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Preisser, E. L., Orrock, J. L. and Schmitz, O. J. (2007), PREDATOR HUNTING MODE AND HABITAT DOMAIN ALTER NONCONSUMPTIVE EFFECTS IN PREDATOR–PREY INTERACTIONS. Ecology, 88: 2744-2751. doi:10.1890/07-0260.1
Available at: https://doi.org/10.1890/07-0260.1

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Ecology, 88(11), 2007, pp. 2744–2751
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PREDATOR HUNTING MODE AND HABITAT DOMAIN ALTER NONCONSUMPTIVE EFFECTS IN PREDATOR–PREY INTERACTIONS

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Abstract. Predators can affect prey populations through changes in traits that reduce predation risk. These trait changes (nonconsumptive effects, NCEs) can be energetically costly and cause reduced prey activity, growth, fecundity, and survival. The strength of nonconsumptive effects may vary with two functional characteristics of predators: hunting mode (actively hunting, sit-and-pursue, sit-and-wait) and habitat domain (the ability to pursue prey via relocation in space; can be narrow or broad). Specifically, cues from fairly stationary sit-and-wait and sit-and-pursue predators should be more indicative of imminent predation risk, and thereby evoke stronger NCEs, compared to cues from widely ranging actively hunting predators. Using a meta-analysis of 193 published papers, we found that cues from sit-and-pursue predators evoked stronger NCEs than cues from actively hunting predators. Predator habitat domain was less indicative of NCE strength, perhaps because habitat domain provides less reliable information regarding imminent risk to prey than does predator hunting mode. Given the importance of NCEs in determining the dynamics of prey communities, our findings suggest that predator characteristics may be used to predict how changing predator communities translate into changes in prey. Such knowledge may prove particularly useful given rates of local predator change due to habitat fragmentation and the introduction of novel predators.

Key words: habitat domain; hunting mode; nonconsumptive effects; predator–prey interactions.

Introduction

Predator–prey interactions can promote persistence or hasten extinction among competing prey (Savidge 1987), affect community composition (e.g., predator-mediated coexistence), alter biological invasions (Torchin et al. 2003), and influence the nature and strength of top-down limitation in food webs (e.g., trophic cascades). Our ability to predict why predators influence systems in these various ways remains limited because the outcomes are often contingent upon system-specific components of the predator–prey interaction. Inasmuch as progress in community ecology depends upon the ability to generate general across-community predictions (Lawton 1999), explaining the sources of contingency of predator–prey interactions is a major goal of ecologists.

In predator–prey interactions, contingent effects may arise in part from the diverse ways that predators can impact prey. Although traditionally viewed through the lens of prey consumption (consumptive effects, CEs), predators can also affect their prey through predator-induced alterations in foraging, habitat use, morphology, and other traits (nonconsumptive effects, NCEs; Abrams 1984, 1995). The energetic costs of such antipredator responses can yield changes in prey growth, fecundity, and survival that can affect the population dynamics of both the prey and the prey's resources (Werner and Peacor 2003, Schmitz et al. 2004). A recent meta-analysis suggested that NCEs can equal or exceed CEs in determining the population-level effect of predators on their prey and their prey's resources (Preisser et al. 2005). Given the steadily increasing awareness of their importance, an effective framework for predicting NCE strength based upon the functional characteristics of predators and their prey would provide a powerful tool for predicting otherwise unexpected outcomes of predator–prey interactions.

Schmitz (2005) proposed that combining knowledge of predator hunting mode with information on the habitat domains of both predators and prey could provide a framework for predicting NCE strength. Because information on both hunting mode and habitat domain is relatively straightforward to obtain, this framework may be applicable to systems for which only rudimentary information on predator–prey ecology is available. If the combination of domain and hunting mode effectively predicts the dynamic interplay (sensu Lima 2002) between predators and their prey, this framework could be used to identify when NCEs might be important and suggest when the role of NCEs in predator–prey interactions must be considered.

Manuscript received 16 February 2007; revised 23 May 2007; accepted 30 May 2007. Corresponding Editor: J. T. Cronin.
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TABLE 1. Comparative strength of nonconsumptive effects (NCEs) of predator cues on broad-domain prey, classified by predator hunting mode and habitat domain.

Predator hunting mode	Predator habitat domain	Mode–domain combination	Representative predator species	Predicted magnitude of prey response
Active (ACT)	broad (B)	ACT-B	ladybird beetles, weasels	weak
Active (ACT)	narrow (N)	ACT-N	crabs, largemouth bass	weak
Sit-and-pursue (SAP)	broad (B)	SAP-B	wolf spiders, hawks	intermediate
Sit-and-pursue (SAP)	narrow (N)	SAP-N	dragonfly larvae, banded sunfish	intermediate
Sit-and-wait (SAW)†	broad (B)			
Sit-and-wait (SAW)	narrow (N)	SAW-N	praying mantids, web spiders	strong

Notes: Across predator hunting mode, we expect active predators to elicit the lowest nonconsumptive effect on prey, whereas sit-and-wait and sit-and-pursue predators should elicit the greatest nonconsumptive effect on prey. Across predator habitat domain, we expect broad-domain prey to exhibit the greatest nonconsumptive response to narrow-domain predators. Overall ranking of prey NCE is predicted to be SAW-N > SAP-N > SAP-B > ACT-N > ACT-B.

† Broad-domain, sit-and-wait predators (SAW-B) do not exist because this combination of domain and hunting mode is ecologically incompatible.

A hunting mode/habitat domain framework for predicting NCE strength

The concept of predator hunting mode expands upon earlier ideas about predator hunting strategies (Schoener 1971, Huey and Pianka 1981) by classifying predators into three distinct hunting "modes." "Active" predators continuously patrol for prey; examples of this hunting mode include shrews and jumping spiders. "Sit-and-pursue" predators remain in a fixed location but move to attack prey that move within the predator's pursuit distance; examples include dragonfly nymphs and pike. Finally, "sit-and-wait" predators remain at a fixed location for prolonged periods (days to weeks) whether they are hunting or not; this hunting mode includes ambush species such as praying mantids and web spiders. Although some predators may move between modes as environmental conditions change (Scharf et al. 2006), this framework provides a starting point for considering whether hunting mode shapes how predators affect their prey.

The "habitat domain" of an organism is the portion of available microhabitat used by that organism. Habitat domain differs from conventional definitions of microhabitat use because it considers both microhabitat choice and the extent of spatial movement within the chosen microhabitat. Broad-domain organisms can range throughout the available microhabitat (i.e., are able to pursue prey or escape predators via relocation in space), while narrow-domain organisms use a subset of the available microhabitat. For example, the microhabitat of three spider predators in an old-field system can be crudely defined as patches of grass and herbs (Schmitz and Suttle 2001). But, within that microhabitat, one species occupies a narrow domain in the grass and herb upper canopy, one species ranges broadly throughout the canopy, and one species occupies a narrow domain in the lower canopy and ground. Another example occurs in freshwater ponds: broad-domain bluegill sunfish hunt in the water column, in vegetation, and on the pond bottom, while narrow-domain crayfish hunt only on the pond bottom (Turner et al. 1999). By accounting for the location and spatial extent to which individuals move within their chosen microhabitats, an organism's habitat domain both refines and extends the concept of microhabitat choice.

Predictions arising from the habitat domain/hunting mode framework

Changes in prey activity, growth, survival, and density in response to predators should reflect the information content of the predator cue (Sih 1992, Luttbeg and Schmitz 2000). Because both sit-and-wait and sit-and-pursue predators are relatively sedentary, the presence of their cues should be strongly indicative of predation risk. Broad-domain prey may respond to such predators by moving to other microhabitat locations. Similar habitat shifts appear less common when the prey is confronted by actively hunting broad-domain predators (Schmitz 2005). Cues generated by continuously moving active predators may saturate a given microhabitat and provide less information regarding risk compared to point-source cues (Table 1). Prey in such cue-saturated habitats must balance the costs of continuous vigilance and between-habitat movement (Lima 2002) against the low likelihood of encountering the actively hunting predator(s). If cues from actively hunting predators provide less information about local predation risk than cues from sedentary predators, prey may be less responsive to cues from active vs. sit-and-wait or sit-and-pursue predators (Lima and Bednekoff 1999).

We report the results of a meta-analysis of previously published literature testing whether several critical components of predator–prey interactions can be distilled into the two variables (i.e., predator hunting mode and predator habitat domain) that interact to determine the relative importance of NCEs in predator–prey interactions. Our analysis used a comprehensive database of 300 papers reporting the strength of NCEs in a wide range of terrestrial, marine, and freshwater ecosystems. Our findings suggest that predator hunting mode is an especially important determinant of NCE strength, and that, across a variety of taxa, knowledge of

simple predator characteristics can provide insight into how prey respond to their predators.

Methods

Literature survey

We expanded upon the data set compiled by Preisser et al. (2005) by searching the published literature for studies reporting on experimental manipulations involving predator risk treatments (e.g., caged predator, predator cues) and controls (e.g., no caged predator, absence of predator cues). We performed key word searches in several online databases (BIOSIS, JSTOR, and the Web of Knowledge Science Citation Index) as well as manually searching all volumes of *American Naturalist, Ecology, Oecologia,* and *Oikos* dating from 1990 to 2005 (for more detail, see Preisser et al. [2005]). We examined the bibliographies of pertinent papers for additional references. We searched for papers measuring one or more of the following prey-level variables: (1) growth (mass gain per time); (2) fecundity (offspring per female, offspring per brood); and (3) density (number of individuals per cage, population growth rate). In studies measuring one or more of those variables, we also searched for data on prey activity (proportion moving, number active per observation period, and so on).

Data extraction

For each study, we collected information on the sample size (individual organisms per replicate and replicates per treatment), mean, and variance (standard deviation or standard error) of the response variable in both the predator risk and control treatments. We extracted data directly from tables or text. We used digital calipers (Mitutoyo CD-6" C; Mitutoyo, Tokyo, Japan) to measure data in figures or graphs to within $\pm 1\%$ of the actual value (see Bolnick and Preisser [2005] for details).

Conditions other than habitat domain and predator hunting mode were sometimes manipulated within different experiments in the same study (e.g., some studies conducted independent experiments assessing the same interaction under low vs. high density or resource levels). Such studies may not be strictly independent (if only because they were conducted on the same pair of species by the same researchers), an issue that often arises in ecological data sets used for meta-analysis (Englund et al. 1999, Gurevitch and Hedges 1999, Gates 2002). Because it is important to examine predator–prey interactions across the full breadth of conditions in which they occur, and because decisions regarding data used for analysis can affect results and conclusions (Englund et al. 1999), we follow the general recommendations of Gates (2002; also see Gurevitch and Hedges 1999). We conducted a meta-analysis using our full data set as well as a more conservative ("truncated") analysis that uses one randomly selected observation for each case where there are multiple context-specific interactions for each predator–prey species pair in a given paper (Appendix A). This approach allows us to fully explore habitat domain and predator hunting mode across all possible ecological contexts, facilitates comparison with other meta-analyses of predator–prey interactions (Preisser et al. 2005, Stankowich and Blumstein 2005), and guards against the "pseudo-rigor" (sensu Englund et al. 1999) of conducting an analysis only on the full data set. Because of the qualitative agreement of these analyses (Fig. 1; Appendix A), we focus our discussion on the case where the full data set is used, but highlight areas where comparison of full and truncated data sets may be informative.

We classified each predator species in the database by hunting mode and each predator and prey species by habitat domain using information presented in the papers, searches through taxonomic databases and other published literature, and by directly consulting authors. We classified species about which we could find no information, or those species whose hunting modes or habitat domains varied as a function of ecological context, as "unknown." If predators were classified to genus rather than species (e.g., *Anax* spp. dragonfly larvae), we assigned modes and domains only where we felt confident that the entire genus behaved similarly.

The 806-line data set used for the analyses was generated using 193 papers, and included data on 103 predator species and 153 prey species (Appendices C–E). The database was biased towards aquatic systems (664 lines from freshwater systems and 72 lines from marine systems, compared with 70 lines from terrestrial systems). There was also a slight bias towards invertebrate predators (507 lines for invertebrate predators, 297 lines for vertebrate predators) and prey (427 lines for invertebrate prey, 379 lines for vertebrate prey).

Data analysis

We assessed the across-study effects of predator hunting mode, predator habitat domain, and the predator mode–domain combination using two effect size metrics; the use of multiple metrics is recommended for quantitative reviews of published data (Lajeunesse and Forbes 2003). We present results for the log response ratio, ln(RR), calculated as the ln of the mean experimental response divided by the mean control response (Hedges et al. 1999), and Hedges' d, calculated as the difference between a treatment and control mean standardized by the pooled standard deviation (Hedges and Olkin 1985). Because the use of log response ratios is recommended for ecological data (Hedges et al. 1999), we present results from the log response ratios in the text and, for cases where we used one randomly selected interaction per predator–prey species pair per paper, in Appendix A. We also provide the corresponding Hedges' d effect sizes in Appendix B; the results generated using Hedges' d were in qualitative agreement with those generated using the log response ratio.

We calculated mean effect sizes using a random-effects model in MetaWin 2.1.4 (Rosenberg et al. 2000).

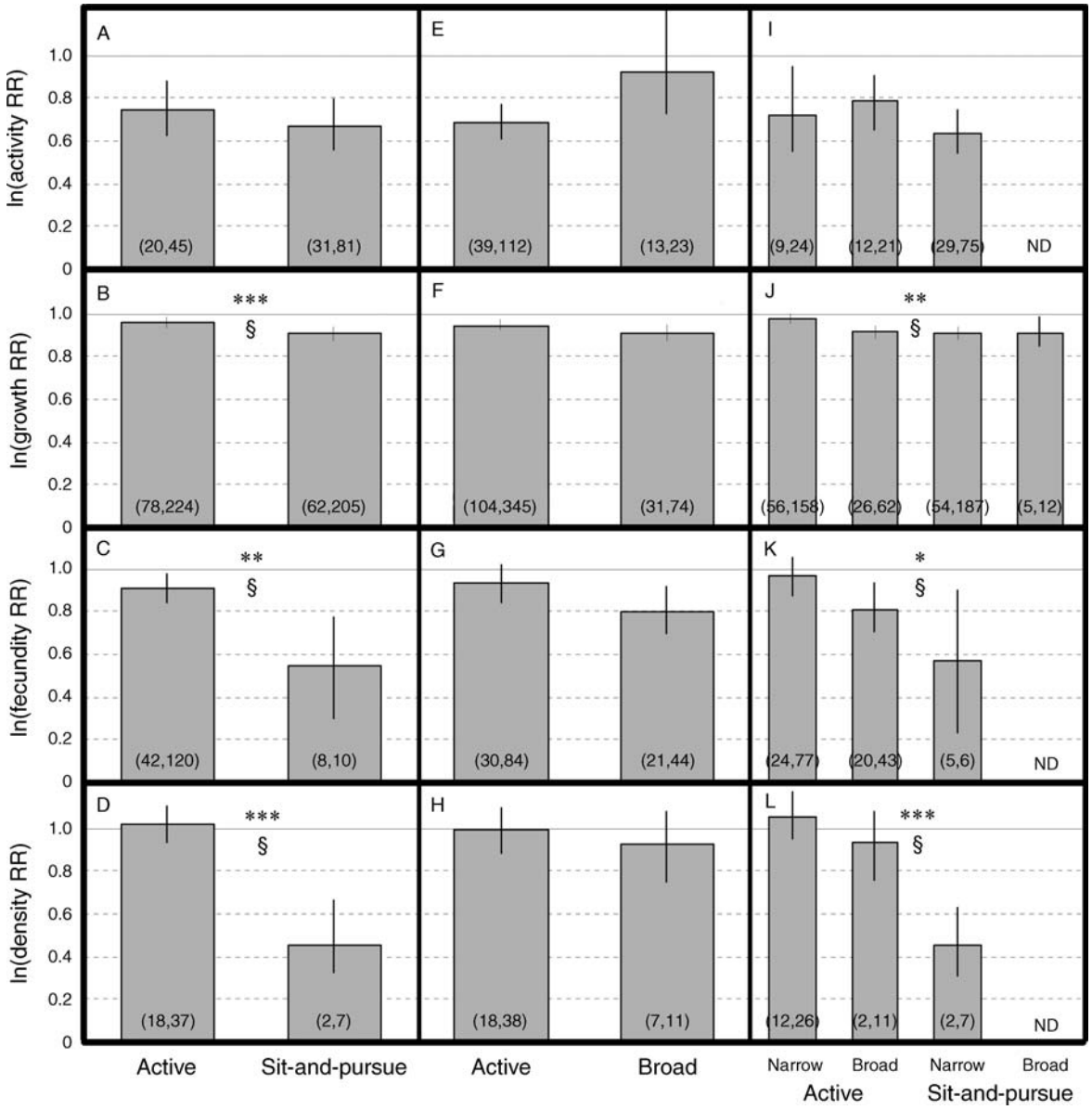

FIG. 1. Results of a meta-analysis using log response ratio effect sizes to examine the effect of predator hunting mode and predator habitat domain on the strength of nonconsumptive effects (NCEs) for a variety of prey response metrics. Values of ln(response ratio [RR]) <1.0 indicate predator presence has a harmful effect; values >1.0 indicate predator presence has a beneficial effect. Mean effect sizes were generated using a random-effects model, and a bootstrapping routine was used to generate the accompanying 95% confidence intervals. Numbers in parentheses at the base of each bar represent the number of published papers followed by the number of independent experiments contributing to a given mean. ND = insufficient data (fewer than five independent experiments). For initial values, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$. For adjusted values, § indicates significance at $\alpha = 0.05$ after using step-up false discovery rate (FDR) Bonferroni-type correction (Benjamini and Hochberg 1995). Because some species could not be classified by both habitat domain and hunting mode, the number of observations used for analyses of only habitat domain and only hunting mode are always greater than the summed number of observations across all habitat modes and domains.

We chose this model based on our expectation that different systems and ecological contexts have different "true" effect sizes (Gurevitch and Hedges 1999). Before beginning our analyses, we dealt with obviously outlying values by removing studies that were more than four standard deviations from the mean; all of these studies were $|d| > 5$ (33/839 total lines). The 33 removed studies represented 15 papers (19/33 studies came from five papers), and had a mean $|d| \pm \text{SE} = 9.86 \pm 1.649$. Because our data appeared non-normally distributed, we used a bootstrapping routine to calculate confidence intervals. We calculated mean effect sizes and bootstrapped confidence intervals separately for each response variable and used chi-square tests to assess the

significance of predator hunting mode and habitat domain. In addition to reporting the initial P values, we also report adjusted 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 tested for the effect of potential publication bias by calculating Spearman's rank-order correlation, r_S, a statistic describing the relationship between the standardized effect size and across-study sample size (Begg and Mazumdar 1994, Rosenberg et al. 2000). If potential publication bias was detected (Spearman's r_S with $P < 0.05$), we used funnel plot analysis to visually identify outliers for removal (Begg and Mazumdar 1994, Palmer 1999, Rosenberg et al. 2000). We also calculated Rosenthal's fail-safe number, the number of unpublished studies of zero effect necessary to reduce d to negligible ($0.2 > d > -0.2$) levels, for each data set.

Results

Only five of 153 prey species in our data set could be classified as having a narrow habitat domain (Appendix C). Given the relative lack of data on this group, we chose to exclude data from narrow-domain prey and limit our analyses to prey with broad habitat domains. Although we found data on 68 actively hunting predator species and 23 sit-and-pursue predator species, we were only able to find data on six predator species with a sit-and-wait hunting mode. We obtained habitat domain data on 29 active broad-domain (ACT-B) predator species, 33 active narrow-domain (ACT-N) species, four sit-and-pursue broad-domain (SAP-B) species, 15 sit-and-pursue narrow-domain (SAP-N) species, and six sit-and-wait narrow-domain predator species (Appendix D). Rather than attempt to draw general conclusions from such a small number of sit-and-wait predator species, we chose to exclude sit-and-wait predators from our analyses. Although we found only four predator species that had both a sit-and-pursue hunting mode and a broad habitat domain, we chose to analyze data from these species in order to examine all four mode × domain combinations. In light of the small sample size, however, the results from this group should be treated with caution.

Predator hunting mode

Prey activity in the presence of sit-and-pursue predator cues was not significantly lower than in the presence of active predators (Fig. 1A; $Q = 1.32$, $P = 0.41$, P_{adj} nonsignificant [NS] at $\alpha = 0.05$). However, life history variables showed that prey discriminated between cues from sit-and-pursue vs. active predators. Prey exposed to sit-and-pursue predator cues experienced greater reductions in growth (Fig. 1B; $Q = 24.7$, $P = 0.004$, $P_{adj} < 0.05$), fecundity (Fig. 1C; $Q = 16.1$, $P = 0.008$, $P_{adj} < 0.05$), and density (Fig. 1D; $Q = 11.8$, $P = 0.009$, $P_{adj} < 0.05$) than when exposed to cues from active predators. In the truncated analysis, cues from sit-and-pursue predators decreased both activity and fecundity more than did cues from active predators (Appendix A); although the adjusted P values were nonsignificant, these results remain qualitatively consistent with the findings of the full analysis.

Predator habitat domain

Predator habitat domain did not affect any prey life history variables (Fig. 1E–H). There were, however, marginally significant trends towards a greater reduction in prey activity ($Q = 6.10$, $P = 0.055$, P_{adj} = NS) and fecundity ($Q = 5.44$, $P = 0.077$, P_{adj} = NS) in the presence of cues from broad-domain vs. narrow-domain predators. There was no effect of predator habitat domain on any of the response metrics in the truncated analysis (Appendix A).

Predator mode–domain framework

When the predator hunting mode–habitat domain combinations were compared with each other, the strongest differences were between narrow-domain predators with a sit-and-pursue vs. active hunting mode (Fig. 1I–L). The life history variables growth, fecundity, and density showed a consistent pattern: prey were least responsive to cues from ACT-N predators, marginally more responsive to ACT-B predators, and most responsive to SAP-N predators (growth, Fig. 1J, $Q = 36.4$, $P = 0.007$, $P_{adj} < 0.05$; fecundity, Fig. 1K, $Q = 16.9$, $P = 0.012$, $P_{adj} < 0.05$; density, Fig. 1L, $Q = 31.1$, $P = 0.002$, $P_{adj} < 0.05$). When the broad-domain vs. narrow-domain comparison was limited to actively hunting predators, there was no effect of habitat domain on either activity ($Q = 2.66$, $P = 0.15$, P_{adj} = NS) or density ($Q = 2.09$, $P = 0.37$, P_{adj} = NS). However, both prey growth ($Q = 15.1$, $P_{adj} < 0.05$) and fecundity ($Q = 7.37$, $P_{adj} < 0.05$) were more affected by cues from ACT-B than ACT-N predators. Only the growth data set was large enough to allow us to compare prey response to SAP-B predators to the other combinations. There was no difference between this mode–domain combination and the other three (Fig. 1J); this may, however, be at least partially due to the relative lack of data on SAP-B predators (five studies, 12 lines). Although there was no significant effect of predator mode–domain on any of the response metrics in the truncated analysis (Appendix A), the results qualitatively agree with those emerging from the full analysis.

Publication bias

There was no indication of publication bias (Spearman's r_S with $P > 0.05$) in Hedges' d analyses using prey activity, fecundity, and density (Rosenthal's fail-safe number = 42 809, 2097, and 77, respectively). However, Spearman's r_S for the growth data set was significant ($P < 0.05$). We therefore used a funnel plot analysis to identify and remove five (out of 449 lines in the growth data set) unusually large negative outliers with d values of −4.97, −4.79, −3.63, −2.86, and −2.42. Removing

these outliers removed the effect of potential publication bias (Spearman's r_S with $P > 0.05$, Rosenthal's fail-safe number = 90 263). In response ratio (RR) analyses, none of the data sets showed signs of publication bias (all r_S with $P > 0.05$).

Discussion

Predators affect prey populations via consumption or the induction of energetically costly antipredator traits (nonconsumptive effects, NCEs). An important challenge in community ecology is identifying a set of functional characteristics capable of predicting changes in the strength of CEs and NCEs. Previous efforts to identify such characteristics have focused on predator density or traits such as body size and gape width; these efforts have had mixed success because the specific characteristics do not lead to consistent outcomes (for a review, see Chalcraft and Resetarits [2003]). Our analyses indicate that a predator's hunting mode and, to a lesser extent, habitat domain provides important information for predicting the relative strength of the response of broad-domain prey to predator cues (Fig. 1). Especially in the case of aquatic systems, our work suggests that prey from a variety of taxa can discriminate among predator cues and assess the information provided by these cues regarding predation risk.

Although prey activity was affected by neither hunting mode nor habitat domain in the full analysis, it was dramatically reduced by the presence of predator cues (Fig. 1). The lack of a main effect of hunting mode and habitat domain on activity may underscore the effectiveness of activity reduction as a general strategy (especially in marine and freshwater systems) for avoiding predation (Lima and Bednekoff 1999). Similar "general" strategies for risk reduction may also operate in terms of habitat selection (e.g., rodents avoid risky places rather than specific predator cues; Orrock et al. 2004). Although the truncated analysis used fewer total observations than the full analysis, it still found greater reductions in activity due to sit-and-pursue predators (before adjustment for multiple tests; Appendix A). This difference may reflect the context-dependent nature of prey behavioral changes; for instance, predation risk may substantially impact well-fed prey but have little effect on hungry prey. In contrast to the full analysis, the truncated analysis lessens the potential impact of ecological context on the overall effect size by randomly choosing a single predator–prey species pair interaction per paper.

Cues from sit-and-pursue predators evoked greater reductions in prey growth, fecundity, and density than did cues from active predators (Fig. 1). These responses may arise because cues from relatively sedentary predators (i.e., those species with sit-and-wait or sit-and-pursue hunting modes) may provide reliable information on predator proximity that substantially increases the ability of prey to avoid attack. Similarly, cues from actively hunting predators, however, may be less indicative of actual predator presence and imminent predation risk, so they provide relatively little information to prey and thus evoke less response. Since the movement of freely ranging active predators might result in the dilution of their cues over a wide area, an alternate interpretation of our results might be that the observed difference between predator hunting modes can be attributed to prey encountering dilute cues from active predators and concentrated cues from sit-and-pursue predators. This explanation seems unlikely, however, in light of the fact that the vast majority (>80%) of the surveyed studies employed designs in which the predator was either (A) caged or otherwise confined, or (B) present via the deliberate introduction of cues. Results from the truncated analysis qualitatively support the full analysis (Appendix A), although the growth responses are no longer significant and we had too little data to calculate a density response for sit-and-pursue predators. The fact that SAP predator cues were more than twice as effective at reducing prey growth (8.0% decrease vs. 3.5% decrease for sit-and-pursue and active predators, respectively) in the full analysis suggests that the reduced number of observations in the truncated analysis (202 total observations, vs. 429 in the full analysis) decreased our ability to detect such subtle but important differences in effect size.

In contrast to the strong main effect of hunting mode when averaged across predator habitat domain, there was no significant main effect of predator habitat domain on NCE strength when studies were pooled across predator hunting mode. Although this result ran counter to our expectation that narrow-domain predator cues should evoke a greater response than cues from broad-domain predators (Table 1), we can envision several potential explanations for this finding. One possible explanation is that the diffusion of cues across habitat boundaries may reduce the importance of habitat domain relative to hunting mode. Predators are also often more mobile and have a larger home range than their prey; it is possible that the home range of even narrow-domain predators may be so large relative to that of their prey that both narrow-domain and broad-domain predators evoke the same response. Predators may also change their patterns of habitat use depending upon prey availability and/or abiotic factors (Sih 2005). In contrast, the clear behavioral and morphological correlates of predator hunting mode (Schoener 1971, Huey and Pianka 1981) may make this characteristic less labile (e.g., sit-and-pursue predators may not readily become active predators) and more indicative of the threat posed by that predator. Finally, because the vast majority of broad-domain studies involved active predators, our analysis of habitat domain unavoidably compared active broad-domain (ACT-B) predators with narrow-domain predators from both hunting modes; this lack of sit-and-pursue broad-domain (SAP-B) predators may effectively reduce our ability to detect the main effect of habitat domain when pooling across hunting mode.

An explicit comparison of the three most common mode–domain combinations helps shed light on the patterns observed for main effects. First, cues from sit-and-pursue narrow-domain (SAP-N) predators evoked large changes in prey growth, fecundity, and density (Fig. 1). In contrast, active narrow-domain (ACT-N) predators consistently caused the smallest response in prey growth, fecundity, and density. Prey responses to ACT-B predators were either intermediate or more similar to the response evoked by SAP-N predators. While the substantial difference between SAP-N and ACT-N predators is likely responsible for the significant effect of hunting mode, averaging across hunting modes to calculate a "mean" narrow-domain response may obscure differences between narrow-domain and broad-domain predators. When only actively hunting predators are compared, cues from ACT-B predators caused greater reductions in prey growth and fecundity than cues from ACT-N predators. Analyses of these mode–domain combinations suggest that, at least within a particular foraging mode, predator domain may affect NCE strength.

The paucity of SAP-B predators may reflect an ecological tradeoff among hunting modes and habitat domains. Sit-and-pursue predators are likely to be more effective when they are stealthy and cryptic, characteristics that may require specialization on a narrow range of potential habitats for maximal effectiveness (Scharf et al. 2006). Similarly, the lack of narrow-domain prey may simply reflect the ecological reality that most prey species have the potential to flee predators by moving through alternate habitats. Since the size and scope of our database makes it unlikely that sampling error per se is responsible, future studies are needed to ascertain whether the apparent paucity of SAP-B predators truly reflects the "ecological likelihood" of such a combination or merely a tendency for researchers to work with specific predator types.

The hunting mode–habitat domain hypothesis also has implications for predicting contingency in multiple predator effects on shared prey species (Schmitz 2007). Empirical synthesis indicates that these contingencies boil down to four general cases: substitutable, nonlinear due to predator–predator interference, nonlinear due to intraguild predation, and nonlinear due to predator–predator synergism (Schmitz 2007). Multiple predator species should have substitutable effects on a common prey species whenever the predators have spatially complementary habitat domains and the prey species have broad habitat domains. Nonlinear interference effects should arise when predator species have identical hunting modes and the habitat domains of predators and prey overlap completely in space. Nonlinear intraguild predation effects should arise whenever prey species have broad habitat domains and predators have overlapping narrow habitat domains with different hunting modes. Finally, nonlinear, synergistic effects should arise whenever prey species have narrow habitat domains and predator species have the same hunting mode and broad but overlapping habitat domains.

Our work adds to a growing consensus that predator identity "matters," while suggesting a new and testable hypothesis that the nonconsumptive effect of predators on prey may nonetheless be largely predictable based on a few readily determined functional predator traits. Although we were unavoidably limited by the relative lack of data on terrestrial systems, the size and scope of our database further suggests that our findings are relevant to a range of systems and taxa. In practical terms, the fact that sit-and-pursue predators evoke large NCEs means that estimates of direct prey mortality may underestimate the full impact of introduced or newly dominant species with this hunting mode. This may be important when, for example, the loss of top predators in an ecosystem results in an increase in smaller generalist predators (Crooks and Soule 1999) with different hunting modes and habitat domains. Similarly, introduced predators can hamper reintroductions of rare prey (e.g., Short et al. 1992) or drive some prey species extinct (Savidge 1987). The mode–domain framework thus provides a way to predict the strength of NCEs evoked by newly dominant predator species, and may also be useful for anticipating the impact of introduced predators on native prey populations. Finally, when modeling predator–prey interactions, our results also provide insight into when NCEs must be considered and when they may play a lesser role (for instance, in interactions involving active narrow-domain predators).

Acknowledgments

This work was improved by comments from Peter Abrams, Jon Grabowski, Scott Peacor, and two anonymous reviewers. This work was conducted as part of the "Does Fear Matter?" Working Group supported by the National Center for Ecological Analysis and Synthesis (NSF Grant #DEB-0072909) and the University of California, Santa Barbara. J. L. Orrock also acknowledges the National Science Foundation (NSF Grants #DEB-0444217 and #DEB-0502069) and NCEAS for support.

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APPENDIX A

A figure showing meta-analysis results calculated using the log response ratio effect size metric and a single randomly selected interaction per predator–prey species pair per published source (*Ecological Archives* E088-170-A1).

APPENDIX B

A figure showing meta-analysis results calculated using the Hedges' *d* effect size metric (*Ecological Archives* E088-170-A2).

APPENDIX C

A table showing the number of published references and total number of lines used in the meta-analysis for each combination of predator hunting mode, habitat domain, and taxonomic class (*Ecological Archives* E088-170-A3).

APPENDIX D

A table showing the number of published references and total number of lines used in the meta-analysis for each combination of prey habitat domain and taxonomic class (*Ecological Archives* E088-170-A4).

APPENDIX E

A table showing citation, system, predator hunting mode, habitat domain, and species (or closest given approximation), and prey species (or closest given approximation) for each article used in the meta-analysis (*Ecological Archives* E088-170-A5).