table 1). Second, treatments I, II, IV and VII were used to estimate the baseline mortality of the prey and to estimate the respective cannibalism rate of each size class (M, ML, L) independent of each other. Together, all treatments allowed me to test whether effects of predatory size classes are independent of each other. The experiment was terminated after 16 days. This duration allowed for significant cannibalism while simultaneously avoiding the emergence of the largest size class during the experiment. At the end of the experiment, cage contents were removed, and I counted and photographed all surviving dragonfly larvae.

POPULATION MORTALITY

To test for differences in mortality rates across treatments, I calculated the mortality rate within a cage using the survival model $N_t = N_0 e^{-mt}$, with N_t = final prey density, N_0 = initial prey density and t = duration of the experiment and solving for $m = -\ln(N_t/N_0)/t$. To test whether the effects of different size classes were linear, independent of each other, I calculated the expected mortality rate for the small size class (m_{Exp}^s) for each mixed size class treatment under the null hypothesis of no interaction effects between size classes and that the per-capita interaction strength is constant (see Appendix S1 for full model description and statistics). The null model prediction was then compared to the observed mortality using a general linear mixed model followed by planned linear contrasts between observed and expected values for each treatment. A significant difference between observed and expected mortality rates indicates that size classes are not substitutable, i.e. their effects are not independent of each other.

SIZE STRUCTURE

To gain additional insight into the different effects of cannibal size classes on the prey population, I tested whether the size distribution within the smallest size classes differed between treatments. Prior to the experiment, I photographed and measured the HW and BL of 110 randomly selected small *P. lydia* using IMAGE J (<http://imagej.nih.gov/ij>) as a reference for the initial size distribution. At the end of the experiment, all surviving individuals were photographed and measured. BL varies with food intake and is variable within instar, while HW varies across but little within instar. I analysed treatment effects on the size structure using a one-way MANOVA, with the mean, maximum, minimum, skewness and standard deviation for HW and BL within a cage as dependent variables, followed by individual ANOVAS to test for the treatment effects on each statistic.

Results

SIZE-SPECIFIC CANNIBALISM RATES

The size-structured survival model provided a good fit to the observed survival of small *P. lydia* (Fig. 2). Survival of small *P. lydia* significantly decreased in the presence of the three cannibalistic size classes ($a = 0.626 \pm 0.087$ SE, $t = 7.22$, d.f. = 15, $P < 0.001$) and differed significantly across size class ($b = -0.129 \pm 0.035$ SE, $t = -3.77$, d.f. = 16, $P = 0.0019$); cannibalism rates were 1.7 and 2.6 times higher in the large size classes than in the ML and medium size classes, respectively. Separate analyses for each size class

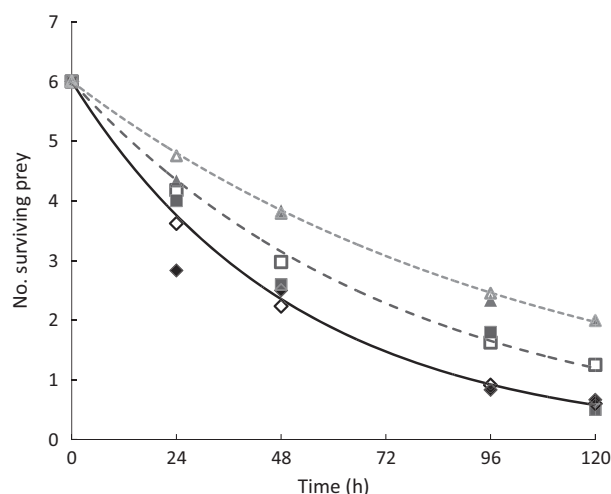


Fig. 2. Observed and predicted average survival of small *Platthemis lydia* in the presence of different cannibalistic size class in the laboratory feeding trial experiment: M = medium (\blacktriangle), ML = medium-large (\blacksquare), L = large (\blacklozenge) (see Materials and Methods for size details). Filled symbols indicate average observed survival, open symbols indicate average values predicted by the survival model, and lines indicate fitted trend lines. Only means are represented for clarity; analysis of the full data set was performed using a generalized nonlinear mixed model that accounted for repeated observations within individuals (see Materials and Methods for details). Survival significantly declined over time ($P < 0.001$), and predation rates differed significantly across predator size classes ($P = 0.0019$).

obtained similar size-specific a values within the 95% CI of the full model.

BEHAVIOURAL-MEDIATED INDIRECT INTERACTIONS BETWEEN CANNIBAL SIZE CLASSES

In the absence of larger conspecifics, no cannibalistic attacks were observed among small *P. lydia* larvae. Consumption of small conspecifics increased to 18% ($\pm 4.6\%$ SE) in the presence of only medium-sized larvae (Cann) ($Z = 3.28$, $P = 0.001$, $N = 7$). However, the presence of a non-lethal, large larva (Cann + Lg) significantly reduced cannibalism of small larvae to 2.7% ($\pm 1.8\%$ SE) ($Z = 2.5$, $P = 0.0124$, $N = 7$), indicating that the non-lethal presence of large *P. lydia* larvae indirectly reduced cannibalism rates of medium-sized *P. lydia*.

IMPACT OF SEASONAL CHANGES IN SIZE DISTRIBUTION OF CANNIBALS ON CONSPECIFIC PREY MORTALITY

Changes in the size distribution of the different cannibalistic size classes significantly affected the total mortality rate of the population ($F_{6,30} = 12.92$, $P < 0.0001$) and the mortality of small *P. lydia* ($F_{6,30} = 11.49$, $P < 0.0001$) (Fig. 3a). For both mortalities, except treatments with only small *P. lydia* ($P = 0.405$), all treatments were significantly different from zero (all $P < 0.02$). Relative differences between treatments were similar for both mortalities (Fig. 3a). There was a general trend for mortality rates to increase with

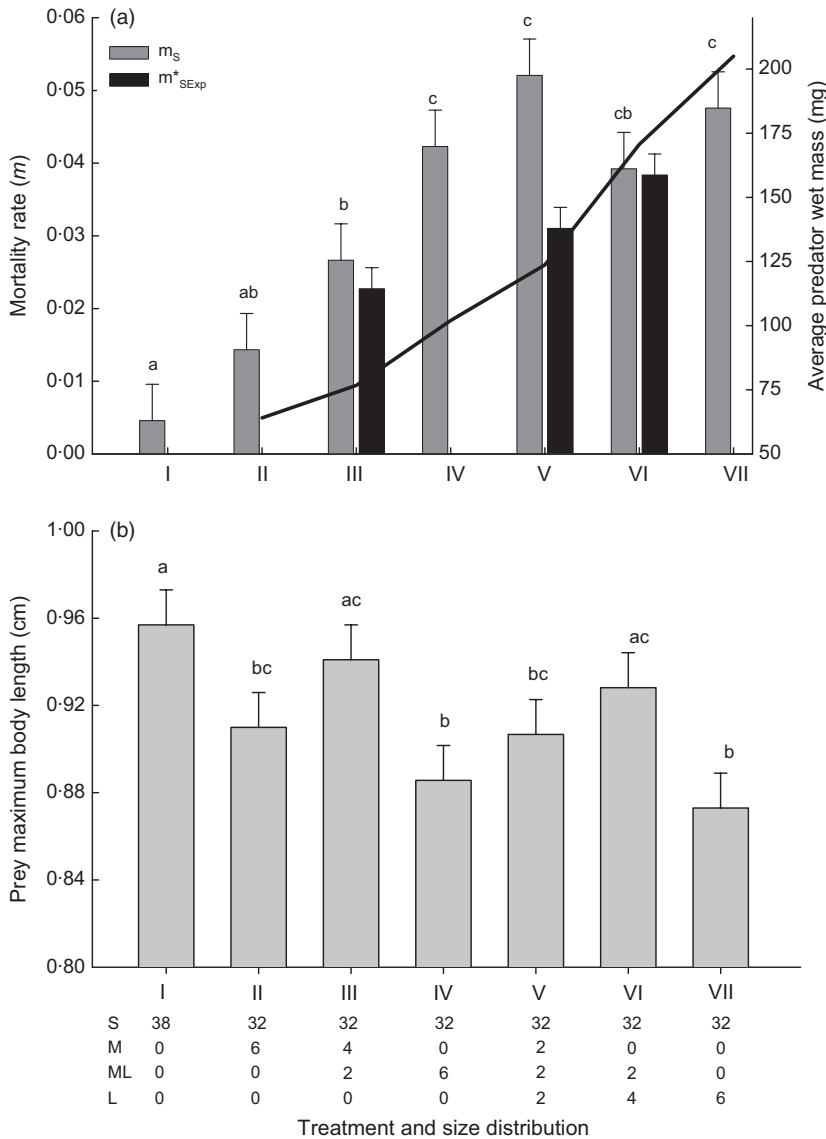


Fig. 3. (a) Mean (± 1 SE) observed mortality rates for small individuals (prey) only (m_s), and corresponding expected mortality rates for small prey only (m_{SEXP}^*) predicted by the null model assuming independent effects of different predatory size classes (see Materials and Methods for details). The solid black line indicates the average predator wet mass for a given predator treatment. (b) Average (± 1 SE) maximum body size of small individuals (prey) as a function of size structure in predatory size classes. Different letters between treatments for a given mortality (or body length) indicate significant differences between treatments ($\alpha = 0.05$) after correcting for the false discovery rate (FDR) to control for the type I error because of the multiple comparisons (Benjamini & Hochberg 1995). The size distribution (number of individuals in each size class S-L) for each treatment is given below the treatment number (see Table 1). Mean and SE are based on least square model estimates after accounting for block effects.

average mass of cannibals (regression analysis: $R^2 = 0.520$, $F_{1,40} = 43.28$, $P < 0.0001$). However, when only one cannibalistic size class was present (M, ML or L), mortality rates only differed between M and ML or L but not between the two largest size classes (Fig. 3a), and mortality rates peaked at intermediate average body size when all three cannibal size classes were present, indicating that mortality rates did not consistently increase with average body size of predators. In treatments with all size classes (M + ML + L), observed mortality rates were 68% higher than expected from the null model ($t_{1,25} = -2.50$, $P = 0.019$) assuming no indirect interactions between size classes (see Appendix S1), indicating that different size classes were not substitutable in this scenario (Fig. 3a). Observed mortalities with only two cannibalistic size classes were consistent with predictions of the respective null models (for M + ML: $t_{1,25} = -0.29$, $P = 0.078$, for ML + L: $t_{1,25} = 0.95$, $P = 0.34$). The total number of individuals in all cannibalistic size classes (i.e. M + ML + L) at the end of the experiment did not differ significantly between treatments ($F_{5,25} = 0.72$,

$P = 0.614$) and was 5.7 (range 3–6) on average across treatments (Fig. 4).

SIZE STRUCTURE

The MANOVA revealed a significant difference in the different size statistics within the smallest size class across treatments (Wilks' lambda: $F_{60,141.28} = 1.41$, $P = 0.0421$). Subsequent individual ANOVAs indicated that this difference was largely driven by differences in the maximum prey BL across treatments ($F_{6,36} = 3.48$, $P = 0.0084$), which was largest in treatments without a cannibalistic size class and smallest when only large (L) or medium (M) predator size classes were present (Fig. 3b). Other size statistics did not differ significantly between treatments (all $P > 0.13$).

Discussion

Body size is a key trait of individuals and is known to influence the type and strength of species interactions (De Roos,

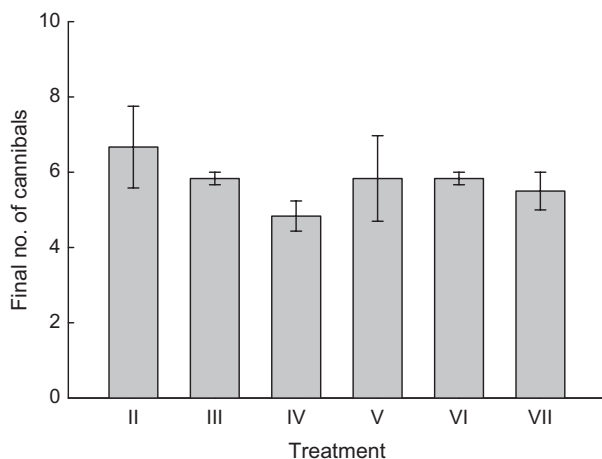


Fig. 4. Mean (± 1 SE) number of cannibals (i.e. total number individuals summer over M, medium–large and L size class) at the end of the experiment in each cannibal treatment. There was no significant difference between treatments ($F_{5,25} = 0.72$, $P = 0.614$).

Persson & McCauley 2003a; Yang & Rudolf 2010). In natural communities, the size distribution of predators commonly differs between communities and within a season. However, the consequences of variation in the size distribution of predator communities on predator–prey dynamics are not well understood. Here, I show the per-capita strength of prey suppression is altered by seasonal changes in mean predator (cannibal) size but also through changes in the size distribution within a predator population. This suggests that seasonal variation within a single trait, body size, can influence predator–prey dynamics in natural communities.

AVERAGE PREDATOR SIZE AND PREY MORTALITY

The relative difference in body size between a predator and its prey is known to be a key factor in determining per-capita predation rates (e.g. Thompson 1975; Wahlstrom *et al.* 2000; Aljetlawi, Sparrevik & Leonardsson 2004; Brose *et al.* 2008; Rudolf 2008a). This would suggest that changes in mean body size of predators are also likely to alter the strength of top-down control imposed by predators on their prey. Although laboratory experiments clearly indicated that per-capita predation rates increased with predator size and significantly differed between predator size classes (Fig. 2), prey mortality did not consistently increase with average predator size in the field and was similar among treatments with the two largest size classes (Fig. 3a). While predation rates are expected to be lower in the field compared to laboratory experiments (e.g. owing to more complex habitat structure and alternative food in the field), the question is why the relative differences between size classes disappeared.

Although it is possible that the increased variation in mortality reduced statistical power to detect a difference, effect size (i.e. mean difference) between the two largest predator size classes was very small. In addition, when considering both single and mixed sized predator treatments, mortality

did not consistently increase with the average size of the predator within treatments either (Fig. 3a) but instead peaked when all three predatory size classes were present. It is possible that the interference among similar sized individuals in the field reduced per-capita predation rates. Recent experiments suggest that interference among similar sized predators may increase with absolute size (V. H. W. Rudolf, unpublished data), which would reduce the differences in prey mortality between treatments with different size classes in the field. However, it is unlikely to explain why mortality rates were highest when all three size classes were present and not when only large predators were present. This suggests that changes in the distribution of predator body sizes were also an important component determining the effect of predators on prey survival. The study was designed to mimic natural seasonal changes in body size distribution within a predator population and not to explicitly compare the relative effects of changing the mean and distribution of sizes of predators or how both variables interact. This will require future studies that manipulate both statistics independently. Nonetheless, the results clearly indicate that given a fixed predator density, changing the size structure within a predator population can alter prey suppression through changes in the mean size and size distribution of predators.

SEASONAL CHANGES IN VARIATION OF PREDATOR BODY SIZES

Mortality rates of the prey were significantly altered by changes in the predator size distribution, clearly indicating the importance of seasonal shifts in predator body size composition. However, the pattern did not simply follow a general increase in average size of predators (Fig. 3a). Instead, contrary to the expectations, mortality rates peaked when all three predator size classes were present. In addition, mortality rates in this treatment were significantly higher than expected based on the individual effects of each size class, indicating that size classes were not substitutable. This indicates an increase in prey suppression with higher body size diversity. The finding seems to be contradictory to results from other studies and my laboratory experiment. In previous studies on odonates, predatory crabs and salamanders, pairing two different size classes always resulted in lower prey mortality rates than expected based on individual effects, irrespective of whether the small size class consisted of conspecifics or heterospecifics (Crumrine 2005, 2010; Griffen & Byers 2006; Rudolf 2006). In all four studies, the authors argue that risk of predation (or cannibalism) increases within the predators when two different size classes are present, resulting in concurrent behavioural changes (i.e. anti-predator behaviour) in the smaller size class that led to the lower-than-expected prey mortality. Consistent with these studies, my laboratory experiment indicated strong behavioural effects; the presence of a large size class dramatically reduced predation rates of smaller predators. In addition, the probability of cannibalism is known to increase with increasing size differences between individuals in the study species (see

Results) (Wissinger 1988, V. H. W. Rudolf, unpublished data). Cannibalism among large cannibalistic size classes was also present in the field experiment, although cannibalism rates did not differ between treatments. Why then were prey mortality rates higher than expected when all three size classes were present?

Increasing the size range within predators can have at least three key effects besides altering mean size (Fig. 1): (i) it could alter behavioural interference among predators altering the per-capita predation rate of individuals (i.e. non-consumptive indirect effects), (ii) it could alter the rate of predation within the predator community (i.e. large predators cannibalizing small predators), leading to indirect 'consumptive effects' (consumptive mediated indirect effects), and (iii) it could increase top-down control if different sized predators have different feeding niches. In the field experiment, interference between predators was present (i.e. cannibalism occurred), and the laboratory experiment indicated that smaller predators alter their behaviour and consumption rates in the presence of large predators. Yet, the higher-than-expected prey mortality at the highest body size diversity suggests that both factors did not substantially reduce prey mortality. It is however possible that behavioural interactions between different size classes increased prey mortality. For example, previous studies (Ferris & Rudolf 2007; Rudolf 2008b) indicated that small predators alter their behaviour in the presence of larger conspecifics. If large predators caused changes in the spatial dispersion of small predators and prey or cause both to use the same refuge/microhabitat, this would increase encounter rates among small predators and prey.

It is also possible that interference is stronger within size classes than between size classes. In that case, reducing the density within a size class would result in an increase in the per-capita predation rate of individuals, leading to higher-than-expected prey mortality (Greig & Wissinger 2010). Given the substitutive experimental design in this experiment, which held total density constant, this scenario would also result in an increase in consumption rate in the mixed predator treatment. However, given that large predators strongly reduced foraging rates of small predators in the laboratory experiment, we would expect that this increase in foraging rate would only occur in the largest predator size class.

Alternatively, niche complementarity (i.e. differences in feeding niches) among different sized predators could have been responsible for increased prey mortality. Previous studies suggest that risk enhancement (i.e. higher-than-expected prey mortality) can arise when predators differ in their microhabitat use (Soluk & Collins 1988; Schmitz 2007). Thus, if different sized predators inherently use different microhabitats, this could explain why the observed mortality was higher than expected when multiple predator size classes were present. Unfortunately, it was not feasible to test for differences in microhabitat use as larvae bury in the substrate and are typically impossible to see in the field experimental set-up. However, different sized individuals often vary in habitat use (e.g. Werner & Hall 1988; Persson & Eklov 1995; Biro, Post

& Parkinson 2003; Rudolf 2006; Rudolf & Armstrong 2008), so it is plausible that this could have been the case in this study as well.

Finally, differences in feeding niches may arise because predation rates vary with the relative body size of predators and prey. In most species, optimal attack rates and preferences change with relative size differences of predator and prey (e.g. Thompson 1978; Mittelbach 1981; Aljetlawi, Sparrevik & Leonardsson 2004). Thus, given a sufficient size distribution in the prey, increasing the size range of predators is likely to increase prey mortality. In this scenario, one would expect that (i) the mean size and size distribution of the prey differ between treatments with single sized predators and (ii) the skewness of prey sizes should differ between treatments with single or multiple size classes. While results indicated significant treatment effects on prey size structure, only the maximum prey size differed between treatments. As expected, maximum prey size decreased as predator size increased when only one predator size class was present. However, maximum prey size was higher in all treatments with mixed predator size classes than in any single predator size class. There was no difference in minimum prey size, skewness or mean prey size among predator treatments. Thus, there is some limited evidence that different sized predators may favour different prey sizes. Although the signal seems weak, this may partly explain why prey mortality was higher than expected when all predator size classes were present. While there was some size variation in the prey, the size range in the prey had to be constrained to avoid cannibalism within the prey. A larger prey size range may have increased predator niche complementarity and resulted in higher prey mortality in mixed predator treatments. Irrespective of the underlying mechanisms, the results clearly show that increasing the size range within predators can increase prey mortality. This suggests that we cannot simply predict prey mortality based on the average body size of predators. Instead, we also need to account for the size distribution within predators.

While the present study used seasonal variation in size within a cannibalistic population as a model system, it is likely that the results apply to many other systems where body size differs between predator species. Empirical data indicate that the ecological variation among size classes within species is often similar or larger than ecological differences between similar sized species within a predator community (Polis 1984; Munoz & Ojeda 1998; Woodward & Hildrew 2002; Rudolf & Armstrong 2008). Focusing on size variation within a species has the benefit that size is the main factor that varies, while most other traits (e.g. general morphology or feeding mode) remain constant. Using different sized species would introduce additional differences between predators, which would make it more difficult to isolate the single effects of body size. However, species may differ in their anti-predator behaviour [including showing no anti-predator response (Greig & Wissinger 2010)], or individuals may respond differently to intra- vs. interspecific predators (Ferris & Rudolf 2007; Rudolf & Armstrong 2008), which

could lead to different indirect interactions and thus consequences of increasing the size variation within a predator community than what I observed in this study. Thus, the next important step will be to test whether the findings of this study hold true across species that differ in other aspects of their biology and whether size variation remains an important predictor despite these differences. Ecologists increasingly recognize that average body size of individuals or species determines dynamics of predator–prey interactions, the stability of complex food webs and dynamics of entire ecosystems (Brose, Williams & Martinez 2006; e.g. De Roos & Persson 2002; De Roos, Persson & Thieme 2003b; De Roos *et al.* 2008; Otto, Rall & Brose 2007; Rudolf 2007a,b). The current study suggests that variation in body size could also be an important conduit that links the effects of changing biodiversity to the functioning of ecosystems.

Classical unstructured predator–prey models assume that the per-capita interaction strength among species is constant. However, almost all species grow during the course of a season. Previous studies have demonstrated that seasonal changes in body size can alter the strength or even the type of species interactions (reviewed in Yang & Rudolf 2010). This study extends previous research by demonstrating that seasonal variation in the size structure of predators can alter the interaction strength between predators and prey, and the effects often cannot be predicted by averaging among size classes. Thus, seasonal changes may result in nonlinear dynamics that cannot be predicted by the average body size during a season. Given the importance of the strength of species interactions for dynamics and stability of complex communities (McCann, Hastings & Huxel 1998), this suggests that seasonal variation in size structure can have important implications for the dynamics of natural communities.

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