Allometric scaling of indirect effects: body size ratios predict non-consumptive effects in multi-predator systems

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Summary

1. Non-consumptive effects (NCES) frequently lead to non-independent effects of multiple predators. While such emergent predator effects are ubiquitous in natural communities, the strength of these effects varies among studies and systems, making it difficult to predict a priory how changes in predator diversity influence prey suppression. Thus, identifying general scaling rules which can explain this variation of non-independent effects is vital for modelling natural communities and how they respond to biodiversity loss.

2. Body size is a key trait determining the nature and strength of ecological interactions. While great progress has been made using allometric relationships to predict the interaction strength of predator–prey pairs, it is unknown whether similar relationships explain variation in the strength of NCEs, and how they are related to consumptive effects.

3. Here, we experimentally manipulate the relative size difference of multiple predators to determine whether NCEs follow general allometric scaling relationships in an aquatic multi-predator system.

4. Results demonstrate that the presence and strength of NCEs can vary dramatically across predator combinations. However, this variation scaled predictably with the size ratio of predators, increasing the size difference among predators increased NCEs. This pattern was driven by a size-mediated shift in 'food web motif' from competition to intraguild predation and a positive correlation of NCEs and intraguild predation rate.

5. Results indicate that models which assume that consumers have independent effects are particularly likely to make erroneous predictions when predators differ substantially in size, but simple allometric relationships of NCEs could be used to correct this bias.

Key-words: biodiversity, interaction modification, intraguild predation, ontogenetic niche shift, trait-mediated, trophic cascade

Introduction

Identifying general scaling relationships that can be used to predict the strength of species interactions and dynamics of natural communities has been a longstanding challenge in ecology. For instance, there has been an increasing effort to identify general allometric relationships that can be used to predict per-capita interaction strength among predator–prey pairs (e.g. Peters 1983; Yodzis & Innes 1992; Cohen *et al.* 1993; Woodward *et al.* 2005a; Hildrew, Raffaelli & Edmunds-Brown 2007; Petchey *et al.* 2008; Brose 2010). However, in natural communities, pairwise interactions can be modified through

non-consumptive effects (NCEs) arising from indirect interactions with other individuals in the community (reviewed in Lima 1998; Werner & Peacor 2003; Schmitz 2007). NCEs are ubiquitous in natural communities (Preisser, Bolnick & Benard 2005) and ignoring them can lead to erroneous predictions on how communities respond to changes in community structure (e.g. Sih, Englund & Wooster 1998; Bolker *et al.* 2003; Schmitz, Krivan & Ovadia 2004; Rudolf 2007). Thus, identifying general relationships that predict the strength of NCEs is critical to develop mechanistic food web models and predict impacts of biodiversity loss.

While previous studies have suggested a number of potential factors that could influence the strength of NCEs (Trussell, Ewanchuk & Matassa 2006; Schmitz

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2007; Grabowski, Hughes & Kimbro 2008), little attention has been paid to the role of body size (but see Rudolf 2006, 2008b,a; Preisser & Orrock 2012; Rudolf 2012). Yet body size is a key trait for predicting the strength and type of species interactions (Woodward *et al.* 2005b; Brose 2010; Miller & Rudolf 2011). For instance, in multi-predator systems, increasing the relative size difference between two predators can shift the 'food-web motif' from competition to intraguild predation (IGP). A further increase in relative size can potentially shift the IGP system to a food chain if one predator stops consuming shared prey (e.g. because the prey is too small to be profitable) (Fig. 1). Such changes in food web motive due to shifts in relative size of consumers are frequent in terrestrial and aquatic system in a variety of taxa (e.g. beetles (Yasuda *et al.* 2004), fish (Persson *et al.* 1999), crustaceans (Maly 1976; Griffen & Byers 2006), dragonflies (Rudolf & Armstrong 2008), salamanders (Boone, Scott & Niewiarowski 2002; Rudolf 2008b), etc.). Indeed, they are likely to occur whenever predators that share resources have overlapping size ranges (Yang & Rudolf 2010; Miller & Rudolf 2011). Importantly, such changes in food web motives can alter the potential for indirect interactions. For instance, if predators consume each other, the concurrent reduction in predator density also reduces their total combined consumption rates and thereby indirectly increase prey survival. Thus, changing the relative size of predators can lead to so called 'emergent multi-predator effects' (MPEs), where the effect of predators is not independent of each other (Ives, Cardinale & Snyder 2005; Casula, Wilby & Thomas 2006; Rudolf 2012).

While such density (consumptive)-mediated indirect effects are well documented, it remains unknown how NCEs scale with relative size of predators. Yet identifying this relationship is imperative to determine the net effect of multi predators on their shared prey. In the absence of NCEs, we would expect that the strength of multiple-predator effects scales positively with the size difference, and thus intraguild predation rate, of predators. However, if NCEs are present this scaling relationship will depend on how NCEs scale with intraguild predation rates. Based on optimal foraging theory, we would expect that increasing the risk of intraguild predation should decrease foraging rates of predators (Lima & Dill 1990; Lima 1998). This should lead to an increase of NCEs with size difference of predators leading to higher than expected prey survival. However, many other scenarios are possible. For instance, if small predators alter habitat use to avoid predation, increasing intraguild predation risk could decrease habitat overlap and thereby reduce predator interference and promote niche-complementarity (Schmitz 2007). This could lead to a reduction of NCEs and thus lower than expected prey survival with increasing size difference. Previous studies have found mixed results for size-mediated NCEs and focused on only two size classes and/or did not estimate risk of intraguild predation (Crumrine 2005, 2010; Griffen & Byers 2006; Rudolf 2006, 2008a,b; Hill & Weissburg 2013). Consequently, it is unclear whether general allometric scaling relationships of NCEs exist and how they influence emergent multiple-predator effects.

Here, we experimentally test the hypothesis that multi-predator effects scale positively with the size ratio of predators and that this relationship is driven by a positive
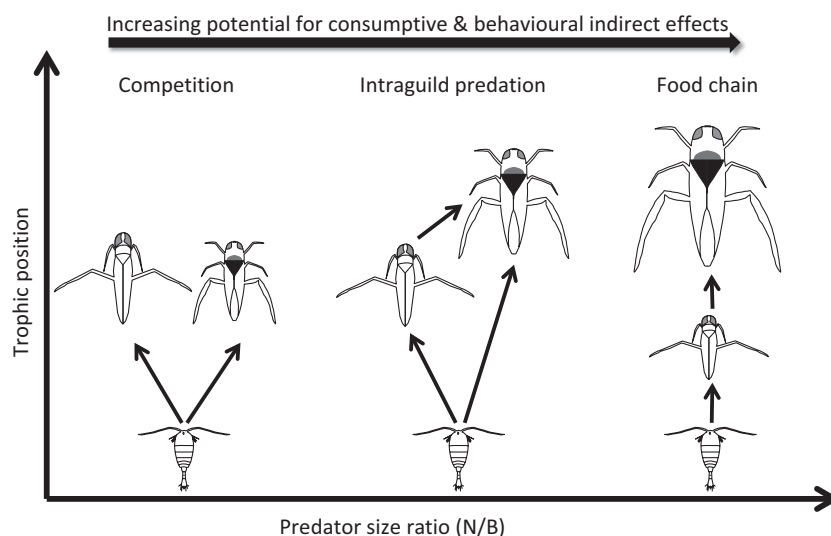

Increasing potential for consumptive & behavioural indirect effects

Competition   Intraguild predation   Food chain

Trophic position

Predator size ratio (N/B)

Fig. 1. Example of size-mediated shifts in food web motif in multi-predator systems. Increasing size differences among predators shifts the system from competition, where both species compete for a common resource, to intraguild predation, where one predator consumes the other predator, to a food chain, where one predator drops the shared pray from its diet and only consumes the other predator. This change from competition to intraguild predation creates the potential for both consumptive (density)- and non-consumptive (e.g. behaviour)-mediated indirect effects which can lead to emergent multi-predator effects (MPEs) of both predators. Example depicts food web motif change observed in this study, where increasing the size of *Notonecta indica* (N) relative to *Buenoa scimitra* (B) increases the risk of intraguild predation, leading to larger than expected survival of their copepod prey when both predators are present.

correlation between NCEs and size-driven intraguild predation rates. In particular, we manipulated the presence and size ratio of two predators to isolate and determine the strength of multiple-predator effects on survival of their shared prey and identify how they are correlated with a change from competition to intraguild predation food web motifs.

Materials and methods

STUDY SYSTEM

We experimentally manipulated the relative size of two aquatic predatory Hemipterans, *Notonecta indica* and *Buenoa scimitra*, which co-occur in local ponds in South East Texas. Each species goes through five distinct instars before reaching the adult stage. Adult *N. indica* is generally larger than *B. scimitra*, with a heavier body build and stronger legs to hold larger prey. While both species consume zooplankton (Murdoch, Scott & Ebsworth 1984; Arnér *et al.* 1998; Hampton, Gilbert & Burns 2000), *N. indica* also readily attacks larger animals, including *B. scimitra*. We used a Calanoid copepod as prey, which was the most dominant zooplankton species, comprising >90% of zooplankton biomass, in our focal ponds at the time of the experiment. The species is an active swimmer in the open water column, and it is readily consumed by both predators. All specimens for this experiment were collected between September 12 and October 12 from one fishless pond at the Center for Environmental Studies, Sam Houston State University, Huntsville, TX.

EXPERIMENTAL DESIGN

We independently manipulated the presence and absence of both predators and their relative size to determine how the relative size differences of predators influence multi-predator effects (MPEs) (Table 1). Depending on the specific question, two experimental designs are commonly used to test for MPEs (and NCEs): additive and substitutive designs (Sih, Englund & Wooster 1998; Griffen 2006). Additive designs keep the densities of species constant across single and multi-species treatments, while substitutive designs keep total predator density constant regardless of how many species are present. Substitutive experiments are designed to test whether species are functionally equivalent. We already knew that species are not substitutable in our system (i.e. *N. indica* eat *B. scimitra* but never the other way round), and we were instead explicitly interest in how adding predators alters prey. Furthermore, substitutive designs would confound biomass effects among treatments given the size differences among predator combinations. Thus, we used an additive design with fixed species density (two individuals/container) rather than a substitutive design.

Size classes were chosen in order to best match sizes between the species (Table 1). We used *B. scimitra* of either instar IV [= small (S): average body length (BL): 3·2 mm, average dry mass (DM): 0·6 mg], instar V [= medium (M): BL: 4·3 mm, DM: 1·5 mg), or adult stage (= large(L): BL: ~5·5 mm, DM: 3·0 mg], and *N. indica* individuals of either instar III of [= medium (M): BL: 3·9 mm, DW: 0·83 mg] or instar IV [= large (L): BL: 5·6 mm, DW: 2·6 mg]. Because of the seasonal change in the size distribution in natural populations, we had to run treatments with medium and large *N.indica* size classes sequentially. To

Table 1. Predator combinations and size classes in the treatments used to determine how non-consumptive effects (NCEs) scale with relative size differences and predation risk of the two predators *Notonecta indica* (N) and *Buenoa scimitar* (B). S = small, M = medium, L = large (adult). Size differences are based on body length which gave the best model fit

Notonecta size class	Buenoa size class	Average body length [mm]/dry mass[mg]	Size difference [(N-B)/N]
0	0[a]		
0	S[a]	3·2/0·6	
0	M[a]	4·3/1·5	
0	L[a]	5·5/3·0	
M	0	3·9/0·8	
L	0	5·6/2·6	
M	S		0·180
M	M		−0·103
M	L		−0·410
L	S		0·429
L	M		0·232
L	L		0·018

[a]These treatments were repeated twice to serve as a control for time effects and reference for each *Notonecta* treatment.

account for potential changes in *Buenoa* or copepods over time, we repeated all single *Buenoa* size treatments and predator-free control treatments for each *Notonecta* size treatment. Thus the study consisted of two 2 (presence or absence of *Notonecta*) × 4 (no, small, medium, or large *Buenoa*) full factorial designs, each with their own controls.

All experiments were performed in plastic containers (L × W × H: 30·5 cm × 17·8 cm × 10·2 cm) filled to a depth of 7 cm with a mixture of filtered pond and RO water. Three artificial plants which covered ~1/3 of the container volume served as refuge and structure for predators. The containers were kept in environmental chambers at 24 °C under a 13:11 h light/dark photoperiod. The experimental containers were checked three times per day, every six hours during the day and every 12 h overnight, at which point moulted and dead individuals were replaced, and *B. scimitra* mortality was noted. We found that intraguild predation generally did not occur during the dark cycle. Replacing dead individuals allowed us to estimate intraguild predation while removing or at least strongly reducing any indirect consumptive effects (i.e. due to reduction in predator density, see Discussion) to isolate the strength of non-consumptive effects (e.g. due to changes in IG prey behaviour) in the system. The experiment was terminated after 36 h, when all predator and prey specimens were removed and counted. The duration of the experiment was based on pilot studies and assured enough time to significantly reduce prey levels without the risk of depleting prey in any treatment. All backswimmers were starved 24 h prior to the start of the experiment to equalize hunger levels, and 100 copepods served as shared prey. Each treatment was replicated 10 times (split into three temporal blocks with 3–4 replicates per treatment for logistic reasons).

STATISTICAL ANALYSES

Prey survival

We tested how predator identity and size affected proportional prey survival with a GLM analysis, with *N. indica* and *B. scimitra*

treatments as fixed effects and binomial error distribution corrected for over dispersion. Because copepod survival and *B. scimitra* consumption rates differed significantly among *N. indica* size treatments, we treatments with medium and large *N. indica* separately.

Intraguild predation

To confirm that *N. indica* influences *B. scimitar* survival, we used a GLM with the number of dead *B. scimitra* as dependent variable and the *N. indica* and *B. scimitra* size class as fixed factors. There was no significant ($P = 0.391$) difference in survival rates of *B. scimitra* in the absence of *N. indica* between both *N. indica* size treatments (see 'experimental design' above). Thus, we pooled both sets of experiments for this analysis. To account for heterogeneity in variances among size treatments, we used a GLM approach that modelled different variances for the respective treatments using a likelihood estimation in the 'proc mixed' procedure in SAS and corrected the degrees of freedom using the Kenward–Roger correction (Littell *et al.* 2006). Then, we determined whether and how differences in body size among predators scale with intraguild predation rates using a GLM with binomial distributed error terms with size-specific mortality risk of *B. scimitra* [no. of *B. scimitra* dead with *N. indica* in size class j – average (no. of *B. scimitra* dead in absence of *N. indica*)] as dependent variable and size difference (body length (BL) *N. indica* – BL *B. scimitra*) as independent variable. A similar analysis with dry mass differences provided similar results (not shown), but body length (BL) differences provided a much better fit of the model. *Notonecta* size (and corresponding interaction terms) was not significant, so we dropped it from the final analysis.

Multiple-predator effects (MPEs)

To determine whether MPEs are present and how they scale with the size ratio of predators, we used an independent (multiplicative) risk model to calculate expected proportional survival rates of prey as: $\hat{C}_{Nj+Bj} = (C_{Nj}*C_{Bj}/C_0)$, where C_{ij} indicates the proportion of surviving prey in the specific predator treatments [$i = Nj$: *N. indica* of size class j (L or M), $i = Bj$: *B. scimitra* of size class j (L, M, or S), $i = 0$: predator-free control] (Vonesh & Osenberg 2003). Following previous studies (e.g. Trussell, Ewanchuk & Matassa 2006), the numerator is provided by each replicate of a given predator combination, while the denominator is always the average of all predator-free controls within a block. We then calculated the strength of MPEs on prey survival as the log ratio of observed versus expected prey survival as MPE = ln $(C_{Obs(Nj+Bj)}/\hat{C}_{Nj+Bj})$. This statistic is one of the least-biased metrics for comparing effect sizes with several desirable statistical properties (Hedges, Gurevitch & Curtis 1999). It is also easy to interpret with a clear biological meaning in our system: zero indicates no MPEs, negative values indicate lower than expected prey survival ('risk enhancement') while positive values indicate the opposite ('risk reduction').

We tested whether MPEs scaled with the probability of intraguild predation (i.e. size-specific mortality risk of *B. scimitra*, see above) or predator size difference (see above) and block as random factor using GLM analyses with normal distributed error terms. Initial GLM included *N. indica* size as fixed effects, but *N. indica* size or its interaction with other fixed effects was never

significant and therefore dropped from the final analysis. Because we could not instantly replace dead predators, it is possible that a short-term reduction in predator density was at least partly responsible for the observed MPEs. Thus, we calculated the total predator hours (TPH) for a given tank (= total hours predators were alive, summed for both predators). This was performed by assuming that individuals were on average consumed half way between checks (e.g. if a predator was consumed during a six hour period, we subtracted 3 h from the total predator hours). We then tested whether there was any significant relationship between TPH and MPEs across all treatments. Changing the assumption about when individuals were killed (e.g. beginning, middle or end of the 6-h period) did not change the results. Since we believe that the mean is the biological most realistic scenario, we only present these results here. Unless stated otherwise, all GLM analyses were carried out with 'proc glimmix' statement in SAS, and all data met underlying assumptions. All figures are based on back-transformed data for ease of interpretation.

Results

PREY SURVIVAL

The proportion of prey surviving was significantly affected by the size class of *B. scimitra* ($F_{3,67} = 83.4$, $P < 0.0001$), the presence/absence of large *N. indica* ($F_{1,67} = 91.2$, $P < 0.0001$), and the interaction of both ($F_{3,67} = 24.0$, $P < 0.0001$) (Fig. 2). The same pattern was observed in trials with medium-sized *N. indica* (*B. scimitra* size: $F_{3,70} = 176.5$. $P < 0.0001$, *N. indica* presence/absence: $F_{2,70} = 130.7$, $P < 0.0001$, *B. scimitra***N. indica*: $F_{3,70} = 17.33$, $P < 0.0001$). In both species, each predator size class
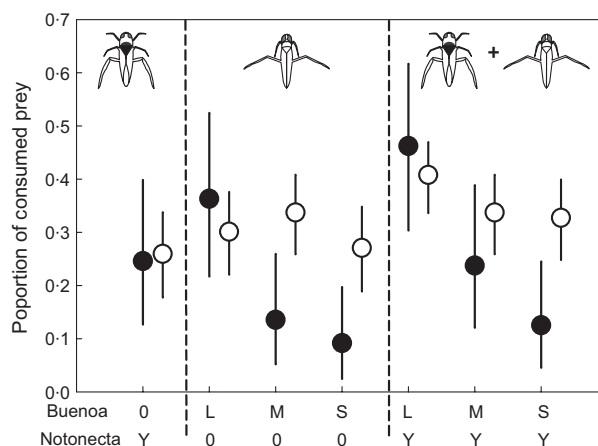

Fig. 2. Mean (with 95% CI) proportion of copepod prey consumed as a function of presence and size class/stage of two predators, *Notonecta indica* and *Buenoa scimitar*. *Buenoa scimitra* was either absent (0) or present at three differently sized stages (large (L), medium (M), small (S)). *N. indica* indicates whether this species was present (Y) or absent (0). Filled and open circles indicate experiments with medium or large *N. indica*, respectively. Treatments are standardized relative to prey survival in their respective predator-free controls. Values are back-transformed estimates from GLM with binomial distribution and logit-link function.

significantly reduced prey survival compared with the control (all $P < 0.0008$) (Fig. 2). In both treatments, the interaction was largely driven by the fact that adding *N.indica* to large *B. scimitra* treatments increased mortality more than adding it to treatments with medium or small *B. scimitra* relative to the respective single *B. scimitra* treatments.

RISK OF INTRAGUILD PREDATION

Buenoa scimitra mortality was significantly affected by *B. scimitra* size treatment ($F_{2,33} = 22.7$, $P < 0.0001$), *N. indica* treatment ($F_{2,39.2} = 46.1$, $P < 0.0001$) and their interaction ($F_{4,31.2} = 5.9$, $P = 0.0011$). Post hoc comparisons showed that *B. scimitra* mortality was on average significantly higher in treatments with large *N. indica* compared to treatment with medium-sized *N. indica* ($P < 0.0001$), and both treatments differed significantly from the control without *N. indica* present (both $P < 0.0013$). Overall, mortality decreased significantly with increase in relative size of *B. scimitra* stages versus *N. indica* ($F_{1,58} = 13.7$, $P < 0.0005$) (Fig. 3a), but did not change with size in control treatments without *N. indica*, indicating that the risk of intraguild predation was size specific.

SCALING RELATIONSHIPS OF EMERGENT MULTI-PREDATOR EFFECTS (MPES)

In general, all MPEs were positive, indicating higher prey survival than expected from a null model assuming that predators had independent effects when both co-occurred. MPEs significantly increased with the average risk of intraguild predation ($F_{1,58} = 7.6$, $P = 0.0072$) (Fig. 3b). Similarly, MPEs significantly increased with increasing size difference between *N. indica* and *B. scimitra* ($F_{1,58} = 5.9$, $P = 0.0182$) (Fig. 3c). Importantly, we found no significant relationship between reduction in predator density (i.e. total predator hours, see methods) and the strength of MPEs ($R^2 = 0.0001$, slope $= -0.00048$, $P = 0.930$) indicating that this pattern was largely driven by NCEs.

Discussion

Predicting how the addition or loss of predator species influences prey suppression is challenging because consumptive and non-consumptive effects (NCES) frequently lead to non-independent effects of predators which vary among systems (Preisser, Bolnick & Benard 2005; Vance-Chalcraft & Soluk 2005; Schmitz 2007). Thus, identifying general scaling rules of non-independent effects would be invaluable for modelling natural communities and how they respond to changes in biodiversity. Consistent with previous studies (Sih, Englund & Wooster 1998; Vance-Chalcraft & Soluk 2005; Schmitz 2007), our results demonstrate that the joint effects of predators are often less than expected based on models assuming independent predator effects but the presence and strength of these
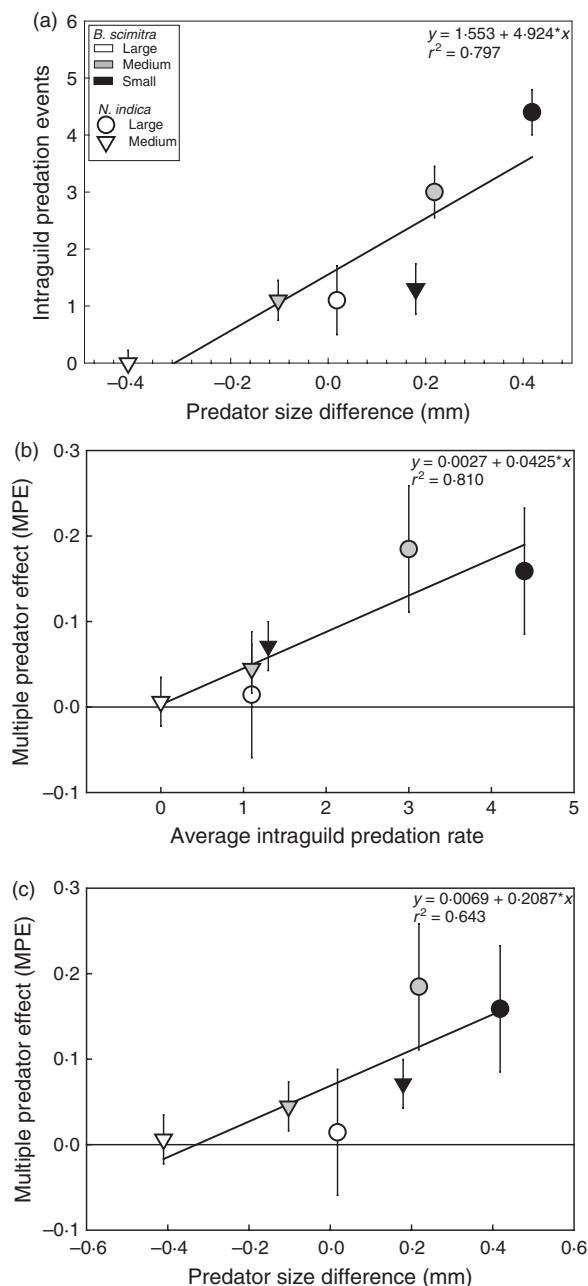

Fig. 3. (a) Mean ($\pm$ 1SE) number of intraguild predation events (no. dead *Buenoa scimitra* with *Notonecta indica* – average no. dead *B. scimitra* in respective control) as a function of the average difference in body length between the two predators *N. indica* and *B. scimitra*; positive values indicate that *N. indica* is larger than *B. scimitra*. (b–c) Relationship between mean ($\pm$ 1SE) emergent multi-predator effect and (b) average intraguild predation rate and (c) average difference in body length between the two predators *N. indica* and *B. scimitra*. Triangles and circles indicate treatments with medium or large stages of *N. indica*, respectively, open, grey and black symbols indicate treatments with large stage (L), medium stage (M) and small stage (S) of *B. scimitra*, respectively. Black lines indicate the significant relationship between relative predator size or intraguild predation rate and non-consumptive effect.

emergent multiple-predator effects (MPEs) varied dramatically across different predator combinations, even though the species identity of predators remained unchanged. However, this variation scaled predictably with the size ratio of predators, increasing the size difference among predators increased the strength of MPEs. Importantly, because we experimentally reduced indirect effects through changes in predator density, this pattern was largely driven by a positive relationship of non-consumptive effects with intraguild predation risk and predator size difference. Our additive design is also expected to underestimate the magnitude of the risk reduction because of prey depletion, suggesting that our NCE estimates are conservative (McCoy, Stier & Osenberg 2012). This indicates that models based on independent predator effects are particularly likely to make erroneous predictions when predators differ substantially in size. However, our results suggest that this bias could be corrected using simple allometric scaling relationships of NCEs.

The positive relationship between MPEs and the size ratio of predators reflects the transition from a competitive to an intraguild predation system (Fig. 1). When the intermediate predator was large enough to prevent intraguild predation, both predators acted as competitors and their effects were additive. However, once the size ratio of both predators exceeded a certain threshold, intraguild predation occurred and increased linearly with increasing size differences among predators. Importantly, the increase in intraguild predation rate was positively related to the strength of MPEs, emphasizing the importance of accounting for size-mediated shifts in species interactions (Miller & Rudolf 2011; Rudolf 2013).

In our experiment, we aimed to isolate the strength of non-consumptive indirect effects (NCEs) by replacing killed predators. Because it was logistically not feasible to replace them instantly, predator density was temporarily reduced. However, we found absolutely no correlation between effective predator density (i.e. total predator hours) and the strength of the MPEs. Importantly, these results are robust to the underlying assumption of when individuals were killed. In contrast, mortality risk (i.e. average number of predator consumed) was a highly significant predictor, clearly indicating that NCEs but not changes in predator density were responsible for this pattern. The habitat complexity in our setup provided predators with potential refuges which are often important for NCEs (Trussell, Ewanchuk & Matassa 2006), but it also obscured the view of observers preventing us from accurately monitoring potential changes in predator behaviour. However, many studies have identified potential pathways leading to NCEs (Werner & Peacor 2003; Schmitz 2007) and even identified what cues are used to distinguish between different sized predators (Hill & Weissburg 2013). Yet, to the best of our knowledge, no previous study has systematically determined whether general relationships exist between NCEs and predator size differences which was the focus of this study. Thus, it was more important for us to make the

experimental setup as realistic as possible to estimate the strength of NCEs and their relationship with predator size rather than identifying the system-specific pathways for NCEs. While identifying the exact mechanisms underlying NCEs was outside the scope of our study, results suggest that *B. scimitra* decreases its foraging rate with increasing risk of predation. Such size-specific changes in behaviour have been observed in backswimmers and many other species (Sih 1982; Persson & Greenberg 1990; Biro, Post & Parkinson 2003; Griffen & Byers 2006; Rudolf 2006, 2008a, b; Rudolf & Armstrong 2008). While we cannot exclude other potential mechanisms (e.g. change in prey behaviour, prey switching, etc.), this change in feeding behaviour would be consistent with optimal foraging theory (Lima & Dill 1990) and provide one possible explanation for why NCEs increased with risk of intraguild predation, rather than with the actual mortality in a given treatment.

Body size ratios are known to strongly influence consumer–resource interactions and food web dynamics (reviewed in De Roos, Persson & McCauley 2003; Woodward *et al.* 2005a; Miller & Rudolf 2011), but they have received surprisingly little attention when studying NCEs (Rudolf 2013). Yet, NCEs can result in trophic-level effects that frequently rival or even exceed consumptive effects (Schmitz, Beckerman & Obrien 1997; Preisser, Bolnick & Benard 2005). Thus, identifying how NCEs scale with body size differences is imperative if we want to accurately predict the impact of multiple predators on prey using general allometric relationships. To the best of our knowledge, our study is the first to show a clear relationship between the size ratio of multiple predators and the strength of NCEs. Previous studies have found mixed support for size-specific NCEs (Griffen & Byers 2006; Rudolf 2006, 2008a, 2012; Preisser & Orrock 2012) and typically only focused on two size classes. One meta-analysis, however, looked at a size range across different species and did not find a clear relationship between NCEs and prey survival (Preisser & Orrock 2012). While this may seem in contrast with our results, we suggest that there is no reason to believe that there is a universal scaling relationship of NCEs and size ratios. The ultimate cause for NCEs in predator–prey systems is the risk of predation (i.e. fitness cost) and the size differences of species simply serves as a proxy for this risk. Importantly, how predation scales with the size ratio of species depends on specific life-history traits of individuals. For instance, some predators have to swallow prey whole (e.g. many fish, salamander and bird species) which requires that they are substantially larger than their prey, while predators that can chew or pierce (and suck-out) their prey can even be smaller than their prey (as in our study). Thus, how the risk of predation scales with predator: prey size ratio varies among systems (Nakazawa, Ohba & Ushio 2013) and the same should apply for NCEs. Such differences in life-history traits across species could explain why some systems exhibit size-specific NCEs but others do not given the same size difference (Griffen & Byers 2006). We used

different size classes of the same species to assure that feeding modes and thus scaling relationships did not vary among different predator size combinations. Consequently, we found that predation risk clearly increased with increasing predator size ratios, which explains why we observed a strong relationship between the size ratio and the strength of NCEs. Our results also indicate that when predation risk does not increase sufficiently with size differences, NCEs will not change much either (Fig. 2). Unfortunately, while previous studies have suggested that the risk of predation could be an important factor driving the strength of NCEs, they did not test it explicitly (e.g. Vance-Chalcraft & Soluk 2005; Griffen & Byers 2006; Preisser & Orrock 2012). Future studies which examine how NCEs scale with size and predation rates across a range of species that differ in feeding mode and gape limitation will provide important insight into how general allometric scaling relationships of indirect interactions are and how they vary with species traits. Only then can be proceed to use size-based approaches to model the complex dynamics of natural communities.

Acknowledgements

Data accessibility

All data associated with the study are freely available online at the Dryad Digital Repository: http://doi.org/10.5061/dryad.276j5 (Krenek & Rudolf 2014).

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