

The cost of safety: Refuges increase the impact of predation risk in aquatic systems

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Abstract. Although use of refuge habitats by prey can reduce their risk of predation, refuge use may also involve costs such as increased within-refuge competition for resources. Despite the ubiquity of refuge use by prey, it is unknown whether predator-induced use of refuges has widespread, negative nonconsumptive effects on prey growth, survival, and fecundity. We performed a meta-analysis of 204 studies of aquatic taxa containing data on 271 distinct predator–prey pairs and found strong evidence that the negative effect of predation risk on prey activity, growth, and fecundity increases when prey have access to refuge habitats. Moreover, the effect of refuge habitats on growth and activity depends upon whether the refuge provides partial or total protection from predators. These results suggest that prey choosing whether to use refuges face a trade-off between lowering the immediate risk of being consumed and increased nonconsumptive costs of refuge use. Our results suggest that changes in nonconsumptive effects in the presence of refuge habitats may alter prey population dynamics, coexistence, and metapopulation dynamics. Moreover, our results reveal key pragmatic considerations: the magnitude and direction of nonconsumptive effects may depend on the presence of refuge habitat and whether the refuge provides partial or total protection from predators.

Key words: anti-predator behavior; growth; meta-analysis; nonconsumptive effects; survival.

INTRODUCTION

The risk of predation often induces the use of safer ‘refuge’ habitats by prey. Indeed, refuge use under predation risk is commonly observed in a wide range of systems (Lima and Dill 1990, Bell et al. 1991, Lima 1998, Brown and Kotler 2004, Caro 2005, Stankowich and Blumstein 2005, Cooper 2009). Refuge habitats can change prey behavior (Cooper 2005, Stankowich and Blumstein 2005), influence population dynamics (Cooper and Frederick 2007), alter the outcome of predator–prey interactions (Orth et al. 1984, Hugie 2003), change the strength and direction of trophic cascades (Schmitz et al. 1997, Grabowski 2004, Trussell et al. 2006a), influence energy transfer among trophic levels (Trussell et al. 2008, 2011), and mediate indirect effects in ecological communities, such as apparent competition (Orrock et al. 2010a).

Although refuge habitats provide direct benefits to prey by reducing their likelihood of being consumed (Lima 1998), refuge habitats may also modify the nonconsumptive effects (NCEs) of predators on prey. Nonconsumptive effects refer to risk-induced changes in prey habitat use, activity, growth, survival, reproduc-

tion, and abundance (also called “trait-mediated effects” or “risk effects;” see Abrams 2007, Creel and Christianson 2008). For example, reduced foraging activity in response to predation risk can significantly reduce prey growth, reproduction, and ultimately population size (Brown and Kotler 2004, Preisser et al. 2005, Creel and Christianson 2008). Refuges might be expected to magnify nonconsumptive effects because prey that face predation risk may be more likely to use refuge habitats, and prey in refuges may strongly compete for limited resources (Persson and Eklöv 1995, Martin et al. 2003, Trussell et al. 2006b) rather than foraging in higher-resource environments outside the refuge (Sih 1992). Moreover, although less often explored (but see Eklöv and Persson 1995, Persson and Eklöv 1995, Cooper et al. 1999), the type of refuge (i.e., whether the refuge provides concealment from or total protection against predators) may also alter the nonconsumptive effects of prey refuge use because the costs and benefits of using a partial refuge may differ from those in a total refuge. For example, although total refuges may provide more protection for some prey species, they may also provide less profitable foraging opportunities (e.g., Eklöv and Persson 1995). Despite the importance of NCEs and the potential for refuge use to exacerbate their impact, it is unclear whether refuge-mediated changes in the strength of NCEs are a common occurrence.

We used meta-analysis to conduct a multi-taxa examination of how prey access to different refuge types

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(none, a partial refuge that provides cover/concealment only, and a total, predator-proof refuge) affects the strength of predator-induced NCEs in aquatic systems (the rationale for focusing on aquatic systems is described in *Methods*, below). Specifically, we examine how the presence of refuge habitats affects the magnitude of risk-mediated changes in prey activity, growth, fecundity, and survival (see Plate 1). Our results provide a comprehensive examination of how refuge habitats alter the strength and importance of NCEs for aquatic prey.

METHODS

We conducted a search of peer-reviewed literature reporting the results of experimental manipulations that compared the responses of prey under predation risk (e.g., caged predators, chemical cues) to prey in control treatments (e.g., cages with no predators, no chemical cues). We searched online databases (JSTOR, BIOSIS, Science Citation Index) as well as issues of *American Naturalist*, *Ecology*, *Oecologia*, and *Oikos* published from 1990 through 2005 (for a detailed description of these methods, see Appendix A). We only included papers that measured one or more of four variables: prey activity, growth, survival, and fecundity (because so little data were available on prey density, we chose not to analyze this variable).

For each paper, data were extracted from the text or from graphics using digital calipers that were accurate to within $\pm 1\%$ of the actual value. We also classified each set of data as to whether it included no refuges (no refuge) or physical structures that prey could use as cover (partial refuge) or protection (total refuge) from predation risk. Typical partial refuges included vegetation, cobble, litter or other substrates that provided cover but where prey could still be attacked. Typical complete refuges included tubes, large rocks or other physical structures where predators could not attack prey; both partial and total refuges could be composed of natural or artificial materials (e.g., PVC pipe). Some articles reported the results of multiple experiments conducted under different conditions (e.g., the impact of predation risk under differing resource levels or prey densities). An issue that often arises in meta-analysis is that some studies may not be considered strictly independent because they were conducted by the same researchers and/or on the same predator-prey species pair (Englund et al. 1999, Gurevitch and Hedges 1999, Gates 2002). Because of our interest in assessing responses to predation risk across the spectrum of ecologically relevant conditions, we followed the recommendation of Gates (2002) and Gurevitch and Hedges (1999) and conducted our meta-analysis using the full data set. To address the potential effect of nonindependence, we also conducted a more conservative, "truncated" analysis using a single data point randomly selected from each paper to ensure independence of observations (Englund et al. 1999).

Because over 91% of the rows in the initial data set were aquatic organisms, we restricted our analyses to aquatic systems only (see Appendix A for a summary of studies and appendices B and C for detailed information). The aquatic-systems-only data set contained 888 rows from 170 papers, with data on 101 predator and 125 prey species (233 distinct predator-prey pairs). Although we gathered a substantial number of studies from diverse taxa (i.e., 125 species; Appendix A), some taxonomic groups were inherently more abundant in our data set. The most common prey classes in aquatic systems were Amphibia (401 lines from 46 species) and Insecta (142 lines from 32 species). To ensure that our results were robust to any confounding of taxonomy and study type (e.g., if all of the studies for total refuges used amphibians), we also conducted ancillary analyses that utilized only prey from Insecta or Amphibia.

Following Lajeunesse and Forbes (2003), we used both the log response ratio and Hedges' d metrics to assess the across-study effects of refuges on prey response to risk. The log response ratio, $\ln(RR)$, is calculated as the $\ln$ of the treatment response divided by the control response; Hedges' d is calculated as the difference between the experimental and control means standardized by the pooled standard deviation (Hedges et al. 1999). Although both metrics provide useful information, effect sizes calculated using $\ln(RR)$ may be preferable because Hedges' d may find significant effects that are due to standard deviation rather than biological effect size, as may occur in studies of predator-prey interactions (see example in Osenberg et al. 1997; see Appendix A for additional details). We thus focus on the $\ln(RR)$ results in our discussions of both the full and truncated analyses (Fig. 1 and Appendix A, respectively), and provide the corresponding Hedges' d effect sizes for both the full and truncated analyses in Appendix A; in general, the Hedges' d results qualitatively agreed with the $\ln(RR)$ results.

Mean effect sizes were calculated using Metawin 2.1 (Rosenberg et al. 2000). We used a mixed-effects model because of our expectation that there may not be a single shared effect size across all of our studies (Gurevitch and Hedges 1999); 95% confidence intervals were generated by bootstrapping. In addition to the initial P values, we also provide P values corrected for multiple comparisons at $\alpha = 0.05$ using step-up false discovery rate (FDR), a sequential Bonferroni-type procedure (Benjamini and Hochberg 1995). We used ANOVA to test whether experimental duration differed among experiments for each of the three refuge types; we corrected for multiple comparisons using the FDR procedure.

RESULTS

Analysis of the full data set showed that aquatic prey generally responded more strongly to predation risk in the presence of a partial or total refuge, as evidenced by significant changes in activity, growth, and fecundity (Table 1, Fig. 1). The significant effect of refuge presence

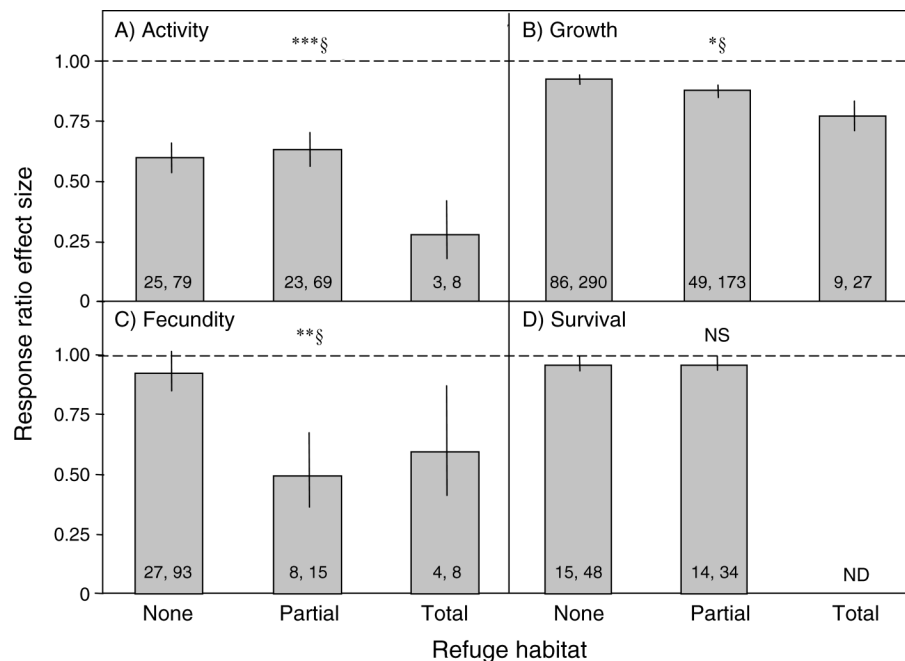


FIG. 1. Results of a meta-analysis using log response ratio effect sizes to examine the effect of prey refuges (no refuge, partial refuge, and total refuge where prey are safe from predators) on the strength of the nonconsumptive effect of predation risk on (A) prey activity, (B) prey growth, (C) prey fecundity, and (D) prey survival. Log response ratio values <1 indicate that predator presence has a harmful effect; values >1 indicate that predator presence has a beneficial effect. Data are means with 95% confidence intervals generated via bootstrapping. Pairs of numbers at the base of each bar represent (left) the number of published papers and (right) the number of independent experiments contributing to a given mean. The asterisks at the top of each panel represent the significance of an overall omnibus test (i.e., testing the hypothesis that at least one of the three values is different from the others). Key to abbreviations: ND, insufficient data; NS, nonsignificant.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.005$ for initial values.

§ For adjusted values, significant at $\alpha = 0.05$ after step-up FDR (false discovery rate) Bonferroni-type correction.

was also found with the Hedges' d effect size metric (Table 1, Appendix A). Total refuges reduced prey activity, but partial refuges did not (Fig. 1A). As the safety provided by the refuge type increased (i.e., no refuge, partial refuge, total refuge), growth was increasingly reduced (Fig. 1B). Fecundity was equally reduced by the presence of a partial or total refuge (Fig. 1C). Because only one study examined prey survival in the presence of a total refuge (Appendix A), our analysis of survival was restricted to no-refuge and partial-refuge situations. Prey survival did not differ in the presence of

a partial refuge (Table 1, Fig. 1D), but was lower in the presence of partial refuge habitats when using the Hedges' d metric (Table 1; Appendix A: Fig. A.2).

Despite the lower sample sizes in the truncated analyses, they qualitatively supported the findings of the full-data-set analyses (Table 1; Appendix A). Results obtained when only using prey from the classes Insecta and Amphibia also largely confirmed the findings of our full analysis. We found no effect of refuge type on activity and a significant effect of partial refuges on survival in the Insecta and Amphibia dataset (Appendix

TABLE 1. Results of meta-analyses testing the effect of refuge type (no refuge, partial refuge, or total refuge) on prey response to predation risk.

Analysis type	Activity			Growth			Fecundity			Survival		
	df	Q_{ref}	P	df	Q_{ref}	P	df	Q_{ref}	P	df	Q_{ref}	P
Response ratio (full data set)	2, 155	20.03	0.004	2, 489	27.68	0.011	2, 115	22.1	0.005	1, 80	<0.01	0.981
Hedge's d metric (full data set)	2, 157	35.31	0.003	2, 494	48.18	0.001	2, 119	25.45	0.007	1, 73	6.60	0.015
Response ratio (truncated data set)	2, 45	9.9	0.042	2, 135	19.73	0.021	2, 37	30.37	0.007	1, 28	0.23	0.651
Hedge's d ratio (truncated data set)	2, 47	17.91	0.013	2, 136	14.8	0.022	2, 38	4.01	0.432	1, 27	3.01	0.098

Notes: Q_{Ref} describes the portion of overall total heterogeneity (Q_{Tot}) explained by refuge type (see Appendix A for Q_{Tot} values). P values are calculated using a chi-square approximation. Boldface P values are significant at $\alpha = 0.05$ after step-up FDR (false discovery rate) Bonferroni-type correction.



PLATE 1. The intertidal snails *Nucella lapillus* rely on refuges to avoid predators at little cost when food (the barnacle, *Semibalanus balanoides*) is abundant. Soon food within the refuge will become depleted, and the benefit of being protected from predators will have the cost of less access to food. Photo: G. C. Trussell.

A: Fig. A.4). When the FDR (false discovery rate) correction was applied, however, only growth was significantly ($\alpha = 0.05$) affected by the presence of a refuge (Appendix A: Fig. A.4).

The findings of our meta-analysis appear unlikely to be a product of publication bias or a correlation between effect size and sample size (see Appendix A). There was no indication of publication bias (Spearman's r_s with $P < 0.05$) in the response ratio analyses of prey activity, fecundity, and growth, and in the Hedges' d analyses of prey fecundity, growth, and survival. There was evidence for publication bias in the response ratio analysis of prey survival ($r_s = 0.276$, $P = 0.006$) and in the Hedges' d analysis of prey activity ($r_s = 0.157$, $P = 0.043$). However, since we detected no effect of refuge on prey survival and results from Hedges' d analyses of activity were in agreement with $\ln(RR)$ (log response ratio) results, it is unlikely that publication bias affected the generality of our findings or conclusions.

For three of the four prey variables, experimental duration did not differ between experiments in the different refuge classes (Appendix A). For the studies that reported experimental duration (677 of 975 rows across the entire database), there was a significant ($P = 0.016$) difference in experimental duration for prey growth, with total-refuge studies having a shorter

duration than no-refuge studies (28.0 ± 8.7 and 49.5 ± 3.47 days; respectively; Appendix A). However, this difference was not significant at $\alpha = 0.05$ once the results were corrected for multiple comparisons, and the nature of the difference would be expected to generate a more conservative test of refuges on growth, i.e., the significant NCE (nonconsumptive effects) of total refuges on growth was evident despite the shorter nature of total-refuge studies (also see Appendix A).

DISCUSSION

Our work suggests that the availability of refuge habitats for prey exposed to predation risk in aquatic habitats generally increases the strength of predator-mediated nonconsumptive effects. Although refuge habitats directly benefit prey by decreasing predation risk, this benefit can have substantial costs by amplifying risk-induced reductions in prey activity, growth, and fecundity (Fig. 1). The implications of these results are that refuges may have significant effects on prey populations, coexistence among competing prey, and predator-prey interactions. Moreover, because predicting the likelihood and importance of nonconsumptive effects (NCEs) is an increasingly common goal of predator-prey research, a key implication of our work is that the presence of refuge habitat may be a strong

indicator of larger risk-induced NCEs, i.e., we find that the presence of refuge habitats, much like habitat domain and predator hunting mode (e.g., Preisser et al. 2007), may provide insight into the nature and strength of NCEs.

Our finding that refuges have negative effects on prey growth and fecundity illustrates that the costs of refuge use can enhance nonconsumptive effects. Although these costs have been documented explicitly for some species (e.g., reduced growth in juvenile roach; Persson and Eklöv 1995), the observed widespread cost of refuge use (Fig. 1) may explain why prey rarely opt to use the refuge in the absence of predation risk, and why the decision to enter or leave a refuge habitat is largely determined by the degree of risk in the environment (Lima and Dill 1990, Kats and Dill 1998, Stankowich and Blumstein 2005, Cooper and Frederick 2007). Competitive interactions within the refuge may also enhance the costs of refuge use because these habitats often contain fewer (due to their limited spatial extent) or inferior resources than non-refuge environments (e.g., Power 1984, Persson 1993). For instance, the shaded environment in some refuge habitats may reduce the prevalence of algal food for herbivorous tadpoles. The effects of strong refuge-based competition may be further compounded by the uncertainty of predation risk. Theory predicts that prey with imperfect knowledge of predator presence should err on the side of caution by staying longer in refuges (Sih 1992), and this prediction is supported by empirical data (Sih 1997). As a result, the combination of variable risk and imperfect information may cause prey to remain in refuge habitats longer, thereby increasing resource competition and further reducing prey growth and fecundity.

Our work also illustrates that refuge type (i.e., partial vs. total refuge) may have different nonconsumptive effects on activity and growth (Fig. 1). Differences in activity suggest a qualitative difference in the way that prey use partial vs. total refuges: prey exhibit a large decrease in activity in total refuges, whereas activity in partial refuges is comparable to habitats without a refuge (reduction of activity in the presence of predation risk is a common nonconsumptive effect). The greater reduction of activity in total refuges may arise because these habitats may be more complex and heterogeneous than partial refuges, so that locating and harvesting resources may be more inefficient (Crowder and Cooper 1982, Bell et al. 1991, Eklöv and Persson 1995). These differences in activity may also exacerbate the strength of competitive interactions in total refuges. Moreover, competition may also be directly related to refuge type if total refuges are generally smaller than partial refuges, so that resources are likely to be readily depleted in total refuges. Both reduced activity and increased competition may lead to increased nonconsumptive effects on growth we observed in total vs. partial refuges (Fig. 1B). Despite the significant differences between partial and total refuges in terms of activity and growth, refuge type did

not affect fecundity (Fig. 1C), although the greater variance exhibited by the fecundity data likely reduces the power of tests among refuge type.

Although the availability of refuge habitats consistently increased the strength of NCEs on prey activity, growth, and fecundity, nonconsumptive effects on prey survival were variable depending on the analysis, with no significant effect on survival in the main analysis (Fig. 1) and the truncated analysis (Appendix A), but a significant effect using Hedges' *d* (Appendix A) and when only Amphibia and Insecta were examined (Appendix A). Importantly, the effect size of refuge habitats on survival was generally very low (Fig. 1), even in the analyses where this effect was statistically significant (Appendix A). Relative to the large effect sizes we observed for activity, growth, and fecundity, the small effect size for survival suggests that the nonconsumptive effect of refuge habitats on survival, though sometimes statistically significant, may not be biologically significant, i.e., the costs of refuge use in terms of activity, growth, and fecundity are worth paying when confronted with predation risk, because they do not appreciably affect survival.

Temporal variation in risk may also be important to refuge use (Lima and Bednekoff 1999), and relatively few studies of this important factor also include predator refuges (but see Sih 1997). Short-term metrics like prey activity may overestimate the true effect of predation risk, because prey under short, intense pulses of risk might readily forego foraging for short time periods. Trussell et al. (2011) suggested that prey activity may be less effective than more integrative metrics of prey fitness (e.g., growth) for understanding NCEs when there is temporal variation in risk. Temporal variation in risk could certainly affect refuge use (e.g., Sih 1997, Sih and McCarthy 2002) and thus alter the strength of NCEs. Our meta-analysis finds that metrics that are generally measured over longer time scales, like prey growth and fecundity, exhibited refuge-mediated changes in NCE strength. Thus, our results illustrate that studies that seek to understand the importance of temporal variation in predation risk must carefully consider refuge availability as well as the time course of the response metric being used.

Because refuge habitats can clearly alter NCE strength and have effects on a variety of prey taxa (Fig. 1), our work suggests that anthropogenic activities that alter refuge quality or quantity may have the consequence of changing prey activity, growth, and fecundity. Habitat destruction, eutrophication, climate change, and exotic plants (e.g., Mattos and Orrock 2010) may all alter the quantity and quality of refuge habitat available for prey. For instance, human activities have reduced structured (i.e., refuge) habitats in coastal and marine systems, with estimates of global seagrass, oyster reef, and coral reef habitat loss ranging from 20% to 85% (Waycott et al. 2009, Beck et al. 2011). Anthropogenic alteration of refuge habitats may also

have unappreciated implications for prey persistence (Orrock et al. 2008) and food-web dynamics (Orrock et al. 2010b) if refuge habitats alter the likelihood of prey dispersal.

Our results highlight several key areas for future study. For example, the probability of refuge use likely changes during development because of ontogenetic changes in resource requirements and susceptibility to predators (Urban 2007). Similarly, covariates that are thought to describe risk (i.e., body size of prey and/or predators; Urban 2007, Preisser and Orrock 2012) may shed considerable light on refuge use if incorporated into future analyses that utilize the studies examined here as well as incorporate newly published studies. Moreover, temporal and spatial variation in risk are likely important, but have only been evaluated in a few studies that also include predator refuges (Sih 1992, 1997). Importantly, taxonomic breadth should also be considered in future studies: our meta-analyses reveal that the majority of our understanding of refuges and NCEs comes from the Insecta and Amphibia and from aquatic ecosystems. Incorporation of trophic guild and natural history will also be important for future studies of refuge-mediated effects, as the costs of refuge use may depend upon trophic guild (e.g., shading in refuge habitats may reduce food for herbivorous prey), and these costs need not be negative (e.g., insectivorous fish may find greater food and safety within partial refuges compared to outside the refuge).

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SUPPLEMENTAL MATERIAL

Appendix A

Descriptive details including methods for assembling database, tables that summarize the kinds of studies examined, and figures that present results from truncated analyses and analyses with Hedges' *d* ([Ecological Archives E094-049-A1](#)).

Appendix B

Descriptive information for all studies used in the meta-analysis, including citation, system, predator and prey species, and number of lines in the database ([Ecological Archives E094-049-A2](#)).

Appendix C

Summary of number of articles and lines in the database, classified by prey species, predator species, and refuge type ([Ecological Archives E094-049-A3](#)).