

LETTER

Resource dynamics influence the strength of non-consumptive predator effects on prey

Evan L. Preisser,^{1*} Daniel I. Bolnick² and Jonathan H. Grabowski³

¹Department of Biological Sciences, University of Rhode Island, Kingston, RI 02881, USA

²Section of Integrative Biology, University of Texas at Austin, One University Station C0930, Austin, TX 78712, USA

³Gulf of Maine Research Institute, 350 Commercial Street, Portland, ME 04101, USA

*Correspondence: E-mail: preisser@uri.edu

Abstract

Predators influence prey populations both by consuming individual prey, and by inducing changes in prey behaviour that limit reproduction and survival. Because prey trade-off predation risk for foraging gains, the magnitude of predators' non-consumptive effects should depend on resource availability. Studies of non-consumptive effects generally adopt either of two strategies: (i) maintaining a static ration of the prey's resources; and (ii) using resource populations that vary dynamically in response to prey behaviour. Contrasting these experimental designs using meta-analysis, we evaluated whether resource dynamics influence the magnitude of non-consumptive effects on prey growth, survival, fecundity, population density, foraging rate and habitat use. Predators had a more negative effect on prey demography in dynamic- vs. static-resource experiments. Our results highlight the importance of resource dynamics in mediating the magnitude of non-consumptive effects of predators on prey, and illustrate the often-unintended impacts of experimental design on estimates of effect size in ecological interactions.

Keywords

Context-dependence, non-consumptive effects, predation, tritrophic interactions.

Ecology Letters (2009) 12: 315–323

INTRODUCTION

The threat of predation often leads prey to adopt a variety of defensive tactics (Abrams 1984; Lima & Dill 1990; Werner & Peacor 2003; Schmitz *et al.* 2004). These anti-predator defenses can be costly. For example, prey that reduce their foraging rates to avoid predators may incur reduced energy income, greater starvation risk, reduced mating success, or increased vulnerability to other kinds of predators (Preisser & Bolnick 2008). Because these costs may influence prey population dynamics, predators can reduce prey abundance through both non-consumptive effects (NCEs, also sometimes called trait-mediated effects or non-lethal effects) as well as the consumptive effects (CEs) more commonly studied by ecologists (Werner & Peacor 2003; Schmitz *et al.* 2004; Abrams 2007). NCEs can be a major component of predator-prey dynamics (Preisser *et al.* 2005), because all members of a prey population may adopt costly defenses even though only a few individuals might actually be killed by a predator. Distinguishing NCEs from traditional CEs may be important because the two effects may operate at different time scales and have very

different consequences for population stability (Abrams 1990), spatial dynamics (Abrams 2008b), energy flows through ecosystems (Schmitz *et al.* 2008), and possibly evolution (Rundle *et al.* 2003).

Given the potentially large impact of NCEs in predator-prey interactions, it is useful to identify settings in which NCEs are likely to be more or less pronounced. The magnitude and even the direction of NCEs may be contingent on many factors, including (but not limited to) resource abundance (Abrams 1984, 1991; Peacor 2002; Luttbeg *et al.* 2003; Bolnick & Preisser 2005), predator hunting mode (Preisser *et al.* 2007), predator and prey life history characteristics (Abrams 1991), and the spatial and temporal scale over which an NCE is measured (Peacor & Werner 2004a; Abrams 2008b). Resource abundance may alter NCE magnitude (Bolnick & Preisser 2005), for instance, because prey balance predation risk vs. foraging rewards (Abrams 1991). However, the impact on resource abundance on NCE magnitude is not straightforward. It may be, for instance, that greater resource availability allows prey to satisfy basic energetic needs more quickly, reducing the fitness costs of reduced foraging effort. Alternatively,

however, greater resource availability may also increase the opportunity cost of reduced foraging effort, thereby magnifying the difference in energy income between individuals that do or do not curtail their foraging.

Because a predator's NCE on prey depends on resource availability, any resource population dynamics should modify the magnitude of NCEs. For example, Peacor (2002) showed that tadpoles exposed to predator cues greatly reduced their foraging activity. The reduced grazing activity released algae from top-down control, causing such a large increase in algal density that the positive effect of increased food abundance on tadpole growth more than offset the negative effect of tadpoles' reduced foraging effort on tadpole growth. Predators thus actually had a positive NCE on prey growth rate, mediated by changes in prey behaviour and subsequent resource dynamics. Alternatively, NCEs may be exacerbated if changing prey behaviour leads to declining resource densities. For instance, grasshoppers exposed to predatory spiders shifted from high-quality grasses onto safer but less nutritious forbs (Schmitz *et al.* 1997). Forb biomass then declined while grasses increased, further reducing grasshopper survival (Schmitz 1998). These case studies illustrate that resource dynamics can either mitigate or exacerbate the negative impact of predation risk on prey populations. We therefore used a meta-analysis of published experiments to evaluate whether the preponderance of examples suggest a general trend towards negative or positive effects of resource dynamics on NCEs.

To evaluate the effect of resource dynamics, we took advantage of a basic dichotomy in how NCE experiments are conducted. Studies of NCEs generally entail at least two experimental treatments: a predator-free control, and a predator-risk treatment in which the prey are exposed to predator cues (usually visual and/or olfactory). Predators in predator-risk treatments are isolated from their prey so that prey perceive risk but cannot be eaten. The between-treatment differences in behaviour (feeding rate, use of refuges) and/or life history parameters (growth, survival, fecundity, population density) measure the NCE of predation risk on prey (but see Abrams 2008a,b for important caveats about this experimental design). In these experiments, the prey may be supplied either with a set ration of food resources (e.g., a fixed quantity of artificial food), or may be left to feed on resource populations (algae, bacteria, etc.) that can reproduce and show dynamic responses to consumption. The former design (static rations) does not permit feedbacks between prey behaviour and resource availability. Consequently, contrasts between experiments with rationed ('static') vs. dynamic resources can evaluate whether resource dynamics have a consistent effect on NCE magnitude. We therefore tested for differences in mean NCE magnitude between static-resource and dynamic-

resource experiments. We emphasize that the exact magnitude of such differences will depend on the study systems and details of experimental designs in the published literature (e.g., time-scales, spatial scales, taxonomic focus, predator densities). Consequently, we focus less on the effect size *per se* and more on whether there is a general across-taxa difference in effect size between studies with static vs. dynamic resources.

METHODS

We assembled and analysed a database of 1002 measurements of NCE magnitude drawn from 214 published papers, recording the mean response from control (predator-free) and predator-risk (risk cue) treatments, along with sample sizes, and standard deviations. The database includes a nearly exhaustive collection of studies of NCEs from the ecological literature from 1970 through 2005, and is available through the National Centre for Ecological Analysis and Synthesis (<http://knb.ecoinformatics.org/knb/metacat/nceas.873.24/nceas>). The database, search methods and response variables are described in more detail elsewhere (Bolnick & Preisser 2005; Preisser *et al.* 2005, 2007). Information about each study (effect sizes, sample sizes, etc.) were checked by at least two people. We categorized studies as static if a constant or renewed supply of resources were provided throughout the experiment. Dynamic resources included any study with living resources whose densities were allowed to fluctuate. Thirty-six published papers that could not clearly be assigned to one of these designs were excluded from our analyses. The data analysed in this paper is provided in the Supporting Information.

We subdivided the database into sets of studies with biologically equivalent response variables (all measured on the prey population): population density, survivorship, fecundity, somatic growth rates, foraging rate and habitat use (% of time spent outside of refuge habitats). We analysed each of these response variables separately using the software package MetaWin (Sinauer Associates, Inc. Sunderland, MA, USA) (Rosenberg *et al.* 2000), calculating a log response ratio (lnRR) for each study and then calculating separate response ratio (RR) means for static- and dynamic-resource experiments (Hedges & Olkin 1985; Gurevitch & Hedges 1999; Hedges *et al.* 1999). In discussing our results, we report the RR rather than its logarithm to make it easier to intuit difference in effect sizes; RR ratios of one represent no difference in response means between experimental (predator risk) and control (no predator) treatments. Conversely, $RR < 1$ (or > 1) indicates that the measured variable is lower (or greater) in predator risk treatments than in the control. The magnitude of RR indicates the size and direction of the between-treatment difference; for example, $RR = 0.5$ indicates that

the response variable is 50% lower in the predator risk treatment than in the control, whereas $RR = 1.5$ indicates a 50% increase in the response variable in the predator risk treatment.

We tested for significant differences between static and dynamic resource experiments using a random-effects Q -statistic of among- vs. within-group heterogeneity, with the P -value calculated from a chi-square distribution (for details of the statistical model, see Rosenberg *et al.* 2000). Using the random effects model reflects our assumption that there is no single correct NCE effect, but rather a distribution of effects. We used a normal quantile plot in MetaWin to confirm that the data fit a normal distribution. In cases with a non-normal distribution, we also report P -values generated using a randomization procedure (Rosenberg *et al.* 2000). In the two cases with moderate departures from normality, the randomization procedure yielded qualitatively similar P -values to the parametric analysis. We also used a random-effects model to estimate 95% CI for the mean effect size of the two experimental designs, and to check whether these intervals included the null expectation of $RR = 1$ (no effect). We performed three parallel analyses on subsets of the dataset that were restricted to prey species in the class Amphibia only, the class Insecta only, and the class Branchiopoda only; these represent respectively the first, second, and third most abundant classes of prey organisms in our database. This set of analyses assessed the potential for a confounding effect of taxa and resource type. In particular, if we observe the same differences between static and dynamic NCEs within taxa, as we observe across the whole database, we can be confident our results are fairly general. It should be noted that some response variables had too few observations within a particular taxonomic group to justify analysis: studies with amphibian prey, for instance, rarely measured individual fecundity. Because other taxa in the database had relatively few case studies in three or more of the six response variables, we did not have sufficient statistical power to justify additional analyses of specific taxa.

We also tested the hypothesis that the results of dynamic resource experiments show greater variation over time than do the results of static resource experiments. This analysis would ideally take into account both prey and resource generation times, as well as the ratio of experimental duration to resource generation time. Since resources are rarely identified to species, however (for instance, many papers refer only to periphyton or zooplankton), a detailed analysis of this sort proved impractical. As a result, we chose to analyse the relationship between mean effect size and experimental duration (in days) for (1) all dynamic resource experiments that employed periphyton, the most common dynamic resource in our database, as the basal resource; and (2) all static resource experiments. We performed these

analyses in MetaWin using weighted least squares regression with experimental duration as a random effect (reflecting our assumption that there is a true random component of variation in effect sizes between studies; Rosenberg *et al.* 2000). Finally, we used the same technique to test whether response ratios in static- and dynamic resource experiments were affected by stochasticity related to prey population size, i.e., for a potential relationship between mean effect size and the number of prey individuals per experimental replicate (coded as a random effect).

Some sets of observations within the database are not fully independent, having been measured on either the same predator-prey species pair or on closely related taxa. There is no generally established solution for this pseudoreplication. Averaging all studies for a given predator-prey species pair may gloss over ecologically important variation in effect sizes arising from different experimental temporal or spatial scales, densities, season, geography, etc. In addition, averaging studies within a given predator-prey pair does not actually eliminate pseudoreplication because of the potential for phylogenetic non-independence among different predator and prey species. Existing methods that account for phylogenetic non-independence are unable to deal with interacting sets of species with incongruent phylogenetic trees. Consequently, we report an analysis of all effect size estimates rather than a summary estimate for each predator-prey species pair. To confirm that no single species or experiment makes up a large enough proportion of effect sizes in our database to create a strong bias, we reran all analyses sequentially omitting the three prey species with the largest number of effect size estimates. Because the qualitative results (significance, or direction of effects) remained unchanged, we report an analysis of the full dataset.

RESULTS

Non-consumptive effects strength differed between experiments employing static vs. dynamic resources. For every response variable examined (prey density, survival, fecundity, growth, feeding rate and habitat use), predators exerted a stronger negative effect on prey ($RR < 1$) when resources were dynamic than when resources were static (Fig. 1 upper panel, Fig. 2 upper panel), though this difference was not significant for behavioural traits (feeding rate and habitat use). This same trend occurred when we analysed data from the three most abundant prey classes separately: the Amphibia (Fig. 1 lower panel, Fig. 2 lower panel), Insecta, and Branchiopoda also recorded stronger negative effects of predators in dynamic vs. static resource experiments. Since the three classes did not differ in their qualitative response to static- vs. dynamic-resource experiments, we present and discuss only the results from the most abundant prey class

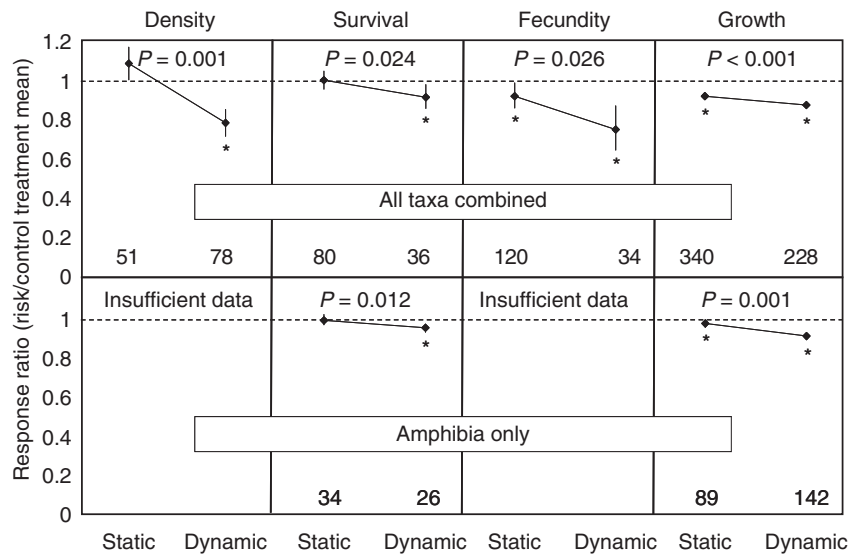


Figure 1 Mean response ratios for traits likely to directly influence prey population dynamics (prey population density, survival, fecundity and somatic growth rates). Top row: all prey taxa combined; bottom row: Amphibia prey only. Sample size and mean \pm 95% CI are provided separately for static- and dynamic-resource experiments. P -values are based on a test of the null hypothesis that static and dynamic resource studies have similar mean effect sizes. P -values are calculated using a chi-square approximation except in cases where the effect sizes were non-normally distributed, in which case P -values from a randomization test are reported (see text). A horizontal line at RR = 1.0 represents the case of no non-consumptive effect, where predator-cue and predator free treatments have similar means. Asterisks next to each mean effect size indicate whether the mean is significantly different from a null value of RR = 1.0.

(Amphibia). The similarity of within-taxon to across-taxon trends suggests that our findings are not an inadvertent result of confounding study taxon with static vs. dynamic resources.

Non-consumptive effect strength in studies measuring prey population density differed between static and dynamic-resource experiments (Fig. 1; χ^2 : $P < 0.0001$; randomization: $P = 0.001$). When resources were not dynamic, prey population density was on average 8.8% higher in predator-risk vs. control treatments (RR = 1.080), although this did not differ significantly from the null hypothesis of no overall effect (95% CI: 0.97–1.175). In contrast, when resources were able to respond dynamically, prey population density in predator-risk treatments averaged 21.5% lower than in the control treatments (RR = 0.785; 95% CI: 0.719–0.856).

Prey survival was unresponsive to predation risk when resources were static (RR = 1.006; CI = 0.962–1.05). In studies with dynamic resources, however, prey survival averaged 8% lower in predator-risk treatments compared to controls (RR = 0.920, CI = 0.860–0.983). The difference between static vs. dynamic resources was significant using the chi-square approximation (Fig. 1; $P = 0.024$) but non-significant with the randomization test ($P = 0.189$). Estimated effect sizes were normally distributed, so the more powerful chi-square test should be valid. Amphibian survival followed the same trend: survival in predator-risk

treatments was lower in dynamic resource experiments (RR = 0.963, CI = 0.943–0.984) but not in static resource experiments (RR = 1.004, CI = 0.978–1.032). The difference between static and dynamic resource treatments was significant using both the chi-square approximation ($P = 0.012$) and the randomization test ($P = 0.008$).

Studies of prey fecundity found that reproductive rates declined by 6.8% (relative to a risk-free control) with predation risk and static resources, compared to a 24% decline when resources were dynamic (Fig. 1; static RR = 0.932, CI: 0.869–0.999; dynamic RR = 0.760, CI = 0.654–0.882; χ^2 : $P = 0.012$; randomization $P = 0.026$). Results were non-normally distributed for fecundity, so the randomization P -value is more appropriate.

Prey growth rates showed a similar trend. When resources were static, predation risk reduced somatic growth by 7.7% (relative to a control), compared with 12.3% when resources were dynamic (static RR = 0.924; CI = 0.909–0.940; dynamic RR = 0.877; CI = 0.858–0.897). This amounts to a roughly 60% increase in the magnitude of NCEs on prey growth (Fig. 1; χ^2 : $P = 0.0002$; randomization $P = 0.021$). The Amphibia-only results again agreed with the all-taxon analysis (static RR = 0.979; CI = 0.960–0.997; dynamic RR = 0.916; CI = 0.902–0.930), and there was a significant difference between static and dynamic resource treatments in the predicted direction in both the chi-square approximation ($P < 0.001$) and the randomization test ($P = 0.005$).

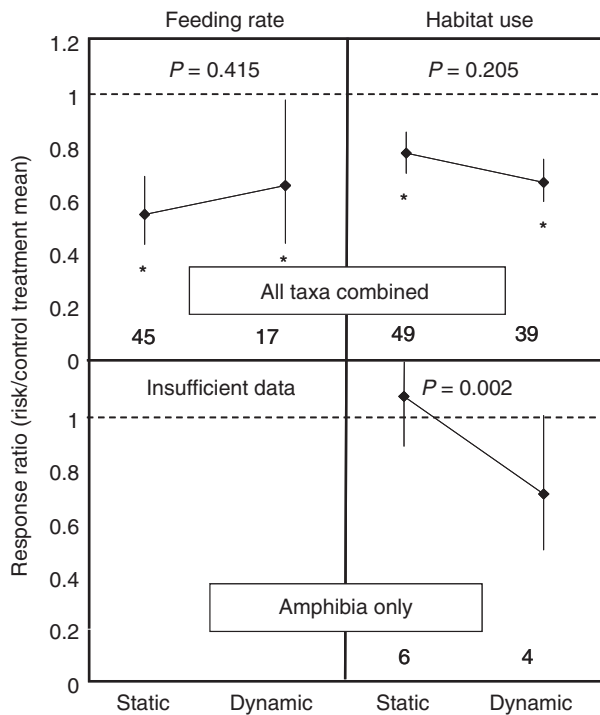


Figure 2 Mean response ratio for prey foraging behaviour traits (foraging rate, habitat use). Top row: all prey taxa combined; bottom row: Amphibia prey only. Sample size and mean \pm 95% CI are provided separately for static- and dynamic-resource experiments. *P*-values are based on a test of the null hypothesis that static and dynamic resource studies have similar mean effect sizes. *P*-values are calculated using a chi-square approximation except in cases where the effect sizes were non-normally distributed, in which case *P*-values from a randomization test are reported (see text). A horizontal line at RR = 1.0 represents the case of no non-consumptive effect, where predator-cue and predator-free treatments have similar means. Asterisks next to each mean effect size indicate whether the mean is significantly different from a null value of RR = 1.0.

In contrast to the life-history metrics described above, measures of prey behaviour showed little difference between static and dynamic experiments although the trends were in the same direction (Fig. 2). Predation risk substantially reduced prey foraging rate relative to risk-free controls (Fig. 2), but there was no significant tendency for this NCE to be stronger in dynamic- vs. static-resource studies (static RR = 0.650, CI = 0.438–0.963; dynamic RR = 0.544, CI = 0.432–0.684; χ^2 : *P* = 0.415; randomization *P* = 0.485). We had relatively few studies of foraging rates in our database, because we only recorded behaviour effect sizes for studies that also reported life-history effect sizes. Consequently, this particular result has fewer case studies (*n* = 17 and 45 for static and dynamic designs, respectively) and lower power.

Predation risk had a general tendency to reduce prey use of non-refuge (risky) habitats relative to risk-free controls (Fig. 2, RR < 1). In static resource experiments, predation risk reduced use of risky habitats by 21.9% (RR = 0.781, CI = 0.6584–0.901). In dynamic resource experiments, this reduction was even larger (RR = 0.674, CI = 0.5672–0.779). A parametric random-effects model found a marginally significant difference between static and dynamic resource studies (χ^2 : *P* = 0.052), whereas the trend was non-significant with a randomization test (*P* = 0.205). Because the normal quantile plot showed some departure from normality, the parametric test is suspect and we do not conclude that there is an appreciable habitat use difference between static and dynamic resource studies. In contrast, a separate analysis of Amphibia revealed that dynamic resource experiments showed stronger effects of predator risk than did static resource experiments regardless of whether a χ^2 approximation (*P* = 0.002) or a randomization test (*P* = 0.007) was used.

Prey demographical variables (density, survival, fecundity and growth) varied more over time in dynamic vs. static resource experiments (Table 1). In dynamic resource experiments, the effect of predation risk on prey survival, fecundity and growth increased significantly over time (Table 1; all *P* < 0.05) and only density was unaffected. Static resource experiments showed no relationship between experimental duration and NCEs on prey density, survival and fecundity (all *P* > 0.05), despite the fact that time and the effect of predation risk on growth were significantly correlated (*P* < 0.001).

Prey density, survival, and fecundity showed no relationship between mean effect size and the number of individuals per replicate (all *P* > 0.05) in either static or dynamic

Table 1 Results of weighted least-squares regressions of study-specific means of the log response ratio vs. experimental duration (in days), for both static (all resource types) and dynamic (periphyton resources only) experiments, for demographical response variables

Experiment type	Prey response variable	Sample size	Response vs. experimental duration		
			Intercept	Slope	<i>P</i>
Static	Density	36	0.077	−0.001	0.085
Static	Survival	63	−0.069	0	0.611
Static	Fecundity	135	−0.105	0	0.756
Static	Growth	379	−0.039	−0.001	< 0.001
Dynamic	Density	12	−1.029	0.008	0.054
Dynamic	Survival	6	−0.239	−0.007	0.037
Dynamic	Fecundity	23	0.031	−0.002	0.029
Dynamic	Growth	155	−0.102	−0.001	0.021

Bolded text indicates *P*-values significant at *P* < 0.05.

resource experiments. Although prey growth in static resource experiments was slightly but significantly negatively correlated with the number of individuals per replicate ($n = 378$, intercept = -0.0568 , slope = -0.0004 , $P = 0.034$), these variables were not correlated in dynamic resource experiments ($n = 184$, intercept = -0.104 , slope = 0.000 , $P = 0.318$). Consequently, our results are not likely to be artifacts arising from the confounding of resource dynamics with experimental population size.

DISCUSSION

Prey that change their foraging behaviour, mating behaviour, physiology, or morphology in response to predation risk may incur costs that affect important demographic parameters and influence prey population dynamics (Lima & Dill 1990; Werner & Peacor 2003). Predators may thus exert NCEs on prey life history measures. Shifts in prey behaviour or phenotype can also modify resource densities as top-down control of resources is relaxed (Bolker *et al.* 2003; Werner & Peacor 2003; Schmitz *et al.* 2004). Because NCE magnitude may depend on resource availability (Abrams 1991; Peacor 2002; Bolnick & Preisser 2005), there may be complex feedbacks between predation risk, prey defense and resource density. Such feedbacks have been demonstrated both theoretically (Abrams 1991; Peacor 2002) and empirically (Peacor 2002). Whether the presence of resource dynamics acts to mitigate or magnify NCEs, however, may depend on the temporal and spatial scale of the study (Peacor 2002; Abrams 2008a) and the natural history of a given predator/prey pair.

Our meta-analysis highlights a general tendency for resource dynamics to exacerbate the NCEs of predators on their prey. Perceived predation risk generally reduces prey density, fecundity, survival and growth relative to risk-free controls. We found that this NCE tends to be stronger in experiments that allow resources to vary, relative to those studies that supply a controlled ration of resources to the prey. The tendency for resource dynamics to exacerbate NCEs was observed for multiple response variables: prey somatic growth, fecundity, survival and population density. Prey behavioural traits (foraging rate and use of risky habitats) showed non-significant trends in the same direction. The latter result is important because it suggests that the differences in prey growth, survival and reproduction observed between static- and dynamic-resource studies cannot simply be attributed to differences in prey behaviour *per se*, and so presumably also involves feedbacks through changes in other interacting species.

We emphasize that the effect sizes and even directions described here reflect aggregate means across diverse systems and that the results from individual studies may depend on system-specific variables beyond the scope of our analyses.

Among-system differences in predator or prey life history, physiology, coevolutionary history, relative body sizes and many other factors might influence NCE sizes. It is beyond the scope of the present study to dissect how all such interacting variables modify NCE magnitude, or its dependence on static vs. dynamic resources. In addition, many cases in our dataset lack relevant information about these other variables. Although we are not able to evaluate all these additional variables at present, the fact that we observe similar results within several distinct taxonomic groups that differ substantially in life history and other biological details suggests that our results are not simply an artifact of these factors. Our work thus confirms that the two experimental designs (static or dynamic resources) lead to systematically different outcomes across a wide range of systems and taxa, although it is likely that additional variation might be explained by examining other variables. Consequently, we focus on the difference between static and dynamic designs rather than on the specific effect size estimates that will be critically affected by the many additional variables and idiosyncrasies of individual study systems.

While there is a tendency for stronger NCEs with dynamic resources, this mean difference obscures high among-study variance within the set of experiments employing either static or dynamic resources. For instance, studies of systems with fast-growing resources such as periphyton have found cases where resource dynamics reduce NCEs. In mesocosm experiments with *Anax* predators and tadpole prey, reduced tadpole foraging effort led to increased algal abundance that ultimately increased tadpole growth rate relative to a no-predator control (Peacor 2002). Consequently, the effect of predation risk on prey growth was negative in the short term but positive in the long term. If such 'overcompensation' was the typical result of such experiments, long-term experiments with dynamically-varying resources should eventually exhibit positive effects of predation risk on prey fitness or growth ($RR > 1$). In contrast, predation risk should have only detrimental effects on prey fitness ($RR < 1$) when resources are static. NCEs would thus tend to be stronger (smaller RR) for static- than dynamic-resource experiments, and the effect of predation risk should decline over time in dynamic resource experiments. Our analysis of the relationship between the effect of predation risk and experimental duration in dynamic resource experiments revealed the opposite pattern: for three of the four prey demographic metrics, the impact of predation risk increased significantly over time (Table 1). While a definitive test for overcompensation requires analyzing multiple experiments with known prey and resource generation times for a polynomial relationship between experimental duration and the effect of predation risk, our findings nonetheless suggest that overcompensation may be atypical (see below for additional

discussion of the temporal scale of both static and dynamic resource experiments).

Possible mechanisms

Why would resource dynamics tend to exacerbate NCEs? A meta-analysis found a tendency for low resource availability to exacerbate NCEs (Bolnick & Preisser 2005). The underlying cause of this trend remains uncertain, but may occur because food limitation reduces individuals' ability to compensate for the energetic costs of anti-predator behaviours, leading to a proportionally larger effect of predators on prey demography. Thus, the stronger NCEs in dynamic-resource studies would be consistent with lower overall resource availability. Most static resource experiments regularly replenished resources, preventing excessive depletion, whereas dynamic resources could reach persistently low levels despite their capacity for reproduction and self-renewal. Alternatively, dynamic resources may exhibit competitive effects such as those seen in the study of grasshopper responses to spiders: when grasshoppers switched to safer forb resources, grasses quickly out-competed forbs, further reducing food availability (Schmitz *et al.* 1997). We therefore predict that static-resource experiments will maintain higher mean resource levels. Testing this prediction requires experiments that repeatedly monitor both prey and resource populations throughout the period of interest. Unfortunately, we are unable to test this prediction via meta-analysis, because not enough case studies provide the necessary multi-species temporal data. Another way to test this prediction would be to compare resource levels between static and dynamic experimental designs. However, no single study used both static- and dynamic-resource designs, preventing us from making direct comparisons of resource availability in the two designs. However, this hypothesis is consistent with fact that prey demographic variables show a strong relationship with experimental duration in dynamic-resource experiments (Table 1). This increasing NCE over time in dynamic studies would be consistent with declining resource availability.

Low availability of dynamic resources could reflect more than simple consumption by the focal consumer. Resources may adopt defensive tactics against their consumers (the focal prey of our collected studies), and hence be subject to direct NCEs of their own. These NCEs may be most pronounced in experiments that allow resource dynamics, because changes in resource growth, reproduction, and movement could further reduce resource abundance in addition to direct consumption. If resource NCEs are more likely in dynamic-resource experiments, it would explain lower resource availability and stronger NCEs. Again, we are unable to definitively test this proposed mechanism under-

lying the observed tendency for resource dynamics to exacerbate NCEs. Although the cascading effects of NCEs on a single species in a food chain have been researched, we are not aware of any studies evaluating the interaction of NCEs due to anti-predator strategies of multiple species at different food chain levels. This underlines the importance of experimental manipulations that collect time-series data on both prey and resource populations and provide the information necessary to differentiate between simple resource diminishment and more complex feedback mechanisms.

Possible sources of bias

Several sources of bias can affect the results of a meta-analysis. The most widespread form of bias is the file-drawer effect, in which studies that fail to reject a null hypothesis tend to remain unpublished. It seems unlikely, however, that negative results would remain unpublished for one experimental design (dynamic resources) but be published for another (static resources). If dynamic resources cause larger NCEs than static resources, it is possible that static-resource studies would be published less often due to their smaller mean effect size. However, we found data on many more static resource experiments (1095 effect size estimates from 154 published papers) than dynamic resource experiments (691 estimates from 69 published papers). As a result, the non-publication of static resource experiments seems unlikely to create an artificial difference between these experimental designs. Another source of bias could arise from differences in study duration, as NCE magnitude can change over the course of a single study (Peacor 2002; Abrams 2008a). The average reported study duration was 34 days (SD = 60), and ranged from a few minutes to as long as three years. Experimental length *per se* seems also unlikely to explain the observed difference between static and dynamic-resource studies, since the two groups did not differ in duration ($P > 0.1$ for all response variables).

Another source of bias might involve logistical constraints influencing which taxa are examined using static- vs. dynamic-resource experimental designs. There are significant differences in occurrence of prey taxa between the two designs ($\chi^2 P < 0.0001$; Appendix S1). There is a tendency for fish and amphibians to be given dynamic resources, and for branchiopods, mammals, and birds to be given static resources. If taxa differed systematically in NCE magnitude, biased representation of taxa might generate spurious differences between the experimental designs. However, the trends observed for the dataset as a whole also hold within major taxonomic groups. We therefore conclude that taxonomic representation is unlikely to be an important source of bias. Individual analyses of the three most abundant prey classes (Amphibia, Insecta, and Branchio-

pod) produced results qualitatively similar to those emerging from the larger analysis. For instance, amphibians make up the majority of studies of NCEs on prey density, and differ in frequency between experimental designs; when analysed separately, however, the results mirror those of the all-taxa analysis (Figs 1 and 2, bottom panel). Results from studies of non-amphibian taxa yield equivalent results, indicating that our results are not driven by the behavioural quirks of amphibians alone (the most heavily-studied taxon).

A final caveat for our study is that the most commonly-used design for NCE experiments may be subject to important biases arising from complicated feedbacks and interactions between NCEs and CEs (Abrams 2007, 2008a,b). Experiments contrasting predator-risk vs. no-predator treatments eliminate CEs in order to measure NCEs. CEs and NCEs may, however, interact: prey with reduced energy income (NCE) may, for instance, become vulnerable to predators (CE). Most experiments also focus on a single type of NCE (e.g., growth, survival, fecundity), ignoring trade-offs between or cumulative effects of multiple NCE pathways (Preisser & Bolnick 2008). Consequently, empirical estimates of NCEs must be treated with caution, and our inferences are only as reliable as the effect size estimates from standard experimental designs in our database.

CONCLUSIONS

Our results highlight the fact that apparently small differences in experimental design can produce very different outcomes. Potential caveats notwithstanding, the diversity of prey taxa (18 classes ranging from bivalves to insects to mammals) and the large number of observations in our dataset allows us to conclude that resource dynamics appreciably affect the magnitude of predator NCEs on prey. This conclusion is strengthened by the fact that we see parallel results across multiple response variables, even though very few predator-prey systems contribute to more than one or two measured responses. Our research provides another illustration of the context-dependence in predator-prey interaction strengths (Peacor & Werner 2004b; Bolnick & Preisser 2005; Preisser *et al.* 2007; Abrams 2008a) that may occur in even simple food web modules. These results have implications for both experimental design in predator-prey studies, and for our understanding of trophic dynamics. Regarding trophic dynamics, our results imply that changing resource density over time can lead to variation in NCE magnitude.

Our results also suggest that experimental assessments of predator effects on prey must acknowledge the potential for resource diminution and feedback loops, and the consequent importance of experimental duration. Had more studies obtained time-series data and measured resource levels, we might have been able to distinguish between the

various mechanisms capable of producing the observed pattern. The scarcity of such datasets underlines the need for experimental manipulations of resource dynamics that take time series data in order to explicitly test these hypotheses. We predict that while resource reduction will affect dynamic systems where the resource's generation time exceeds the experimental duration, longer-term experiments with rapidly cycling resources may yield complex feedback loops capable of producing overcompensation and other outcomes. While the use of dynamic resources appears largely motivated by the laudable desire for ecologically-relevant conditions, our work demonstrates the subtle but important consequences of such realism. Similarly, experimenters employing static resources should be aware that controlled laboratory manipulations may unwittingly but systematically underestimate the response of prey to predation risk.

ACKNOWLEDGEMENTS

We thank S. Peacor and several anonymous referees for comments on the manuscript, and P. Abrams for the discussions that motivated this study. M. Benard and J. Pantel helped assemble the NCE database. This work was conducted as part of the 'Does Fear Matter?' Working Group supported by the National Centre for Ecological Analysis and Synthesis (NSF Grant #DEB-0072909) and the University of California, Santa Barbara.

REFERENCES

- Abrams, P.A. (1984). Foraging time optimization and interactions in food webs. *Am. Nat.*, 124, 80–96.
- Abrams, P.A. (1990). The effects of adaptive behavior on the type-2 functional response. *Ecology*, 71, 877–885.
- Abrams, P.A. (1991). Life history and the relationship between food availability and foraging effort. *Ecology*, 72, 1242–1252.
- Abrams, P.A. (2007). Defining and measuring the impact of dynamic traits on interspecific interactions. *Ecology*, 88, 2555–2562.
- Abrams, P.A. (2008a). Measuring the impact of dynamic antipredator traits on predator-prey-resource interactions. *Ecology*, 89, 1640–1649.
- Abrams, P.A. (2008b). Measuring the population-level consequences of predator-induced prey movement. *Evol. Ecol. Res.*, 10, 333–350.
- Bolker, B., Holyoak, M., Krivan, V., Rowe, L. & Schmitz, O. (2003). Connecting theoretical and empirical studies of trait-mediated interactions. *Ecology*, 84, 1101–1114.
- Bolnick, D.I. & Preisser, E.L. (2005). Resource competition modifies the strength of trait-mediated predator-prey interactions: a meta-analysis. *Ecology*, 86, 2771–2779.
- Gurevitch, J. & Hedges, L.V. (1999). Statistical issues in ecological meta-analysis. *Ecology*, 80, 1142–1149.
- Hedges, C. & Olkin, I. (1985). *Statistical Techniques for Meta-analysis*. Academic Press, New York NY.

- Hedges, L.V., Gurevitch, J. & Curtis, P.S. (1999). The meta-analysis of response ratios in experimental ecology. *Ecology*, 80, 1150–1156.
- Lima, S. & Dill, L. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.*, 68, 619–640.
- Luttbegg, B., Rowe, L. & Mangel, M. (2003). Prey state and experimental design affect relative size of trait- and density-mediated indirect effects. *Ecology*, 84, 1140–1150.
- Peacor, S. (2002). Positive effect of predators on prey growth rate through induced modifications of prey behaviour. *Ecol. Lett.*, 5, 77–85.
- Peacor, S.D. & Werner, E.E. (2004a). Context dependence of nonlethal effects of a predator on prey growth. *Israel J. Zool.*, 50, 139–167.
- Peacor, S.D. & Werner, E.E. (2004b). How dependent are species-pair interaction strengths on other species in the food web? *Ecology*, 85, 2754–2763.
- Preisser, E.L. & Bolnick, D.I. (2008). The many faces of fear: comparing the pathways and impacts of nonconsumptive predator effects on prey populations. *PLoS ONE*, 3, e2465.
- Preisser, E.L., Bolnick, D.I. & Benard, M.F. (2005). Scared to death? the effects of intimidation and consumption in predator-prey interactions. *Ecology*, 86, 501–509.
- Preisser, E.L., Orrock, J.L. & Schmitz, O.J. (2007). Predator hunting mode and habitat domain affect the strength of non-consumptive effects in predator-prey interactions. *Ecology*, 88, 2744–2751.
- Rosenberg, M., Adams, D. & Gurevitch, J. (2000) *MetaWin: Statistical Software for Meta-Analysis*, 2nd edn. Sinauer Associates, Sunderland MA.
- Rundle, H.D., Vamosi, S.M. & Schluter, D. (2003). Experimental test of predation's effect on divergent selection during character displacement in sticklebacks. *Proc. Natl Acad. Sci. USA*, 100, 14943–14948.
- Schmitz, O. (1998). Direct and indirect effects of predation and predation risk in old-field interaction webs. *Am. Nat.*, 151, 327–342.
- Schmitz, O., Beckerman, A. & O'Brien, K. (1997). Behaviorally-mediated trophic cascades: effects of predation risk on food web interactions. *Ecology*, 78, 1388–1399.
- Schmitz, O., Krivan, K. & Ovadia, O. (2004). Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecol. Lett.*, 7, 153–163.
- Schmitz, O., Grabowski, J., Peckarsky, B., Preisser, E., Trussell, G. & Vonesh, J. (2008). From individuals to ecosystem function: toward an integration of evolutionary and ecosystem ecology. *Ecology*, 89, 2436–2445.
- Werner, E. & Peacor, S. (2003). A review of trait-mediated indirect interactions in ecological communities. *Ecology*, 84, 1083–1100.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 The taxonomic distribution of effect size estimates in the static/dynamic database (pooling all response variables).

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

Editor, Marcel Holyoak

Manuscript received 18 August 2008

First decision made 19 September 2008

Second decision made 7 January 2009

Manuscript accepted 28 January 2009