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The allometry of fear: interspecific relationships between body size and response to predation risk

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Citation: Preisser, E. L., and J. L. Orrock. 2012. The allometry of fear: interspecific relationships between body size and response to predation risk. Ecosphere 3(9):77. http://dx.doi.org/10.1890/ES12-00084.1

Abstract. Body size is associated with fundamental biological processes such as metabolism, movement, and the rate of reproduction and evolution. Although allometric principles should also influence the range of potential behavioral responses for a given organism, evidence for such large-scale and cross-taxon relationships is lacking. If they exist, scaling-related changes in behavior should be prominent in predator-prey interactions: body size affects the likelihood of attack and the costs of predator avoidance. We take a interspecific perspective on a traditionally intraspecific topic by using a 142-species data set containing organisms ranging over seven degrees of magnitude in body size to analyze the relationship between mean response to predation risk and both prey size and the predator : prey size ratio. We found a weak but significant relationship between two metrics of prey size (mean species-level prey mass and mean species-level predator : prey size ratio) and two of the five prey response variables: risk-induced changes in prey habitat use and prey fecundity were significantly correlated with prey body size and the predator : prey ratio. Risk-induced reductions in prey activity were positively correlated with prey mass. In contrast, there was no correlation between prey mass or the predator : prey size ratio and risk-induced changes in either prey growth and survival. We also document considerable variation in response to predation risk among taxa, highlighting that many additional factors contribute to the effects of predation risk on prey behavior, growth, fecundity, and survival. The weak but significant large-scale relationships we documented in our work suggest that allometric relationships may play a subtle role in structuring some of a prey organism's response to predation risk.

Key words: allometry; anti-predator behavior; body size; non-consumptive effects; predator-prey interactions.

Received 21 March 2012; revised 18 June 2012; accepted 17 July 2012; final version received 24 August 2012; **published** 18 September 2012. Corresponding Editor: J. Drake.

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Introduction

Body size is associated with many of the most fundamental processes of biology: metabolism and movement (Peters 1983, Schmidt-Nielsen 1984, Brown et al. 2004), rates of reproduction (Blueweiss et al. 1978, Peters 1983) and evolution (Allen et al. 2006), and the likelihood of extinction (Gaston and Blackburn 1995, Allen et al. 2006). Size-related properties can also affect responses to climate change (Gardner et al. 2011) as well as alter food web structure and dynamics (Brose 2010, Thierry et al. 2011). Predator-prey interactions are particularly affected by size considerations (Jackson and Dial 2011, Thierry et al. 2011); size can prove a refuge for both small and large prey (Brooks and Dodson 1965, Urban 2007b), and comparative studies have found broad support for a similar range of body-size ratios among consumers and their resources

(Brose et al. 2006).

Anti-predator behavior often plays an integral role in predator-prey interactions (Lima and Dill 1990, Peacor and Werner 2001, Caro 2005), and the relationship between prey body size and predation risk has been extensively explored in a number of taxa (e.g., Urban 2007b and references cited therein). Within a given taxa, there are a range of potentially interactive reasons why body size might affect anti-predator behavior: body size determines energetic demands (Kleiber 1947, Schmidt-Nielsen 1984, Brown et al. 2004) that, in turn, determine the cost of anti-predator behavior. For instance, larger or better-fed organisms should experience a lower cost of foraging reductions in response to predation risk than smaller or hungry organisms (Stephens and Krebs 1986, Lima and Bednekoff 1999). Larger body size also alters the likelihood of detection, attack, and capture by a predator (Brooks and Dodson 1965, Urban 2007b, Thierry et al. 2011) as well as predator-mediated competitive interactions (Peacor and Werner 2001). As one example, increased body size can increase the likelihood of prey detection but decrease the probability of capture by gape-limited predators (Urban 2007a). A key question emerging from studies that document a strong intraspecific signal of body size on predator-prey interactions is whether similar interspecific patterns also exist and, if so, the nature of the relationship(s).

A recent review (Dial et al. 2008) highlighted the fact that while broad allometric patterns have been explored in fields such as biogeography, community ecology, and evolutionary ecology (e.g., Brown et al. 2004), research into the effect of body-size scaling on behavior has lagged behind. They identify two factors as particular impediments to such efforts. First, inter-taxon comparisons are difficult because the type and range of available behavioral data often varies widely between taxa. Second, the high degree of intraspecific variability that many organisms exhibit is likely to obscure any broader interspecific relationships. Despite these challenges, it is likely that "...size-related functional influences on performance profoundly influence many aspects of animal behavior, such as how animals forage, fight, flee, perceive danger, respond to risk and interact with other individuals" (Dial et al. 2008:394). If so, research addressing such questions may provide important insights into the underlying impact of body size on behavior.

We report the results of the first comprehensive inter-taxon analysis on the role of body size in affecting predation-induced changes in behavior, growth, and fitness. Specifically, we use meta-analysis to examine species-level responses of prey to predation risk (e.g., visual, chemical, and/or tactile predator cues; Preisser and Bolnick 2008) as a function of both prey body size and the predator : prey body size ratio. A broad literature attests to the importance of examining intraspecific patterns: we complement this work with an interspecific analysis of data from 142 prey species from 11 taxonomic classes and 74 predator species from 12 classes whose body size ranges over seven orders of magnitude. Our aim in examining the relationship between prey size, predator : prey ratio, and responses to predation risk is to explore whether allometric principles provide an underlying framework for large-scale interspecific patterns of prey response to predation risk.

Methods

Literature search

We analyzed a large data set containing information on the strength of nonconsumptive effects (NCEs) of predation risk on prey. The data set includes information from 196 papers published prior to 2006. Our search methods are presented in detail elsewhere (Preisser et al. 2007); briefly, we began by carrying out key word searches in three online databases (BIOSIS, JSTOR, and Web of Knowledge Science Citation Index) for papers that reported the results of manipulative experiments reporting the response(s) of prey organisms to non-lethal predation risk (e.g., visual and/or olfactory cues, a caged or nonlethal predator, etc.). In each paper identified using this method, we searched both the cited literature and subsequent literature that cited it. Because we were primarily interested in population-level consequences of NCEs, we only used papers that include measurements of one or more of the following prey variables that have been shown to respond strongly to the risk of predation (Preisser and Bolnick 2008): somatic growth (i.e., mass gain per time), fecundity (i.e., offspring per individual, brood size), density, and survival. Because so little data were available on prey density, we chose not to analyze this response variable. We recorded data from any papers containing information on one or more of these variables. In addition, we recorded data from these papers regarding prey activity (distance moved, moves/hr, or other metrics assessing prey mobility) or open (i.e., non-refuge) habitat use (proportion of time spent in open versus refuge habitats, percentage of individuals in predator-accessible areas, or other metrics assessing prey presence in potentially risky habitats). In summary, our database contained information about five prey response variables: activity, habitat use, somatic growth, fecundity, and survival. To evaluate whether systematic differences in experimental duration and venue size might affect our results, we also recorded data on experimental length (in days) and size of the experimental arena (in m^3).

Body size information

For each study, we recorded any information regarding prey size at the beginning of the experiment. One hundred out of 196 papers (accounting for 483 of 1042 records in the database) used in our analysis reported data on prey mass; of the remainder, 82 papers (424/1042 records) reported data on prey developmental stage sufficient to estimate prey mass and 26 papers (135/1042 records) reported some measurement of prey length sufficient to estimate prey mass (the total number of papers exceeds 196 because some papers that reported data on multiple prey species used different metrics for each species). Because research assessing body-size relationships traditionally uses wet mass measurements (e.g., Kleiber 1947) and most papers provided data on prey mass, we chose this metric for our analyses. When data on prey size were reported using other metrics (e.g., Gosner stage, snout-vent length), we searched published journals, printed reference materials (e.g., Altman and Dittmer 1964), and online databases (e.g., Froese and Pauly 2011) for regressions or other information necessary to convert these measurements into wet mass. We only employed regressions or searched for mass information when organisms were identified to species.

Although we gathered similar data on predators, we found that information regarding predator mass was often lacking or ambiguous (e.g., reporting only the sex of the predator; Trussell and Nicklin 2002). Only 24 of 196 papers (accounting for 100 of 1042 records in the database) provided data on predator mass; of the remainder, 60 papers (309/1042 records) provided data on predator developmental stage sufficient to estimate predator mass, 64 papers (296/1042 records) provided data on some aspect of predator length or width sufficient to estimate predator mass, and the rest provided insufficient or no information. Compounding the problem was the fact that 17 papers (representing 103 records in the database) only identified predators to the genus level (e.g., Anax sp.; Peacor and Werner 2001). Although most of these papers reported some measurement of predator developmental stage and/or length, the lack of species-level information precluded us from confidently estimating wet mass. The relative paucity of predator data, and the consideration that inaccuracy in either species' measurement can induce significant error in calculating size ratios, are important to keep in mind when interpreting results obtained using an analysis of predator : prey ratios. Because of this, our database may be less suited to an analysis of the predator : prey ratio than to prey body size per se.

Data analysis

We used data on the mean and variance in the control and experimental groups in each published study to calculate the log response ratio effect size (predator risk treatment in the numerator, control treatment in the denominator) for each study in the dataset. By standardizing risk-induced changes relative to control values, the approach facilitates the comparison of multiple studies and is recommended for ecological meta-analysis (Gurevitch and Hedges 1999). Because many prey species were the subject of multiple experiments assessing their response to predation risk, we used the effect size and variance from each study to calculate a single cumulative mean effect size per species per response variable. A detailed explanation of the effect size calculation is contained in Appendix A. Data from individual studies was also used to calculate a single value for mean prey mass at the time of the experiment per species per response variable; we accounted for differences in sample size by weighting mass measurements from each study by the total number of individual prey measured.

We used meta-analysis to assess the species-level relationship between prey wet mass in grams and predator : prey wet mass ratio, coded as continuous random variables, and response to predation risk for two behavioral variables (prey activity and open habitat use), somatic growth, and two fitness-related variables (prey fecundity and survival). Our treatment of prey wet mass and predator : prey wet mass ratio as random variables reflects our assumption that there is a truly random component to between-study differences in effect sizes and is consistent with our goal of broad-sense inference. To determine whether taxon-specific patterns were driving our results, we also analyzed the species-level relationship between mass and effect size separately for the two most common classes in each response variable for both prey wet mass and predator : prey mass ratio. All meta-analyses were performed used Metawin 2.14 (Rosenberg et al. 2000).

To determine whether our findings might be the result of confounding factors such as experimental duration or size of experimental venue, we used linear regression to assess the experiment-level relationship between each variable and prey body size. If multiple predator-prey species pairs were tested within the same experiment, data from each predator-prey pair was added as a separate data point. If there was a significant relationship, we used meta-analysis to assess the relationship between the factor, coded as a continuous variable in a fixed effects model, and effect size for the five prey variables.

Results

Meta-analysis of prey body size

Experimental duration and venue size.—There was no experiment-level relationship between experimental duration and prey size (linear regression, $F_{1,150} = 0.53$, $p = 0.47$) or between the size of the experimental venue and prey size ($F_{1,182} = 0.54$, $p = 0.46$). Because there was no significant relationship between prey size and either variable, we did not conduct individual meta-analyses of the relationship between these factors and the response variables.

Taxonomic width and breadth.—Our 196-paper dataset contained data on 142 prey species from 12 classes: Actinopterygii, Amphibia, Arachnida, Aves, Bivalvia, Branchiopoda, Gastropoda, Insecta, Isopoda, Malacostraca, Mammalia, and Reptilia. The classes Amphibia and Insecta dominated the data set, with 42 and 41 species respectively. Conversely, the classes Aves and Arachnida were represented by four and two species, respectively, and the class Reptilia contributed a single species. A list of all species and studies is contained in Appendix B.

Behavioral metrics (Fig. 1).—For both prey activity and open habitat use, the species-level response to predation risk increased (shown by a greater departure from zero) as a function of body mass. In terms of prey activity, every 10-fold increase in body mass increased the magnitude of the response to predation risk by 6.7 ± 4.9% SE ($n = 47$ species; $y = -0.0671x - 0.575$, $p[\text{rand}] = 0.018$). The use of open (i.e., non-refuge) habitats showed a similar trend, decreasing 5.5 ± 6.0% for every 10-fold increase in species-level body mass ($n = 33$ species; $y = -0.0552x - 0.3389$, $p[\text{rand}] = 0.006$).

When the most abundant classes were analyzed individually, there were no consistent within-group relationships between body size and response to predation risk (Table 1). Reductions in activity were not correlated with body mass in either the Amphibia and Insecta, the two most represented classes (20 and 19 species, respectively; $p[\text{rand}] > 0.18$ in both cases). Body mass was correlated with increased use of open habitats for the class Insecta ($y = -0.535x - 1.177$, $p = 0.001$) but not for Amphibia.

Growth and fitness-related metrics (Fig. 2).—Larger-bodied species experienced a slight but significantly higher cost of predation risk for two of three metrics (Fig. 2). Risk-related reductions in fecundity increased by 2.4 ± 2.1% for every 10-fold increase in body mass ($n = 32$ species: $y = -0.0239x - 0.302$, $p[\text{rand}] = 0.001$). There was a marginally significant negative relationship between body size and survival ($n = 37$: $y = -0.0007x - 0.0373$, $p[\text{rand}] = 0.083$). There was no relationship between risk and size in growth, the dataset for which the most species-level information is available ($n = 108$: $y = 0.0139x - 0.0646$, $p[\text{rand}] = 0.133$).

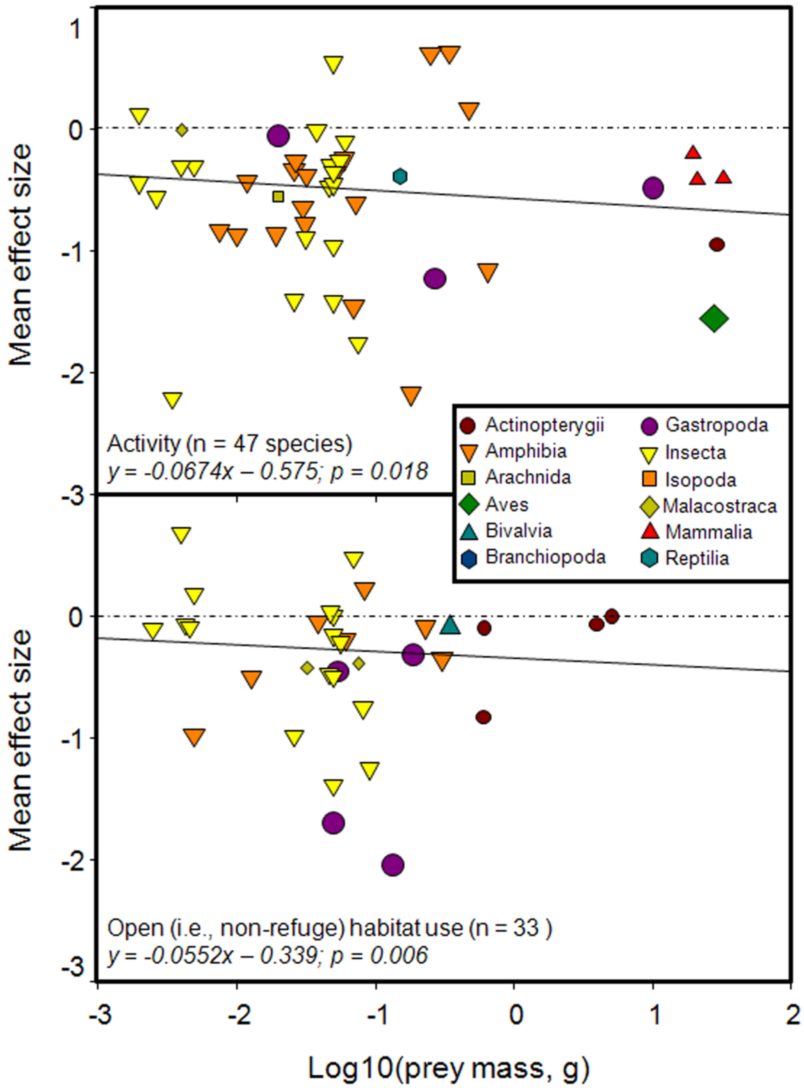

Fig. 1. Relationship between prey body mass and risk-induced behavioral changes, measured as the response ratio effect size. Dotted line indicates zero effect; solid line indicates best-fit linear regression. Symbols indicate cumulative effect size and mean body mass for each prey species included in analysis. Symbol size is weighted by $\log_{10}$ (1/cumulative variance).

As with the behavioral metrics, there was no consistent intra-class relationship between body mass and response to predation risk for the two most abundant classes in each response variable (Table 1). Survival was positively correlated with size in the Insecta (7 species), fecundity was negatively correlated with size in the Mammalia (6 species), and there was no correlation between body size and predation risk within the other five most abundant families.

Meta-analysis of predator : prey body size ratio

Taxonomic width and breadth.—Our dataset contained data on 162 predator-prey species pairs (74 predator species, 106 prey species). There were fewer prey species represented in the analysis of predator : prey ratios (106 species) than in the prey species analysis (142 species) because cases where the prey was identified to species but the predator was identified only to genus were included in the prey species analysis

Table 1. Within-class relationships between prey body mass (top) and predator : prey ratio (bottom) and response to predation risk for species in the two most abundant prey classes for each of the five tested variables. *P*[rand] tests the null hypothesis that the slope of the relationship equals zero.

Response variable	Class	*N*	Slope[SE]	SE	*p*[rand]
Intra-taxon analyses of prey mass					
Activity	Amphibia	18	0.339	0.153	0.975
Activity	Insecta	19	−0.120	0.190	0.181
Refuge habitat use	Amphibia	7	0.244	0.197	0.184
Refuge habitat use	Insecta	16	−0.535	0.208	**0.001**
Growth	Amphibia	41	0.019	0.019	0.164
Growth	Insecta	21	0.001	0.039	0.34
Fecundity	Branchiopoda	6	−0.040	0.068	0.434
Fecundity	Insecta	11	−0.007	0.031	0.341
Fecundity	Mammalia	6	−0.934	0.423	**0.05**
Survival	Amphibia	22	−0.014	0.020	0.35
Survival	Insecta	7	0.148	0.038	**0.01**
Intra-taxon analyses of predator : prey mass ratio					
Activity	Amphibia	26	−0.229	0.107	0.89
Activity	Insecta	11	−0.199	0.087	0.09
Refuge habitat use	Amphibia	7	0.033	0.056	0.091
Refuge habitat use	Insecta	8	0.330	0.173	**0.002**
Growth	Amphibia	60	−0.018	0.011	0.824
Growth	Insecta	15	−0.005	0.019	0.523
Fecundity	Branchiopoda	11	0.042	0.028	0.081
Fecundity	Insecta	8	−0.137	0.058	0.963
Fecundity	Mammalia	2	n/a		n/a
Survival	Amphibia	24	0.004	0.009	0.471
Survival	Insecta	7	0.060	0.020	0.13

Note: For analyses of prey mass, N = number of prey species; for predator : prey mass ratio, N = number of predator-prey pairs.

but not the predator-prey species analysis.

Predators from 12 classes were represented in the dataset: Actinopterygii, Amphibia, Arachnida, Asteriodea, Aves, Gastropoda, Hirudinea, Insecta, Isopoda, Malacostraca, Mammalia, and Reptilia. The classes Actinopterygii (29 species, 114 entries in the dataset) and Insecta (21 species, 109 entries) made up 68% of the predator species and 82% of the entries in the dataset. The other predator classes were represented by six or fewer species and, with the exception of Malacostraca (13 entries), six or fewer entries in the dataset.

Prey species from 11 classes were represented in the dataset: Actinopterygii, Amphibia, Arachnida, Aves, Bivalvia, Branchiopoda, Gastropoda, Insecta, Malacostraca, Mammalia, and Reptilia. The most represented classes were the Amphibia (36 species, 125 entries in the dataset) and Insecta (33 species, 54 entries in the dataset), which made up 63% of species and 66% of entries in the dataset. Aves and Reptilia were the least represented prey classes in the dataset, with one species each and one and two dataset entries, respectively.

Behavioral metrics.—There was no consistent relationship between predator : prey body size ratio and behavioral responses to predation risk (Fig. 3). In terms of open habitat use, every 10-fold increase in the predator : prey body size ratio decreased the magnitude of the response to predation risk by 8.1 ± 4.0% SE (23 predator-prey species pairs; $y = 0.0813x - 0.3375$, $p[\text{rand}] = 0.001$). Thus, prey response decreased as the size of their predators increased. There were more data available for prey activity (46 predator-prey species pairs); for this metric, there was no significant relationship between body size ratio and response to predation risk ($y = -0.169x - 0.251$, $p[\text{rand}] = 0.62$).

Growth and fitness-related metrics.—There was no consistent relationship between the predator : prey body size ratio and fitness-related responses to predation risk (Fig. 4). The effect of predation risk on prey fecundity (33 predator-prey species pairs) decreased significantly by 8.1 ± 2.5% SE for every 10-fold increase in the predator : prey body size ratio ($y = 0.081x - 0.386$, $p[\text{rand}] = 0.001$). In contrast, the two metrics for which more data was available (growth = 108 species pairs; survival = 41 species pairs) showed no relationship between body size ratio and the response to predation risk (both $p >$

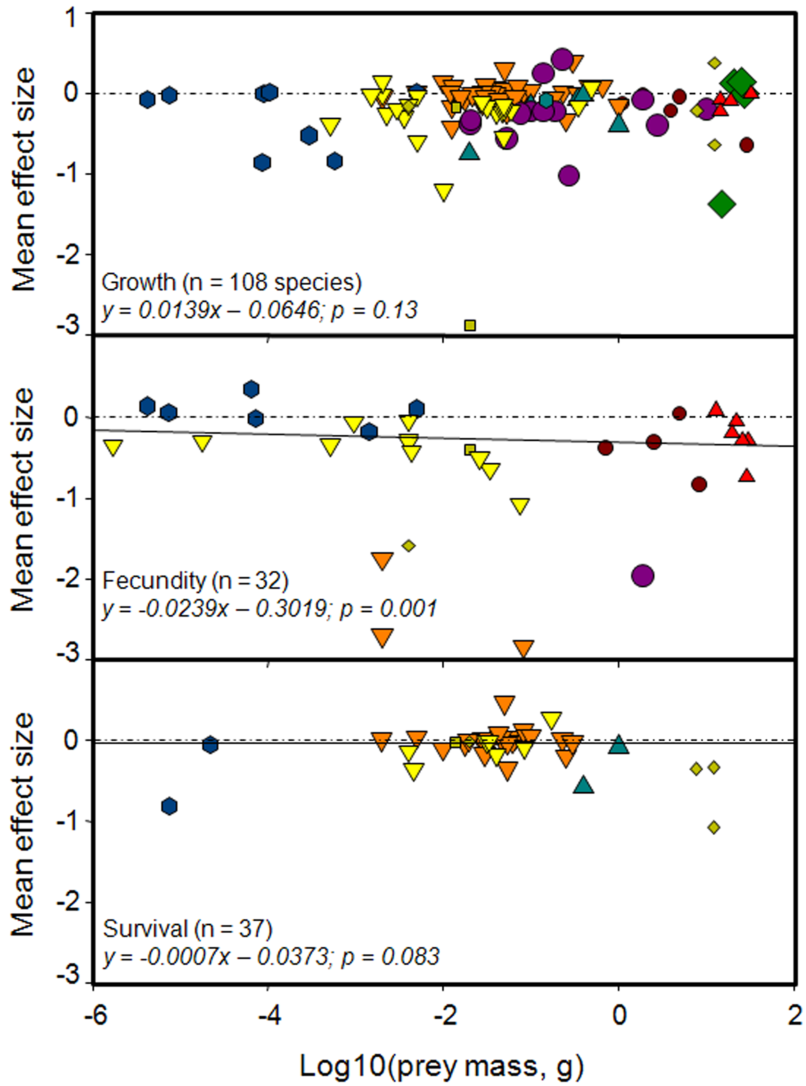

Fig. 2. Relationship between prey body mass and fitness-related metrics due to predation risk, measured as the response ratio effect size. Dotted line indicates zero effect; solid line indicates best-fit linear regression. Symbols indicate cumulative effect size and mean body mass for each prey species included in analysis. Symbol legend and weighting as in Fig. 1.

0.15).

Discussion

Strong interspecific relationships have been documented between body size and a variety of physiological and life-history parameters (Peters 1983, Schmidt-Nielsen 1984, Brown et al. 2004), but the potential for similar large-scale relationships exist between body size and behavior has been largely unexplored. As predicted (Dial et al. 2008),we found that (1) the cross-taxon relationships between body size and response to predation risk, although often significant, were uniformly weak; (2) they depended strongly on the prey characteristic being measured (i.e., behavioral metrics or growth- and fitness-related metrics) and (3) they varied as a function of the size metric (i.e., prey mass or the predator : prey ratio). Taken together, these findings suggest that body size, in addition to its impacts on individual organisms, may also influence some prey

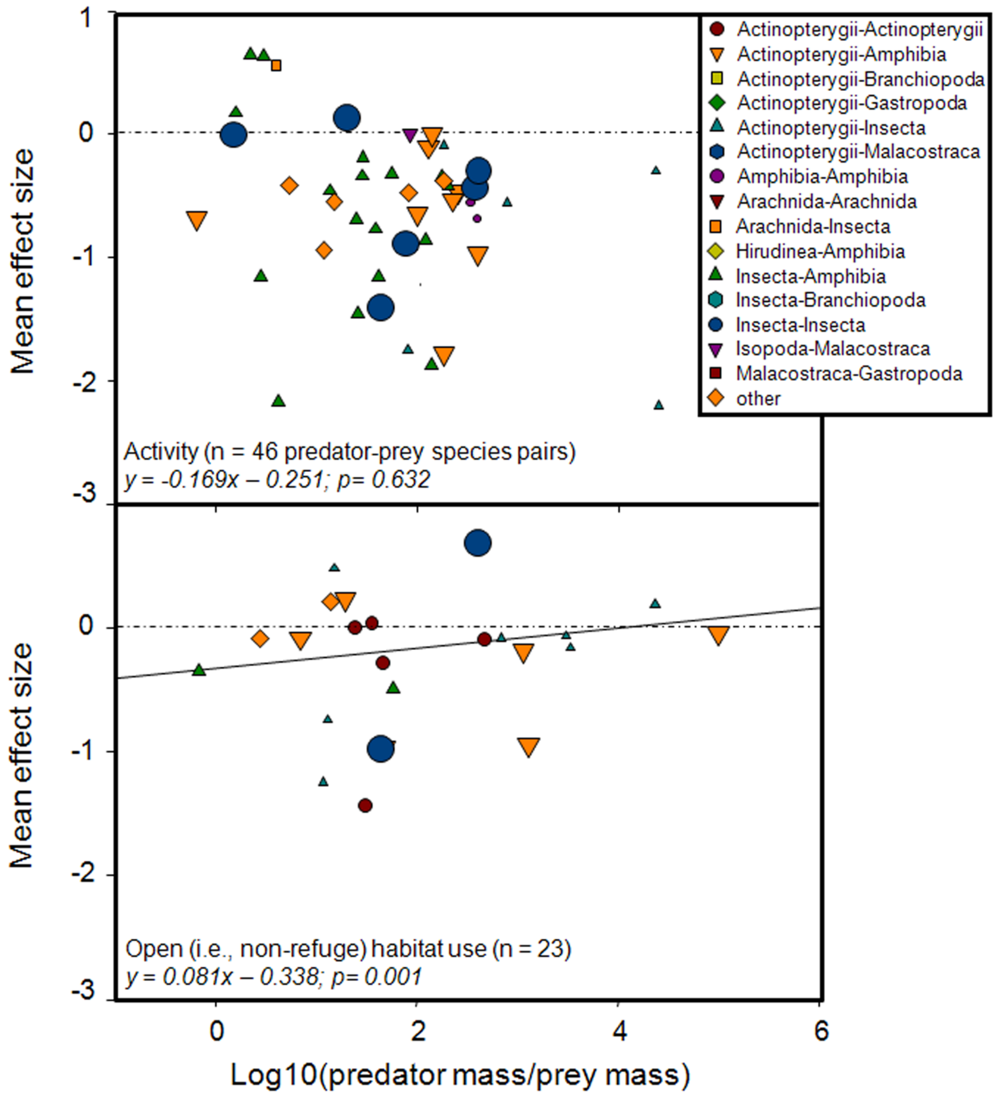

Fig. 3. Relationship between predator : prey body mass ratio and prey behavioral changes due to predation risk, measured as the response ratio effect size. Dotted line indicates zero effect; solid line indicates best-fit linear regression (given only when $p < 0.10$). Symbols indicate cumulative effect size and mean $\log_{10}$ (predator body mass/prey body mass) for each predator-prey species pair included in analysis. Symbol legends give class of predator species before hyphen, and class of prey species after hyphen. Symbol size is weighted by $\log_{10}$ (1/cumulative variance).

responses at the inter-taxon level. Importantly, our analyses of both prey size and predator : prey ratio also documented substantial interspecific variation in the effect of risk on prey, a finding that accords with our understanding of behavior as sensitive to changes in biotic and abiotic conditions (Dial et al. 2008). Despite this variation and the often-weak nature of the relationship, our results regarding prey body size and the predator : prey size ratio imply that allometric principles already known to affect metabolism, life-history characteristics, and evolution (Peters 1983, Brown et al. 2004, Allen et al. 2006) may also provide insights into behavior.

The observed trends in the size-behavior relationship may reflect size-related differences

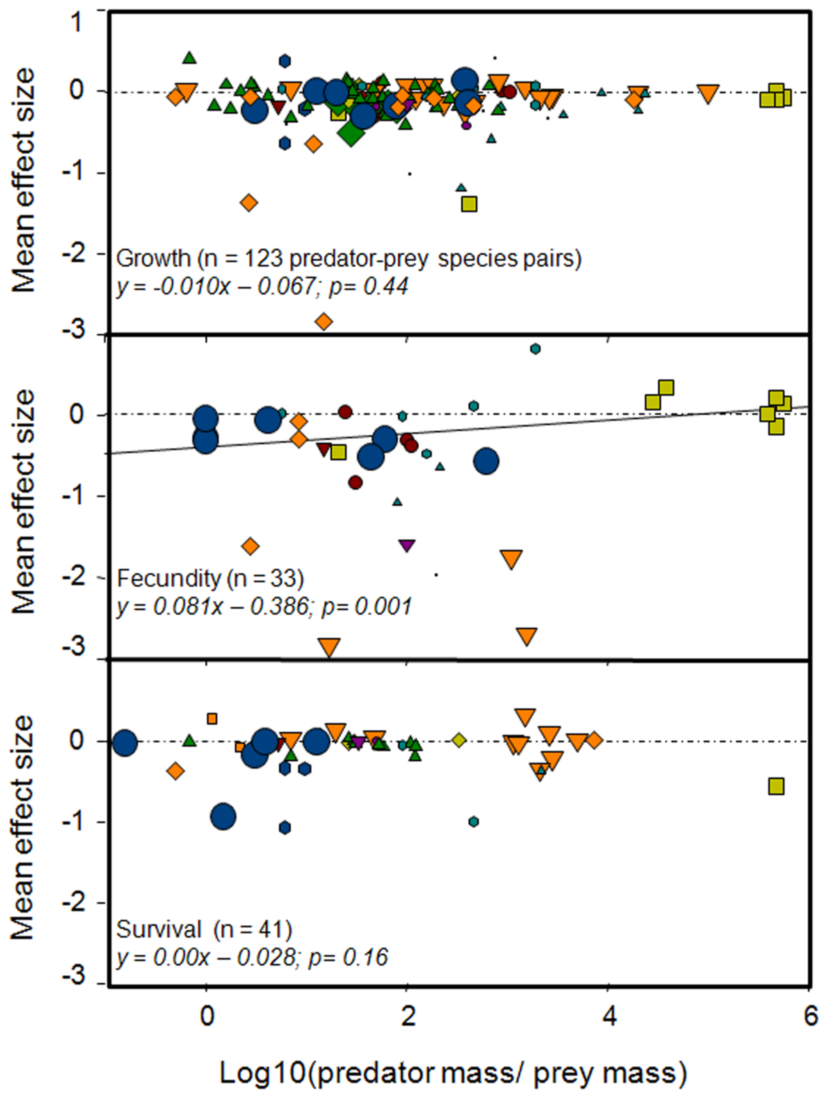

Fig. 4. Relationship between predator : prey body mass ratio and prey growth and fitness-related metrics due to predation risk, measured as the response ratio effect size. Dotted line indicates zero effect; solid line indicates best-fit linear regression (given only when $p < 0.10$). Symbols indicate cumulative effect size and mean $\log_{10}$ (predator body mass/prey body mass) for each species pair included in analysis. Symbol legend and weighting as in Fig. 3.

in metabolic rates. While larger organisms have greater overall metabolic costs, per-gram metabolic costs decrease as a function of body size (e.g., the 'mouse to elephant' curve; Schmidt-Nielsen 1984). Metabolic scaling in mammals (reviewed in Capellini et al. 2010), for instance, means that shrews and other small-bodied predators must spend far more time actively foraging than do larger predators. Predator cues force prey to balance the risk of attack with the rewards of activity (foraging, mating, territorial defense, etc.; Brown and Kotler 2004), and the costs of predator-induced reductions in activity should be higher for smaller organisms. More generally, there is increasing interest in how prey alter anti-predator behavior in response to temporal variation in both the duration and predictability of risk (i.e., the risk allocation hypothesis; Lima and Bednekoff 1999). Although our analyses of species-level data precludes an examination of temporal dynamics, our finding that larger species (organisms that generally possess greater energetic reserves and face a lower risk of predator-induced starvation) are more likely to reduce activity is consistent with the predictions of the risk allocation hypothesis.

Another potential explanation for our results involves scaling-related changes in organisms' power : mass ratios. Across a range of taxa, there is generally a negative relationship between body size and an organism's ability to rapidly accelerate (i.e., burst locomotor performance; Jackson and Dial 2011), change speeds, and maneuver. Such mass-specific differences in burst performance and maneuverability underlie the avian phenomena of 'predator mobbing', where individual or small groups of small-bodied prey surround and attack larger predators (Dial et al. 2008). This apparently risky strategy succeeds because, at close range, smaller birds are quicker and more maneuverable than their predators. These interactions may play out differently in aquatic systems, especially for small-bodied organisms that are expected to experience large differences in drag forces due to their relatively large amount of surface area relative to their volume and the viscosity and density of the surrounding aqueous fluid. Generally, however, size-related differences in propulsion imply that larger prey should require more warning to escape and thus respond more strongly to predation risk.

Body size can also affect response to predation risk by altering the likelihood that prey will detect predators and the likelihood of predator encounter. For some sensory modalities (e.g., vision; Mech and Zollner 2002) size may increase perceptual range and enable larger prey to more reliably detect and respond to cues (Stankowich and Blumstein 2005). Both empirical (Sinclair et al. 2003) and theoretical (Otto et al. 2007) research suggest that larger-bodied prey are fed upon by a less diverse predator assemblage than are smaller-bodied species, which would likely reduce relative predator encounter rates for larger prey. Although large prey may benefit from a size refuge from predation, larger prey are also eaten by larger predators (Brose et al. 2006) that are generally perceived as more threatening than smaller-bodied predators (Stankowich and Blumstein 2005). Because predation risk experiments almost always test prey responses to 'harmful' predators, larger-bodied prey may generally be exposed to cues from rarer but relatively more dangerous predators. In contrast, smaller species may be more likely to come from environments containing cues from a wider range of predator species, such that cues from one particular predator type may not be particularly informative relative to other indicators of risk (e.g., Orrock et al. 2004). Larger organisms also have larger home ranges (Kelt and Van Vuren 2001) and lower per-gram costs of movement (Peters 1983, Schmidt-Nielsen 1984); in addition, large-bodied predators may further reduce the per-unit-time likelihood of predator encounters for larger-bodied prey species. If predator cues are more indicative of an immediate threat to large-bodied prey, they might well react more strongly than do smaller species.

Following an encounter, the likelihood of predator attack (or prey escape) is strongly influenced by the body size of both predator and prey (Domenici 2001, Cooper and Stankowich 2010, Jackson and Dial 2011, Thierry et al. 2011). Although the relationship between body size and predator attack is undoubtedly influential in specific predator-prey interactions, it seems unlikely that this factor could produce a consistent cross-taxa relationship between prey size and predation risk. Predators seeking to maximize the energetic benefits of prey consumption may preferentially target large-bodied prey, providing smaller species with a refuge from attack (Brooks and Dodson 1965). Conversely, large body size reduces the risk posed by gape-limited predators (Urban 2007b). A unimodal size-risk relationship may also occur if predator handling time is lowest with optimally-sized prey: in such cases, prey smaller or larger than optimally-sized individuals are less likely to be attacked (Molles and Pietruszka 1987). Size-dependent anti-predator behavior may also be mediated by ontogenic changes in predator dietary preferences (e.g., Carbone et al. 1999). Another plausible post-encounter explanation for our findings is that large prey typically occur in lower densities than small-bodied organisms (Marquet 2002). As a result, large-bodied organisms that detect a predator cue may be more likely to be attacked since predators have fewer conspecifics from which to choose (i.e., the 'dilution' of predation risk; Lima and Dill 1990, Caro 2005). Because these explanations are likely to be functions of the interplay between predator, prey, and their environment, our cross-taxon study cannot robustly test their contribution to size-dependent anti-predator behavior.

In addition to highlighting significant cross-taxa relationships between body size and anti-predator behavior, another interesting outcome of our work is that, whereas behavioral responses to predation risk, especially refuge habitat use, scale with prey body size (Figs. 1–2), the slope of the relationship is weaker for fecundity, marginally significant for survival, and absent for growth (Fig. 2). The attenuation of the size-risk relationship when moving from behavior- to fitness-related metrics suggests that larger organisms are capable of compensating for their increased response to predation risk. This might arise via allocation towards growth at the expense of fecundity, a hypothesis supported by the non-significant relationship for growth and significant relationship for fecundity. While prey that forego growth are likely to substantially increase their mortality risk, iteroparous species that reduce their fecundity in response to predator cues may be able to compensate by increasing their subsequent reproductive efforts. The interpretation that larger organisms are capable of tolerating greater predator-mediated reductions in activity (Fig. 1) without incurring equivalent fitness-related costs in terms of survival and growth (Fig. 2) is also consistent with the lower relative energetic costs of reduced activity for larger-bodied prey (and thus in agreement with the risk allocation hypothesis; Lima and Bednekoff 1999). It is also possible that prey may be able to compensate physiologically for predator-induced behavioral changes (McPeek 2004). In agricultural systems, for instance, the presence of predators induces *Manduca sexta* caterpillars to reduce their feeding rates. This does not affect growth, however, because the caterpillars compensate via increased digestive efficiency (Kaplan and Thaler 2009).

We found that two different measures of body size, i.e., prey mass and the predator : prey mass ratio, were both correlated with interspecific trends in prey habitat use, fecundity, survival, and growth. However, changes in activity were significant for prey mass but not for the predator : prey ratio. As the number of studies used was similar for both prey mass and predator : prey ratio analyses (47 and 46 studies, respectively), the lack of agreement between these analyses may reflect differences in the quality of data used for each analysis. Perhaps because researchers working in this area use predator cues rather than the predators themselves, data on predator size is rarely reported and/or takes the form of species-specific measurements (e.g., larval instar). In contrast, prey size is virtually always reported, and often in terms of mass or length. The lower quality and quantity of information on predator size may have increased the amount of variation in our data on predator : prey size ratios and thus affected our analyses.

Biological realities may also contribute to the difference between prey mass and predator : prey size ratio we observed for prey activity. For example, experiments exploring predation risk often use chemical cue of predator presence rather than the predators themselves. Such cues may provide little information to the prey regarding predator size, especially for predators that exhibit substantial intraspecific variation in size (e.g., fish predators with indeterminate growth). The decision to reduce activity in such cases may be more reliably linked to prey body size in such experiments because (A) this quantity is known by the prey with much more accuracy than predator body size; and (B) prey size is a primary determinant of the costs of reduced activity, since larger prey are more likely to be able to afford a bout of reduced activity. As such, the prey size, not the ratio of predator : prey size, would be important in determining whether or not to reduce activity in these experiments. This contrasts with experiments on prey behavior when visual information about predators, and thus accurate information regarding predator size, is presented (Stankowich and Blumstein 2005).

While we believe that our work documents a hitherto unrecognized trend in prey behavior, our approach has a number of limitations. Our interest in the relationship between prey behavior and fitness meant that we only analyzed behavioral data from studies that also measured some metric of prey fitness. Relaxing this requirement would have increased the studies from which to draw, but would have precluded our comparisons of behavioral and fitness-level responses. Our reliance on published studies also means that systematic bias could have been introduced if relatively harmful predators were used in research on large-bodied prey species and relatively harmless predators were used in research on small-bodied prey species. While we cannot reject this possibility, we believe that the number of species tested and range of variables assessed makes such bias unlikely. The relatively low number of predator-prey species pairs in our dataset meant that we were also unable to examine predator-specific factors like hunting mode and habitat domain (Preisser et al. 2007). The hunting strategies employed by predators in our analysis varied widely, from actively-hunting species in both terrestrial and aquatic systems to sit-and-wait predators and others that are akin to browsers (e.g., predatory snails 'grazing' on sessile mussels). While such differences clearly affect predator-prey interactions, the data were insufficient to rigorously explore the impact of hunting mode or other subfactors at the cross-taxon level.

More generally, any meta-analytic approach to understanding broad-scale, cross-taxon patterns may be affected by the presence of systemic biases. In this work, we have evaluated our data for the presence of size-related biases where possible. However, although methodological factors like experimental duration or venue size did not correlate with body size and thus appear unlikely to explain our results, we did not account for factors like size-related differences in food resources, cue concentrations, or predator hunting mode. Even if we could address these issues, we cannot reject the hypothesis that another explanation (e.g., size-based variation in predator and/or prey developmental stage) exists for our findings. Such challenges might be better addressed via experiments testing a wide array of differently-sized organisms under standardized conditions. Such an experimental approach would be feasible but logistically challenging and still vulnerable to critique. As one example, experimental duration could be held constant or scaled to prey lifespan; both approaches are justifiable but explore different research questions. Ultimately, a challenge inherent in addressing cross-taxon questions at a broad scale is that many confounding factors may exist; we hope our synthetic work will catalyze the experimentation and methodological advances required to build upon the patterns we present here.

Although the influence of allometry is well-recognized in a number of other fields, our work suggests that cross-taxa constraints may also subtly structure behavioral patterns. Our work supports the prediction of Dial et al. (2008) that similar patterns may not be manifest at the within-class level (Table 1; also see Fig. 3 in Dial et al. 2008); this suggests that the predation risk-body size relationship for a given group of organisms is primarily a function of their ecological and evolutionary context. Our study illustrates that body size is weakly but consistently indicative of broad-scale taxonomic variation in anti-predator behavior. The considerable unexplained variation that we document implies that body size is likely only one of many factors that mediate the effect of predation risk on prey behavior and fitness. Ultimately, discriminating between the mechanisms capable of producing such a large-scale relationship between body size and anti-predator behavior will require research examining behavioral trends at both the within- and between-taxa level and as a function of factors such as prey resources (Preisser et al. 2009). Such questions are especially important given large-bodied organisms' relative vulnerability to anthropogenic disturbance and global warming (Gardner et al. 2011). Future studies that elucidate these mechanisms and traits will be critical for understanding the processes that mediate this and perhaps other equally subtle broad-scale trends in behavior.

Acknowledgments

Both authors contributed equally to this work. A. Beckerman, K. Dial, J. Drake, M. Urban, and two anonymous reviewers provided helpful comments on this manuscript. M. Benard, D. Bolnick, J. Grabowski, and J. Hoisington-Lopez assisted with data collection. 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. ELP acknowledges NSF Grant #DEB-0715504 for support.

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Supplemental Material

Appendix A

Calculations of Mean Effect Size and Variance

Because many prey species were the subject of multiple experiments assessing their response to predation risk, we used the per-study effect size and variance to calculate a single cumulative mean effect size for each species for each response variable:

$$\tilde{E} = \frac{\sum_{i=1}^{n} w_i E_i}{\sum_{i=1}^{n} w_i}$$

where E_i and w_i are the effect size and weight, respectively, for study i, and the study weight is the reciprocal of the study's sampling variance: $w_i = 1/v_i$ (Rosenberg et al. 2000). The cumulative variance for each mean effect size was calculated for each species-response variable effect size as:

$$s^2_{\tilde{E}} = \frac{1}{\sum_{i=1}^{n} w_i}.$$

We used data from individual experiments to calculate a mean prey wet mass for each species-response variable combination. Since different experiments varied in both the number of individuals tested and their mean weights, we calculated a single cumulative mean body mass across all experiments for each species-response variable combination:

$$\tilde{m} = \sum_{i=1}^{n} m_i \left(\frac{x_i}{\sum_{i=1}^{n} x_i} \right)$$

where m_i and x_i are the prey wet mass and number of individual organisms tested in the experiment, respectively.

Appendix B

Table B1. A list of all species and 196 studies.

Reference	Predator class	Predator spp.	Prey class	Prey spp.	Lines in dataset
Allouche and Gaudin 2001	Aves	*Phalacrocorax pygmaeus*	Actinopterygii	*Leuciscus cephalus*	12
Altwegg 2002a	Insecta	*Anax imperator*	Amphibia	*Rana lessonae*	12
Altwegg 2002b	Insecta	*Anax imperator*	Amphibia	*Rana esculenta*	3
Altwegg 2002b	Insecta	*Anax imperator*	Amphibia	*Rana lessonae*	3
Alvarez and Nicieza 2003	Actinopterygii	*Salmo trutta*	Actinopterygii	*Salmo trutta*	9
Alvarez and Peckarsky 2005	Actinopterygii	*Salvelinus fontinalis*	Insecta	*Baetis bicaudatus*	3
Anholt and Werner 1998	Insecta	*Anax junius*	Amphibia	*Rana sylvatica*	5
Anholt et al. 2000	Insecta	*Anax junius*	Amphibia	*Rana catesbeiana*	3
Anholt et al. 2000	Insecta	*Anax junius*	Amphibia	*Rana clamitans*	4
Anholt et al. 2000	Insecta	*Anax junius*	Amphibia	*Rana pipiens*	3
Anholt et al. 2000	Insecta	*Anax junius*	Amphibia	*Rana sylvatica*	4
Appleton and Palmer 1988	Malacostraca	*Cancer productus*	Gastropoda	*Nucella lamellosa*	11
Babbitt 2001	Insecta	*Anax junius*	Amphibia	*Rana spenocephala*	4
Ball and Baker 1995	Actinopterygii	*Lepomis gibbosus*	Insecta	*Chironomus tentans*	5
Ball and Baker 1996	Actinopterygii	*Lepomis gibbosus*	Insecta	*Chironomus tentans*	5
Banks and Powell 2004	Mammalia	*Vulpes vulpes*	Mammalia	*Mus domesticus*	2
Barnett and Richardson 2002	Insecta	*Aeshna palmata*	Amphibia	*Rana aurora*	4
Barnett and Richardson 2002	Insecta	*Aeshna palmata*	Amphibia	*Rana pretiosa*	4
Barry 1994	Insecta	*Anisops gratus*	Branchiopoda	*Daphnia carinata*	2
Barry 2000	Insecta	*Anisops stali*	Branchiopoda	*Daphnia carinata*	2
Beckerman et al. 1997	Arachnida	*Pisurina mira*	Insecta	*Melanoplus femurrubrum*	1
Belk 1998	Actinopterygii	*Micropterus salmoides*	Actinopterygii	*Lepomis macrochirus*	14
Bernot and Turner 2001	Actinopterygii	*Lepomis gibbosus*	Gastropoda	*Physella integra*	1
Bernot and Turner 2001	Malacostraca	*Orconectes rusticus*	Gastropoda	*Physella integra*	1
Binckley and Resetarits 2002	Actinopterygii	*Enneacanthus obesus*	Amphibia	*Hyla squirella*	2
Black and Dodson 1990	Insecta	*Chaoborus americanus*	Branchiopoda	*Daphnia pulex*	6
Black 1993	Insecta	*Chaoborus americanus*	Branchiopoda	*Daphnia pulex*	2
Black 1993	Insecta	*Notonecta undulate*	Branchiopoda	*Daphnia pulex*	2
Brodin and Johansson 2002	Actinopterygii	*Perca fluviatilis*	Insecta	*Lestes sponsa*	3
Brodin and Johansson 2004	Insecta	*Aeshna juncea*	Insecta	*Coenagrion hastulatum*	2

Table B1. Continued.

Reference	Predator class	Predator spp.	Prey class	Prey spp.	Lines in dataset
Brodin et al. 2006	Insecta	*Aeshna juncea*	Insecta	*Coenagrion hastulatum*	10
Burks et al. 2000	Actinopterygii	*Rutilus rutilus*	Branchiopoda	*Daphnia magna*	4
Caro and Castilla 2004	Malacostraca	*Acanthocyclus gayi*	Bivalvia	*Semimytilus algosus*	2
Caro and Castilla 2004	Gastropoda	*Concholepas concholepas*	Bivalvia	*Semimytilus algosus*	2
Caro and Castilla 2004	Gastropoda	*Nucella crassilabrum*	Bivalvia	*Semimytilus algosus*	2
Caudill and Peckarsky 2003	Actinopterygii	*Salvelinus fontinalis*	Insecta	*Callibaetis ferrugineus hageni*	6
Cheung et al. 2004	Gastropoda	*Thais clavigera*	Bivalvia	*Perna viridis*	2
Cheung et al. 2004	Malacostraca	*Thalamita danae*	Bivalvia	*Perna viridis*	2
Chivers et al. 1999	Insecta	*Notonecta* sp.	Amphibia	*Bufo boreas*	2
Chivers et al. 2001	Hirudinea	*Desserobdella picta*	Amphibia	*Hyla regilla*	4
Chivers et al. 2001	Hirudinea	*Desserobdella picta*	Amphibia	*Rana cascadea*	2
Crowl and Covich 1990	Malacostraca	*Orconectes virilis*	Gastropoda	*Physella virgata virgata*	16
de Goeij et al. 2001	Actinopterygii	*Pleuronectes platessa*	Bivalvia	*Macoma balthica*	6
Delgado et al. 2002	Malacostraca	*Panulirus argus*	Gastropoda	*Strombus gigas*	4
Diehl and Eklov 1995	Actinopterygii	*Esox lucius*	Actinopterygii	*Perca fluviatilis*	4
Diehl and Eklov 1995	Actinopterygii	*Perca fluviatilis*	Actinopterygii	*Perca fluviatilis*	4
Dixon and Agarwala 1999	Insecta	*Adalia bipunctata*	Insecta	*Acyrthosiphon pisum*	1
Dixon and Agarwala 1999	Insecta	*Adalia bipunctata*	Insecta	*Acyrthosiphon pisum*	1
Dixon and Agarwala 1999	Insecta	*Adalia bipunctata*	Insecta	*Aphis fabae fabae*	1
Dixon and Agarwala 1999	Insecta	*Adalia bipunctata*	Insecta	*Meguora viciae*	1
Dodson and Havel 1988	Insecta	*Notonecta undulate*	Branchiopoda	*Daphnia pulex*	3
Downes 2001	Reptilia	*Demansia psammophis*	Reptilia	*Lampropholis guichenoti*	2
Duvall and Williams 1995	Actinopterygii	*Oncorhynchus mykiss*	Insecta	*Agnetina capitata*	2
Ejdung 1998	Isopoda	*Saduria entomon*	Malacostraca	*Monoporeia affinis*	3
Eklov and Van Kooten 2001	Actinopterygii	*Esox lucius*	Actinopterygii	*Rutilus rutilus*	1
Eklov and Van Kooten 2001	Actinopterygii	*Perca fluviatilis*	Actinopterygii	*Rutilus rutilus*	1
Eklov 2000	Insecta	*Anax junius*	Amphibia	*Rana catesbeiana*	2
Eklov 2000	Actinopterygii	*Lepomis macrochirus*	Amphibia	*Rana catesbeiana*	2
Fraser and Gilliam 1992	Actinopterygii	*Hoplias malabaricus*	Actinopterygii	*Rivulus hartii*	5
Fuelling and Halle 2004	Mammalia	*Mustela nivalis nivalis*	Mammalia	*Clethrionomys rufocanus*	1
Gliwicz 1994	Maxillopoda	*Acanthocyclops robustus*	Branchiopoda	*Ceriodaphnia reticulata*	1
Gliwicz 1994	Maxillopoda	*Acanthocyclops robustus*	Branchiopoda	*Daphnia hyalina*	1
Gliwicz 1994	Maxillopoda	*Acanthocyclops robustus*	Branchiopoda	*Daphnia magna*	1
Gliwicz 1994	Maxillopoda	*Acanthocyclops robustus*	Branchiopoda	*Daphnia pulicaria*	1
Hanazato and Dodson 1992	Insecta	*Chaoborus americanus*	Branchiopoda	*Daphnia pulex*	2
Hanazato 1995	Actinopterygii	*Lepomis macrochirus*	Branchiopoda	*Daphnia ambigua*	2
Hanazato 1995	Actinopterygii	*Lepomis macrochirus*	Branchiopoda	*Daphnia galeata*	2
Havel and Dodson 1987	Insecta	*Chaoborus americanus*	Branchiopoda	*Daphnia pulex*	2
Hechtel and Juliano 1997	Insecta	*Toxorhynchites rutilus*	Insecta	*Aedes triseriatus*	24
Heikkila et al. 1993	Mammalia	*Mustela nivalis nivalis*	Mammalia	*Clethrionomys glareolus*	2
Heikkila et al. 1993	Mammalia	*Mustela nivalis nivalis*	Mammalia	*Clethrionomys rufocanus*	1
Heikkila et al. 1993	Mammalia	*Mustela nivalis nivalis*	Mammalia	*Clethrionomys rutilus*	3
Hellstedt et al. 2002	Mammalia	*Mustela nivalis nivalis*	Mammalia	*Microtus agrestis*	3
Hill and Lodge 1999	Actinopterygii	*Micropterus salmoides*	Malacostraca	*Orconectes propinquus*	2
Hill and Lodge 1999	Actinopterygii	*Micropterus salmoides*	Malacostraca	*Orconectes rusticus*	2
Hill and Lodge 1999	Actinopterygii	*Micropterus salmoides*	Malacostraca	*Orconectes virilis*	2
Jackson and Semlitsch 1993	Actinopterygii	*Lepomis macrochirus*	Amphibia	*Ambystoma talpoideum*	11
Johansson et al. 2001	Actinopterygii	*Perca fluviatilis*	Insecta	*Lestes sponsa*	2
Johnson et al. 2003	Insecta	*Anax junius*	Amphibia	*Rana spenocephala*	1
Johnson et al. 2003	Insecta	*Cybister sp.*	Amphibia	*Rana spenocephala*	1
Johnson et al. 2003	Malacostraca	*Procambarus nigrocinctus*	Amphibia	*Rana spenocephala*	1
Jones et al. 2003	Actinopterygii	*Lota lota*	Actinopterygii	*Salmo salar*	1
Jones et al. 2003	Actinopterygii	*Salmo trutta*	Actinopterygii	*Salmo salar*	1

Table B1. Continued.

Reference	Predator class	Predator spp.	Prey class	Prey spp.	Lines in dataset
Justome et al. 1998	Asteroidea	*Leptasteria Polaris*	Gastropoda	*Buccinum undatum*	8
Kelly et al. 2002	Actinopterygii	*Salmo salar*	Insecta	*Baetis rhodani*	1
Ketola and Vuorinen 1989	Insecta	*Chaoborus* sp.	Branchiopoda	*Daphnia magna*	1
Ketola and Vuorinen 1989	Insecta	*Chaoborus* sp.	Branchiopoda	*Daphnia pulex*	3
Kiesecker et al. 2002	Amphibia	*Taricha granulosa*	Amphibia	*Rana aurora*	2
Klemola et al. 1998	Aves	*Falco tinnunculus*	Mammalia	*Clethrionomys glareolus*	2
Klemola et al. 1998	Aves	*Falco tinnunculus*	Mammalia	*Microtus agrestis*	2
Kohler and McPeek 1989	Actinopterygii	*Cottus bairdi*	Insecta	*Baetis tricaudatus*	2
Kraft et al. 2005	Insecta	*Anax brevistyla*	Amphibia	*Limnodynastes peronii*	1
Kuhara et al. 1999	Actinopterygii	*Cottus nozawae*	Insecta	*Baetis thermicus*	3
Kuhara et al. 1999	Actinopterygii	*Cottus nozawae*	Insecta	*Glossosoma* sp.	3
LaFiandra and Babbitt 2004	Insecta	*Anax junius*	Amphibia	*Hyla femoralis*	8
Lane and Mahony 2002	Actinopterygii	*Gambusia holbrookii*	Amphibia	*Crinia signifera*	4
Lane and Mahony 2002	Actinopterygii	*Gambusia holbrookii*	Amphibia	*Limnodynastes tasmaniensis*	4
Langerhans and DeWitt 2002	Actinopterygii	*Lepomis cyanellus*	Gastropoda	*Physella virgata*	1
Langerhans and DeWitt 2002	Actinopterygii	*Lepomis gibbosus*	Gastropoda	*Physella virgata*	1
Langerhans and DeWitt 2002	Actinopterygii	*Lepomis macrochirus*	Gastropoda	*Physella virgata*	1
Langerhans and DeWitt 2002	Actinopterygii	*Lepomis megalotis*	Gastropoda	*Physella virgata*	1
Langerhans and DeWitt 2002	Actinopterygii	*Lepomis microlophus*	Gastropoda	*Physella virgata*	1
Langerhans and DeWitt 2002	Actinopterygii	*Micropterus salmoides*	Gastropoda	*Physella virgata*	1
Lardner 2000	Insecta	*Dytiscus marginalis*	Amphibia	*Bufo bufo*	1
Lardner 2000	Insecta	*Dytiscus marginalis*	Amphibia	*Bufo calamita*	1
Lardner 2000	Insecta	*Dytiscus marginalis*	Amphibia	*Hyla arborea*	1
Lardner 2000	Insecta	*Dytiscus marginalis*	Amphibia	*Rana arvalis*	1
Lardner 2000	Insecta	*Dytiscus marginalis*	Amphibia	*Rana dalmatina*	1
Lardner 2000	Insecta	*Dytiscus marginalis*	Amphibia	*Rana temporaria*	1
Laurila and Kujasalo 1999	Insecta	*Aeshna juncea*	Amphibia	*Rana temporaria*	6
Laurila et al. 1998	Insecta	*Aeshna juncea*	Amphibia	*Bufo bufo*	4
Laurila et al. 1998	Insecta	*Aeshna juncea*	Amphibia	*Rana temporaria*	7
Laurila et al. 2004	Insecta	*Aeshna sp.*	Amphibia	*Rana temporaria*	6
Laurila et al. 2006	Insecta	*Aeshna cyanea*	Amphibia	*Rana arvalis*	4
Laurila et al. 2006	Actinopterygii	*Gasterosteus aculeatus*	Amphibia	*Rana arvalis*	4
Laurila et al. 2006	Amphibia	*Triturus vulgaris*	Amphibia	*Rana arvalis*	4
Lefcort et al. 1999	Actinopterygii	*Lepomis macrochirus*	Gastropoda	*Lymnaea palustris*	1
Lefcort et al. 1999	Actinopterygii	*Lepomis macrochirus*	Amphibia	*Rana luteiventris*	1
Lewis 2001	Malacostraca	*Orconectes rusticus*	Gastropoda	*Amnicola limosa*	1
Li and Jackson 2005	Arachnida	*Portia labiata*	Arachnida	*Saxicolla torquata axillaris*	4
Li 2002	Arachnida	*Portia labiata*	Arachnida	*Saxicolla torquata axillaris*	8
Lilliendahl 1997	Aves	*Accipiter nisus*	Aves	*Carduelis chloris*	4
Lilliendahl 1998	Aves	*Accipiter nisus*	Aves	*Emberiza citrinella*	2
Linden et al. 2003	Actinopterygii	*Perca fluviatilis*	Malacostraca	*Neomysis integer*	2
Linden et al. 2003	Actinopterygii	*Perca fluviatilis*	Malacostraca	*Praunus flexuosus*	2
Loose and Dawidowicz 1994	Actinopterygii	*Leucaspius delineatus*	Branchiopoda	*Daphnia magna*	2
Lopez et al. 1995	Gastropoda	*Nucella crassilabrum*	Bivalvia	*Perumytilus purpuratus*	2
Losey and Denno 1998b	Insecta	*Coccinella septempunctata, Harpalus pennsylvanicus*	Insecta	*Acyrthosiphon pisum*	3
Losey and Denno 1998a	Insecta	*Coccinella septempunctata, Harpalus faunus*	Insecta	*Acyrthosiphon pisum*	1
Luning 1992	Insecta	*Chaoborus flavicans*	Branchiopoda	*Daphnia pulex*	4
Luning 1992	Insecta	*Notonecta glauca*	Branchiopoda	*Daphnia pulex*	4
Luning 1994	Insecta	*Chaoborus flavicans*	Branchiopoda	*Daphnia pulex*	16

Table B1. Continued.

Reference	Predator class	Predator spp.	Prey class	Prey spp.	Lines in dataset
Luning 1995	Insecta	*Chaoborus flavicans*	Branchiopoda	*Daphnia pulex*	8
Macchiusi and Baker 1992	Actinopterygii	*Lepomis gibbosus*	Insecta	*Chironomus tentans*	8
Machacek 1993	Actinopterygii	*Rutilus rutilus*	Branchiopoda	*Daphnia galeata*	4
Machacek 1995	Actinopterygii	*Rutilus rutilus*	Branchiopoda	*Daphnia galeata*	2
Magnhagen 1990	Actinopterygii	*Gadus morhua*	Actinopterygii	*Gobus niger*	1
Magnhagen 1990	Actinopterygii	*Gadus morhua*	Actinopterygii	*Pomatoschistus minutus*	1
Mappes et al. 1998	Mammalia	*Mustela nivalis nivalis*	Mammalia	*Clethrionomys glareolus*	2
McCollum and Leimberger 1997	Insecta	*Anax umbrosa*	Amphibia	*Hyla chrysoscelis*	2
McCollum and Van Buskirk 1996	Insecta	*Anax junius*	Amphibia	*Hyla chrysoscelis*	3
McIntosh and Townsend 1996	Actinopterygii	*Galaxias vulgaris*	Insecta	*Deleatidium* sp.	2
McIntosh and Townsend 1996	Actinopterygii	*Salmo trutta*	Insecta	*Deleatidium* sp.	2
McIntosh et al. 2004	Actinopterygii	*Salvelinus fontinalis*	Insecta	*Baetis bicaudatus*	1
McIntyre et al. 2004	Insecta	*Belostoma malkini*	Amphibia	*Rana palmipes*	3
McPeek et al. 2001	Actinopterygii	*Lepomis gibbosus*	Insecta	*Enallagma laterale*	1
McPeek et al. 2001	Actinopterygii	*Lepomis gibbosus*	Insecta	*Ischnura verticalis*	1
Mikolajewski et al. 2005	Insecta	*Aeshna cyanea*	Insecta	*Coenagrion puella*	6
Moore et al. 1996	Actinopterygii	*Lepomis cyanellus*	Amphibia	*Ambystoma barbouri*	1
Moses and Sih 1998	Insecta	*Notonecta undulata*	Insecta	*Gerris marginatus*	6
Nakaoka 2000	Gastropoda	*Busycon caria*	Bivalvia	*Mercenaria mercenaria*	1
Nicieza 2000	Actinopterygii	*Salmo salar*	Amphibia	*Rana temporaria*	6
Nystrom and Abjornsson 2000	Actinopterygii	*Oncorhynchus mykiss*	Amphibia	*Bufo bufo*	2
Nystrom and Abjornsson 2000	Actinopterygii	*Oncorhynchus mykiss*	Amphibia	*Rana temporaria*	2
Oku et al. 2004	Insecta	*Amblyseius womersleyi*	Insecta	*Tetranychus kanzawai*	1
Orizaola and Brana 2005	Actinopterygii	*Salmo trutta*	Amphibia	*Triturus helveticus*	4
Orizaola and Brana 2004	Actinopterygii	*Salmo trutta*	Amphibia	*Triturus alpestris*	2
Orizaola and Brana 2004	Actinopterygii	*Salmo trutta*	Amphibia	*Triturus boscai*	2
Orizaola and Brana 2004	Actinopterygii	*Salmo trutta*	Amphibia	*Triturus helveticus*	2
Orizaola and Brana 2004	Actinopterygii	*Salmo trutta*	Amphibia	*Triturus marmoratus*	2
Palmer 1990	Malacostraca	*Cancer pagurus*	Gastropoda	*Nucella lapillus*	16
Peacor and Werner 1997	Insecta	*Anax longipes*	Amphibia	*Rana catesbeiana*	4
Peacor and Werner 1997	Insecta	*Anax longipes*	Amphibia	*Rana clamitans*	5
Peacor and Werner 2000	Insecta	*Anax longipes*	Amphibia	*Rana catesbeiana*	6
Peacor and Werner 2000	Insecta	*Anax longipes*	Amphibia	*Rana clamitans*	5
Peacor and Werner 2004	Insecta	*Anax junius*	Amphibia	*Rana sylvatica*	5
Peacor 2002	Insecta	*Anax* sp.	Amphibia	*Rana catesbeiana*	6
Peckarsky 1996	Insecta	*Kogotus modestus*	Insecta	*Baetis bicaudatus*	1
Peckarsky 1996	Insecta	*Megarcys signata*	Insecta	*Baetis bicaudatus*	1
Peckarsky et al. 1993	Insecta	*Megarcys signata*	Insecta	*Baetis bicaudatus*	2
Peckarsky et al. 2002	Actinopterygii	*Salvelinus fontinalis*	Insecta	*Baetis bicaudatus*	1
Persons et al. 2002	Arachnida	*Hogna helluo*	Arachnida	*Pardosa milvina*	1
Pierce 1988	Actinopterygii	*Lepomis macrochirus*	Insecta	*Ladona deplanata*	1
Pierce 1988	Actinopterygii	*Lepomis macrochirus*	Insecta	*Sympetrum semicinctum*	1
Pierce 1988	Actinopterygii	*Lepomis macrochirus*	Insecta	*Tetragoneuria cynosura*	1
Pravosudov and Grubb 1998	Aves	*Accipiter striatus*	Aves	*Baelophus bicolor*	1
Rahel and Stein 1988	Actinopterygii	*Micropterus dolomieu*	Actinopterygii	*Etheostoma nigrum*	1
Rahel and Stein 1988	Malacostraca	*Orconectes rusticus*	Actinopterygii	*Etheostoma nigrum*	1
Rasmy et al. 1990	Insecta	*Amblyseius gossipi*	Insecta	*Tetranychus urticae*	2
Rasmy et al. 1990	Insecta	*Phytoseiulus finitimus*	Insecta	*Tetranychus urticae*	2
Rasmy et al. 1990	Insecta	*Phytoseiulus persimilis*	Insecta	*Tetranychus urticae*	2
Rawlings 1994	Malacostraca	*Cancer productus*	Gastropoda	*Nucella emarginata*	2
Reimer and Harms-Ringdahl 2001	Asteroidea	*Asterias rubens*	Bivalvia	*Mytilus edulis*	2
Reimer and Harms-Ringdahl 2001	Malacostraca	*Carcinus maenas*	Bivalvia	*Mytilus edulis*	2
Reimer and Tedengren 1996	Asteroidea	*Asterias rubens*	Bivalvia	*Mytilus edulis*	2

Table B1. Continued.

Reference	Predator class	Predator spp.	Prey class	Prey spp.	Lines in dataset
Reimer et al. 1995	Asteroidea	*Asterias rubens*	Bivalvia	*Mytilus edulis*	1
Relyea and Hoverman 2003	Insecta	*Anax* sp.	Amphibia	*Hyla versicolor*	2
Relyea and Werner 1999	Insecta	*Anax* sp.	Amphibia	*Rana catesbeiana*	2
Relyea and Werner 1999	Actinopterygii	*Lepomis macrochirus*	Amphibia	*Rana catesbeiana*	2
Relyea and Werner 1999	Actinopterygii	*Umbra limi*	Amphibia	*Rana catesbeiana*	2
Relyea and Werner 1999	Insecta	*Anax* sp.	Amphibia	*Rana clamitans*	2
Relyea and Werner 1999	Actinopterygii	*Lepomis macrochirus*	Amphibia	*Rana clamitans*	2
Relyea and Werner 1999	Actinopterygii	*Umbra limi*	Amphibia	*Rana clamitans*	2
Relyea and Werner 2000	Insecta	*Anax* sp.	Amphibia	*Rana pipiens*	2
Relyea and Yurewicz 2002	Amphibia	*Ambystoma tigrinum*	Amphibia	*Rana clamitans*	2
Relyea and Yurewicz 2002	Insecta	*Anax* sp.	Amphibia	*Rana clamitans*	2
Relyea 2000	Insecta	*Anax* sp.	Amphibia	*Rana pipiens*	2
Relyea 2000	Actinopterygii	*Umbra limi*	Amphibia	*Rana pipiens*	2
Relyea 2000	Insecta	*Anax* sp.	Amphibia	*Rana sylvatica*	2
Relyea 2000	Actinopterygii	*Umbra limi*	Amphibia	*Rana sylvatica*	2
Relyea 2002b	Insecta	*Anax longipes*	Amphibia	*Rana sylvatica*	2
Relyea 2002c	Insecta	*Anax* sp.	Amphibia	*Rana sylvatica*	24
Relyea 2002a	Insecta	*Anax longipes*	Amphibia	*Rana sylvatica*	4
Relyea 2002d	Insecta	*Anax longipes*	Amphibia	*Hyla versicolor*	3
Relyea 2003	Insecta	*Anax* sp.	Amphibia	*Rana sylvatica*	4
Relyea 2003	Insecta	*Belostoma* sp.	Amphibia	*Rana sylvatica*	4
Relyea 2003	Insecta	*Dytiscus* sp.	Amphibia	*Rana sylvatica*	4
Relyea 2003	Insecta	*Erythemis* sp.	Amphibia	*Rana sylvatica*	4
Relyea 2004	Insecta	*Anax junius*	Amphibia	*Rana sylvatica*	12
Repka and Pihlajamaa 1996	Insecta	*Chaoborus obscuripes*	Branchiopoda	*Daphnia pulex*	4
Repka et al. 1994	Insecta	*Chaoborus obscuripes*	Branchiopoda	*Daphnia pulex*	8
Repka et al. 1994	Insecta	*Dytiscus* sp.	Branchiopoda	*Daphnia pulex*	8
Repka et al. 1994	Insecta	*Mochlonyx* sp.	Branchiopoda	*Daphnia pulex*	4
Repka et al. 1994	Insecta	*Notonecta* sp.	Branchiopoda	*Daphnia pulex*	7
Resetarits 2005	Actinopterygii	*Enneacanthus obesus*	Amphibia	*Hyla chrysoscelis*	1
Resetarits et al. 2004	Actinopterygii	*Enneacanthus obesus*	Amphibia	*Hyla chrysoscelis*	4
Rieger et al. 2004	Actinopterygii	*Umbra pygmaea*	Amphibia	*Hyla femoralis*	1
Roitberg et al. 1979	Insecta	*Coccinella californica*	Insecta	*Acyrthosiphon pisum*	3
Ronkainen and Ylonen 1994	Mammalia	*Mustela erminea*	Mammalia	*Clethrionomys glareolus*	1
Saenz et al. 2003	Malacostraca	*Procambarus nigrocinctus*	Amphibia	*Rana spenocephala*	1
Schaffner and Anholt 1998	Insecta	*Anax imperator*	Insecta	*Ischnura elegans*	3
Schalk et al. 2002	Hirudinea	*Macrobdella decora*	Amphibia	*Rana clamitans*	2
Scheiner and Berrigan 1998	Insecta	*Chaoborus americanus*	Branchiopoda	*Daphnia pulex*	2
Scheuerlein et al. 2001	Aves	*Lanius collaris*	Aves	*Saxicolla torquata axillaris*	2
Schmidt and Van Buskirk 2005	Insecta	*Aeshna cyanea*	Amphibia	*Triturus carnifex*	2
Schmidt and Van Buskirk 2005	Insecta	*Aeshna cyanea*	Amphibia	*Triturus cristatus*	2
Schmidt and Van Buskirk 2005	Insecta	*Aeshna cyanea*	Amphibia	*Triturus marmoratus*	2
Schmidt and Van Buskirk 2005	Insecta	*Aeshna cyanea*	Amphibia	*Triturus vulgaris*	2
Schmitz 1998	Arachnida	*Pisurina mira*	Insecta	*Chorthippus curtipennis*	1
Schmitz 1998	Arachnida	*Pisurina mira*	Insecta	*Melanoplus femurrubrum*	1
Schmitz et al. 1997	Arachnida	*Pisurina mira*	Insecta	*Melanoplus femurrubrum*	2
Schoeppner and Relyea 2005	Insecta	*Anax junius*	Amphibia	*Hyla versicolor*	6
Scrimgeour and Culp 1994	Actinopterygii	*Rhinichthys cataractae*	Insecta	*Baetis tricaudatus*	8
Sih and Krupa 1996	Actinopterygii	*Lepomis cyanellus*	Insecta	*Aquarius remigis*	2
Sih et al. 1990	Actinopterygii	*Lepomis cyanellus*	Insecta	*Gerris remigis*	6
Skelly 1992	Amphibia	*Ambystoma tigrinum tigrinum*	Amphibia	*Hyla versicolor*	3
Skelly and Werner 1990	Insecta	*Anax junius*	Amphibia	*Bufo americanus*	8
Smith and Jennings 2000	Malacostraca	*Carcinus maenas*	Bivalvia	*Mytilus edulis*	1
Smith and Jennings 2000	Gastropoda	*Nucella lapillus*	Bivalvia	*Mytilus edulis*	1

Table B1. Continued.

Reference	Predator class	Predator spp.	Prey class	Prey spp.	Lines in dataset
Sparrevik and Leonardsson 1999	Isopoda	*Saduria entomon*	Malacostraca	*Monoporeia affinis*	12
Stamp and Bowers 1988	Insecta	*Polistes dominulus, P. fuscatus*	Insecta	*Hemileuca lucina*	2
Stamp and Bowers 1991	Insecta	*Polistes dominulus, P. fuscatus*	Insecta	*Hemileuca lucina*	1
Stamp and Bowers 1993	Insecta	*Podisus maculiventris*	Insecta	*Junonia coenia*	1
Stamp and Bowers 1993	Insecta	*Polistes fuscatus*	Insecta	*Junonia coenia*	1
Stamp 1997	Insecta	*Polistes fuscatus*	Insecta	*Junonia coenia*	1
Stamp 1997	Insecta	*Polistes fuscatus*	Insecta	*Pyrrharctia isabella*	1
Stibor and Luning 1994	Insecta	*Chaoborus flavicans*	Branchiopoda	*Daphnia hyalina*	1
Stibor and Luning 1994	Actinopterygii	*Leuciscus idus*	Branchiopoda	*Daphnia hyalina*	1
Stibor and Luning 1994	Insecta	*Notonecta glauca*	Branchiopoda	*Daphnia hyalina*	1
Stibor 1992	Actinopterygii	*Leuciscus idus*	Branchiopoda	*Daphnia hyalina*	1
Stoks and McPeek 2003	Insecta	*Anax junius*	Insecta	*Lestes congener*	2
Stoks and McPeek 2003	Actinopterygii	*Lepomis gibbosus*	Insecta	*Lestes congener*	2
Stoks and McPeek 2003	Insecta	*Anax junius*	Insecta	*Lestes disjunctus*	2
Stoks and McPeek 2003	Actinopterygii	*Lepomis gibbosus*	Insecta	*Lestes disjunctus*	2
Stoks and McPeek 2003	Insecta	*Anax junius*	Insecta	*Lestes dryas*	3
Stoks and McPeek 2003	Actinopterygii	*Lepomis gibbosus*	Insecta	*Lestes dryas*	3
Stoks and McPeek 2003	Insecta	*Anax junius*	Insecta	*Lestes eurinus*	3
Stoks and McPeek 2003	Actinopterygii	*Lepomis gibbosus*	Insecta	*Lestes eurinus*	3
Stoks and McPeek 2003	Insecta	*Anax junius*	Insecta	*Lestes forcipatus*	2
Stoks and McPeek 2003	Actinopterygii	*Lepomis gibbosus*	Insecta	*Lestes forcipatus*	2
Stoks and McPeek 2003	Insecta	*Anax junius*	Insecta	*Lestes rectangularis*	3
Stoks and McPeek 2003	Actinopterygii	*Lepomis gibbosus*	Insecta	*Lestes rectangularis*	3
Stoks and McPeek 2003	Insecta	*Anax junius*	Insecta	*Lestes vigilax*	3
Stoks and McPeek 2003	Actinopterygii	*Lepomis gibbosus*	Insecta	*Lestes vigilax*	3
Stoks 1998	Insecta	*Notonecta glauca*	Insecta	*Lestes sponsa*	7
Stoks 2001	Insecta	*Aeshna cyanea*	Insecta	*Lestes sponsa*	4
Stoks et al. 1999a	Insecta	*Aeshna cyanea*	Insecta	*Lestes sponsa*	2
Stoks et al. 1999b	Insecta	*Aeshna cyanea*	Insecta	*Lestes sponsa*	6
Stoks et al. 2005	Actinopterygii	*Perca fluviatilis*	Insecta	*Lestes sponsa*	2
Storfer and White 2004	Insecta	*Anax junius*	Amphibia	*Ambystoma tigrinum nebulosum*	1
Storfer and White 2004	Insecta	*Dytiscus* sp.	Amphibia	*Ambystoma tigrinum nebulosum*	1
Teplitsky et al. 2004	Insecta	*Aeshna cyanea*	Amphibia	*Rana dalmatina*	1
Teplitsky et al. 2004	Actinopterygii	*Gasterosteus aculeatus*	Amphibia	*Rana dalmatina*	1
Teplitsky et al. 2004	Insecta	*Aeshna cyanea*	Amphibia	*Rana ridibunda*	1
Teplitsky et al. 2004	Actinopterygii	*Gasterosteus aculeatus*	Amphibia	*Rana ridibunda*	1
Teplitsky et al. 2005	Actinopterygii	*Gasterosteus aculeatus*	Amphibia	*Rana dalmatina*	3
Thiemann and Wassersug 2000	Actinopterygii	*Fundulus diaphanus*	Amphibia	*Rana clamitans*	2
Tollrian 1995	Insecta	*Chaoborus flavicans*	Branchiopoda	*Daphnia pulex*	10
Trussell and Nicklin 2002	Malacostraca	*Carcinus maenas*	Gastropoda	*Littorina obtusata*	4
Trussell and Smith 2000	Malacostraca	*Carcinus maenas*	Gastropoda	*Littorina obtusata*	2
Trussell et al. 2003	Malacostraca	*Carcinus maenas*	Gastropoda	*Littorina littorea*	1
Trussell et al. 2003	Malacostraca	*Carcinus maenas*	Gastropoda	*Nucella lapillus*	2
Turner and Montgomery 2003	Actinopterygii	*Lepomis gibbosus*	Gastropoda	*Physa acuta*	7
Turner 2004	Malacostraca	*Cambarus bartonii*	Gastropoda	*Helisoma trivolvis*	8
Turner et al. 2000	Actinopterygii	*Lepomis gibbosus*	Gastropoda	*Physella gyrina*	1
Van Buskirk and Schmidt 2000	Insecta	*Aeshna cyanea*	Amphibia	*Triturus alpestris*	3
Van Buskirk and Schmidt 2000	Insecta	*Aeshna cyanea*	Amphibia	*Triturus helveticus*	3
Van Buskirk and Yurewicz 1998	Insecta	*Anax junius*	Amphibia	*Rana sylvatica*	6
Vorndran et al. 2002	Insecta	*Aeshna cyanea*	Amphibia	*Bombina bombina*	1
Vorndran et al. 2002	Insecta	*Aeshna cyanea*	Amphibia	*Bombina variegata*	1
Walls et al. 1991	Insecta	*Chaoborus crystallinus*	Branchiopoda	*Daphnia pulex*	12
Walls et al. 1997	Insecta	*Chaoborus* sp.	Branchiopoda	*Daphnia pulex*	4
Walls et al. 2002	Actinopterygii	*Gambusia affinis*	Amphibia	*Gastrophryne carolinensis*	9
Walls et al. 2002	Malacostraca	*Procambarus* sp.	Amphibia	*Gastrophryne carolinensis*	4

Table B1. Continued.

Reference	Predator class	Predator spp.	Prey class	Prey spp.	Lines in dataset
Walls et al. 2002	Actinopterygii	*Gambusia affinis*	Amphibia	*Hyla squirella*	5
Weber and DeClerk 1997	Insecta	*Chaoborus americanus*	Branchiopoda	*Daphnia galeata*	4
Weber and DeClerk 1997	Actinopterygii	*Perca fluviatilis*	Branchiopoda	*Daphnia galeata*	4
Weber 2001	Insecta	*Chaoborus* sp.	Branchiopoda	*Daphnia galeata*	2
Weber 2001	Actinopterygii	*Perca fluviatilis*	Branchiopoda	*Daphnia galeata*	2
Weber et al. 2003	Insecta	*Chaoborus americanus*	Branchiopoda	*Daphnia galeata*	1
Weetman and Atkinson 2002	Actinopterygii	*Gasterosteus aculeatus*	Branchiopoda	*Daphnia pulex*	18
Werner and Anholt 1996	Insecta	*Anax junius*	Amphibia	*Rana catesbeiana*	12
Werner and Anholt 1996	Insecta	*Anax junius*	Amphibia	*Rana clamitans*	12
Werner and Peacor 2006	Insecta	*Anax junius*	Amphibia	*Rana clamitans*	3
Werner 1991	Insecta	*Anax junius*	Amphibia	*Rana catesbeiana*	2
Werner 1991	Insecta	*Anax junius*	Amphibia	*Rana clamitans*	2
Wilder and Rypstra 2004	Insecta	*Tenodera aridifolia sinensis*	Arachnida	*Pardosa milvina*	2
Wolff and Davis-Born 1997	Mammalia	*Mustela vison*	Mammalia	*Microtus canicaudus*	2
Yamada et al. 1998	Malacostraca	*Cancer productus*	Gastropoda	*Littorina sitkana*	6
Ylonen and Ronkainen 1994	Mammalia	*Mustela erminea*	Mammalia	*Clethrionomys glareolus*	7
Ylönen 1989	Mammalia	*Mustela nivalis nivalis*	Mammalia	*Clethrionomys glareolus*	1