

SCARED TO DEATH? THE EFFECTS OF INTIMIDATION AND CONSUMPTION IN PREDATOR–PREY INTERACTIONS

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Abstract. Predation is a central feature of ecological communities. Most theoretical and empirical studies of predation focus on the consequences of predators consuming their prey. Predators reduce prey population densities through direct consumption (a density-mediated interaction, DMI), a process that may indirectly affect the prey's resources, competitors, and other predators. However, predators can also affect prey population density by stimulating costly defensive strategies. The costs of these defensive strategies can include reduced energy income, energetic investment in defensive structures, lower mating success, increased vulnerability to other predators, or emigration. Theoretical and empirical studies confirm the existence of these induced costs (trait-mediated interactions, TMIs); however, the relative importance of intimidation (TMI) and consumption (DMI) effects remains an open question. We conducted a meta-analysis assessing the magnitude of both TMIs and DMIs in predator–prey interactions. On average, the impact of intimidation on prey demographics was at least as strong as direct consumption (63% and 51% the size of the total predator effect, respectively). This contrast is even more pronounced when we consider the cascading effects of predators on their prey's resources: density effects attenuated through food chains, while TMIs remained strong, rising to 85% of the total predator effect. Predators can thus strongly influence resource density even if they consume few prey items. Finally, intimidation was more important in aquatic than terrestrial ecosystems. Our results suggest that the costs of intimidation, traditionally ignored in predator–prey ecology, may actually be the dominant facet of trophic interactions.

Key words: *behavioral effects; density-mediated interactions; higher-order interactions; predation risk; predator–prey ecology; trait-mediated interactions; trophic cascades.*

INTRODUCTION

Food webs, “the ecologically flexible scaffolding around which communities are assembled and structured,” (Paine 1995:ix) are defined by interactions between predators and their prey. Most ecological theory has viewed predator–prey interactions in terms of consumption: predators capture and consume their prey. This interaction reduces prey population density while facilitating predator reproduction. Such density interactions, driven by consumption, have been subjected to extensive empirical and theoretical studies that form the basis of much of our understanding of species interactions and community dynamics (Murdoch et al. 2003).

Predators do not, however, only affect prey by eating them; far from being hapless players on the ecological stage, prey can alter phenotypic traits to reduce their risk of mortality. These predator-induced phenotypic changes can be developmental, morphological, physiological, or behavioral (Werner and Peacor 2003) and

may have significant demographic costs. For instance, *Daphnia* develop defensive spines when exposed to chemical cues from fish. The energetic cost of this structure significantly reduces lifetime fitness (Barry 1994). More generally, defensive tactics can reduce the prey's foraging effort (Morrison 1999), energy income (Downes 2001), the conversion of energy into progeny (Barry 1994), the prey's vulnerability to other predators (Losey and Denno 1998, Eklov and Van Kooten 2001), or emigration rates (Hurd and Eisenberg 1984, Forrester 1994). Predators can thus reduce prey density both through direct consumption (a “density-mediated interaction,” or DMI) and by stimulating costly defensive traits (a “trait-mediated interaction,” or TMI). TMIs can thus be thought of as the strategic changes in prey phenotype, behavior, etc., in response to the presence of a predator. We distinguish between TMIs in two-level food chains (the effect of a predator on its prey) and TMIs in three-level food chains (the effect of a predator on the resources of its prey, also known as a “trait-mediated indirect interaction,” or TMII).

Researchers can independently estimate trait-mediated, density-mediated, and total effects of predators on their prey or the prey's resource using a variety of techniques. The most common is to estimate the effect of nonlethal predator treatments, in which the prey is exposed to the presence of the predator but the predator

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cannot actually kill the prey. For instance, Schmitz and others (Beckerman et al. 1997, Schmitz 1998) measured the total impact of spiders on grasshoppers by comparing predator-present treatments against a control. They eliminated direct consumption in a third treatment by gluing spiders' mouthparts shut, thereby measuring the trait-mediated component of this interaction. Intimidated grasshoppers nonetheless experienced elevated mortality rates: to avoid spiders, grasshoppers switched from eating grasses to eating safer but less energetically rewarding forbs. The reduced energy income led to a higher mortality rate.

An alternative approach is to separately estimate the DMI and TMI components by directly measuring each variable (i.e., measuring consumption rates by gut content analyses and emigration rates by drift-traps [Forrester 1994]). In another example, Rahel and Stein (1988) found that the presence of bass (*Micropterus salmoides*) increases darter mortality in two ways. Bass both eat darters themselves (DMI of bass) and elevate the darter's risk of mortality to another predator, crayfish (TMI of bass). Darters tend to hide in rocky shelters to avoid bass, but this increases their vulnerability to substrate-dwelling crayfish. These components of the predator effect can be estimated by measuring bass consumption rates, crayfish consumption rates, and the increase in crayfish consumption rates caused by the presence of bass.

Experiments have confirmed that trait-mediated interactions are a very common feature of predator-prey interactions (reviewed in Lima and Dill [1990], Lima [1998], Werner and Peacor [2003], Schmitz et al. [2004]). Both theoretical (Abrams 1984) and experimental work suggests that defensive costs (TMIs) can equal or exceed the effects of direct consumption (Werner and Peacor 2003). While it is now clear that TMIs are common and potentially powerful, there have been no general conclusions about the relative strength of trait- and density-mediated effects (but see Abrams [1984, 1991, 1995] for a theoretical perspective).

To draw general conclusions about the relative strength of trait-mediated, density-mediated, and total predator effects, we performed a meta-analysis of published experiments. We surveyed the ecological literature to find studies that estimated the magnitude of the trait-mediated, density-mediated, and total effects of predators on prey survival or population density. We found a total of 166 studies drawn from 49 references (Appendices A and B). We then used standard meta-analytic techniques (Hedges and Olkin 1985) to determine the average strength of trait- and density-mediated effects, expressed as a ratio of the total predator effect.

METHODS

Literature search

We reviewed ecological literature for studies that simultaneously estimate at least two of the following:

(1) The total effect of the predator on its prey, found by comparing prey demography in predator-absent vs. predator-present treatments. We assessed the demographic effects of predators on prey fecundity, survival, density, or population growth rates. (2) The effect of density-mediated interactions (DMIs) between the predator and its prey. This can be estimated by directly assessing the per-predator rate of prey consumption. (3) The effect of trait-mediated interactions (TMIs) between the predator and its prey. Trait-mediated effects can be measured by comparing prey demography in predator-absent vs. "nonlethal" predator-present treatments, in which predators threaten but cannot consume prey. It is also possible to directly record changes in prey emigration rates or nonconsumptive mortality in the presence of a lethal predator.

We excluded studies measuring TM effects without clear demographic consequences (microhabitat shifts, etc.). We also excluded response variables such as growth rate and feeding success: these may have important demographic effects but cannot be directly compared to mortality rates. By excluding such effects, our analysis should be conservative, i.e., tend to underestimate the magnitude of TM effects.

We searched the online citation databases BIOSIS, ISI Science Citation Index, and JSTOR for the following key words: behavior modification, behavioral interaction, density mediated, higher-order interaction, indirect effect, indirect interaction, interaction modification, nonlethal, predator avoidance, predator-risk, risk and foraging, sublethal, trait-mediated. We read all papers whose titles and/or abstracts appeared relevant and pursued pertinent citations within those papers. We also exhaustively examined the journals *American Naturalist*, *Ecology*, *Oecologia*, and *Oikos* from 1990 onwards.

Data collection

We categorized studies by: food chain length (two- or three-level, where a two-level food chain is a predator-prey interaction and a three-level food chain is a predator-prey-resource interaction); ecosystem (freshwater, marine, terrestrial); experimental scale (field, laboratory); experimental duration; and suggested mechanism of the trait-mediated effect (reduced activity, predator-predator facilitation, emigration). Although emigration is not a demographic parameter in the same sense as birth and death, we included it in our analyses because of its effect on local prey density (the scale at which many predator-prey experimental manipulations are performed). We distinguish between microhabitat shifts and actual emigration from the local population in our analyses. Emigration removes individuals from the local breeding population, whereas microhabitat shifts alter population distribution on a finer scale. While there is a continuum between these two processes, we include the former but not the latter. We classified controlled environments like greenhouses

and cattle tanks as “laboratory,” while larger man-made ponds were considered field experiments.

Some articles reported multiple estimates of TM, DM, and total predator effect. We treated multiple estimates as independent data points (“studies”) if they involved different species pairs or if the same species pair was evaluated in different environments, seasons, or population densities. We did this because the importance of TM effects in a predator–prey interaction may depend on environmental conditions (Luttbeg et al. 2003). For repeated estimates of the same interaction, we averaged the effects to produce a single estimate. If a reference measured multiple variables for a given experiment, we chose the variable most closely linked to population density or dynamics.

For each interaction, we recorded the mean and standard deviation for the control, TMI, DMI, and total predator effect (when available), and the per-treatment sample size. The data was taken directly from the text, tables, or calculated by measuring figures (accurate to $\pm 1\%$ of the actual value).

Most studies did not measure all three treatments listed above (total effect, TMI, DMI). One common experimental design was to measure TMI (comparing nonlethal predator treatment to a control) and total predator effect (comparing lethal predator treatment to a control) without a direct measure of DMI. Other studies quantified TMI and DMI only, such as the decrease in prey density due to emigration (TMI) and consumption (DMI; e.g., number of prey found in predator gut contents). In these cases, we inferred the total predator effect using an additive model (total effect = TMI + DMI – predator-absent control). We calculated the variance of the inferred total effect as the square root of the sum of the component variances, assuming that the covariances between TMI, DMI, and the predator-absent control are zero. This inference assumes that TMI and DMI are additive and do not interact. While such interactions are known to exist (Peacor and Werner 2001), they are very rarely measured. It is unclear what bias interactions would introduce to our study, since it is unknown whether or not interactions tend to be in a consistent direction. To test for such a bias, we checked to see whether our inference process had a significant effect on our conclusions.

Effect size

We used two test statistics to estimate the magnitude of TMI and DMI effects: the log response ratio and Hedge’s d . The response ratio (RR) measures the ratio of TMI (or DMI) effect size relative to the total predator effect:

$$RR_{TMI} = \text{abs} \left(\frac{TMI - \text{Control}}{\text{Total} - \text{Control}} \right)$$

$$RR_{DMI} = \text{abs} \left(\frac{DMI - \text{Control}}{\text{Total} - \text{Control}} \right).$$

We took the absolute value of the ratio to assess the

magnitudes of TMI and DMI relative to the total predator effects, without the confounding influence of effect directions. A RR_{TMI} value of zero indicates that there are no trait-mediated effects. A RR_{TMI} value of 1.0 indicates that the trait-mediated effect is the same magnitude as the total predator effect. This does not necessarily imply that the effect of direct consumption is negligible, as RR_{TMI} and RR_{DMI} do not have to sum to 1.0. Nonadditivity can either reflect sampling error in estimating effects or can occur when TMIs and DMIs can have opposite effects (Huang and Sih 1991). Consider a hypothetical TMI effect of +0.5 and a DMI effect of –1.0; the total effect (TMI + DMI) sums to –0.5. The TMI effect has the same magnitude as the total predator effect, but the DMI effect may still be nonzero. The possibility of opposing TM and DM effects means that our response ratios are best interpreted as measuring the relative magnitude of TMI (or DMI) vs. the total effect, rather than as assessing the relative contributions of each interaction type to the total effect.

We used a second test statistic, Hedges’ d , to more directly compare the magnitude of trait- and density-mediated effects to each other. We applied this index of effect size to independently measure TMIs, DMIs, and total effects. For instance,

$$d_{TMI} = \frac{(TMI - \text{Control})}{SE_{\text{pooled}}}.$$

The drawback of this approach is that it compares effect sizes scaled by their respective standard errors, so that differences in d could be attributed to different effects on the mean response variable or different error terms. We calculated the mean Hedges’ d across studies in two ways, first by taking into account effect direction and secondly by focusing solely on effect magnitude. In the former case, d was multiplied by 1 if an increase in the response variable was “beneficial” to the prey (e.g., survival, fecundity), and –1 if an increase in the variable was “detrimental” (e.g., mortality). Measuring magnitude, we took the absolute value of all d .

Statistical analyses

All statistical analyses were conducted using MetaWin (Rosenberg et al. 2000). We first estimated the mean $\ln(RR)$ using a random effects model. However, $\ln(RR)$ is undefined when the response ratio is zero or negative. We therefore calculated the mean value of $\ln(RR + 1)$, taking the exponent and subtracting one from the mean to recover the magnitude of TMI (or DMI) relative to total predator effects. We also calculated the mean Hedges’ d separately for each effect. In calculating the mean d , we only used effects that were reported in the original papers, leaving out cases where we inferred an effect using our additive model. Because of this, the sample sizes for d_{DMI} and d_{total} (both of which had to be inferred in some studies) were less than the sample size for d_{TMI} (available in nearly all cases).

Because our data were non-normal, we report confidence intervals derived from a bootstrapping routine implemented in MetaWin. We used random effects models to test whether characteristics of studies (categorical variables: food chain length, ecosystem, TMI mechanism, field vs. laboratory experiment) explained any variation in effect size. MetaWin estimates the mean effect size and corresponding confidence intervals for each category within a particular variable. All categorical tests were conducted separately for two- and three-level food chains. We used a continuous regression to test whether the effect size is a function of experimental duration.

We ran several diagnostic tests to evaluate the robustness of our results. We used a random effects model to check whether our method for inferring the total effect (total effect = TMI + DMI) introduced bias. We compared the mean response ratio of studies reporting TMI (or DMI) and total effects against the mean of studies reporting TMI and DMI only. We also conducted four tests to assess the potential effects of publication bias: (1) a Spearman rank-order correlation to check for correlation between variance and effect size, (2) Rosenthal's fail-safe test, (3) Orwin's fail-safe test with a cut-off of 0.18, and (4) a cumulative meta-analysis by year.

RESULTS

Trait-mediated effect sizes were on average 63.3% (95% CI: 55–71%) as large as the total predator effect size (Fig. 1A). Density-mediated effects were slightly weaker, averaging 51% the magnitude of the total predator effect (95% CI: 43–59%) (Fig. 1B). However, this overall average confounds studies assessing predator effects on both prey and the prey's resources. Analyzing two- and three-level food chains separately, intimidation has a larger impact on the prey's resources than on the prey themselves ($P = 0.011$; Table 1). TMI effects were 58% of predator effects on prey (two-level food chains), but 85% of predator effects on the prey's resources (three-level chains). Our estimate of cascading effects must be treated with caution, as we have only 30 measures (from 14 papers) of trait- vs. density-mediated effects in three-level interactions. In contrast to increasing TMIs, consumption effects attenuated through food chains (Table 1). DMI effects were 54% of predator effects on prey, but only 33% of predator effects on the prey's resources. While the TMI and DMI response ratios are not strictly additive (see *Methods*), they lead to similar conclusions: the effect of intimidation on prey is at least as large as the effect of direct consumption, and trait-mediated effects dominate trophic cascades.

At first glance, Hedges' d appears to give a very different picture of the relative magnitude of intimidation and consumption effects on prey. While TMIs, DMIs, and total effects all reduced prey density relative to controls ($d = -0.61, -1.87, -1.71$, respectively),

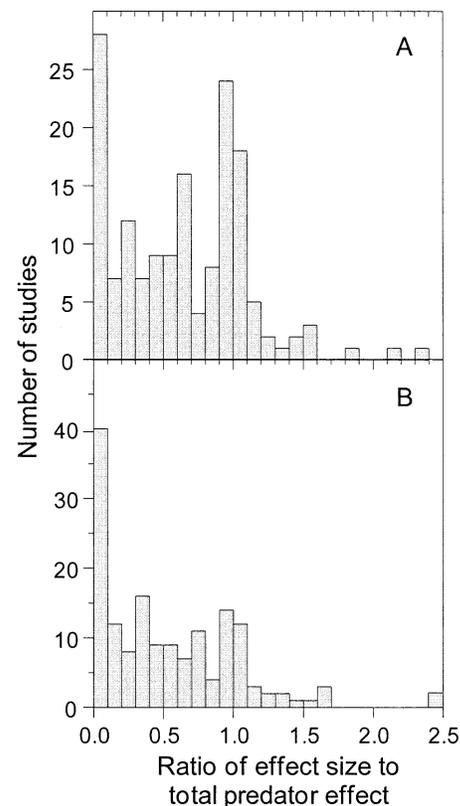


FIG. 1. The distribution of (A) trait-mediated and (B) density-mediated effect sizes (measured relative to the magnitude of the total predator effect) across studies used in this meta-analysis. For a meta-analysis, not all studies contribute equally to the overall mean: studies with lower variance are weighted more heavily than studies with high variance. Hence, the means of these unweighted histograms (60.6% trait-mediated interactions, 50.7% density-mediated interactions) are slightly different from the meta-analysis mean. Either component can exceed the total predator effect due to (a) experimental error or (b) the density-mediated effect and the trait-mediated effect having opposing effects on population density (canceling each other's effect and thus lowering the total net impact of the predator).

the effect of consumption was three times that of intimidation. The problem with this interpretation is that consumption always reduces prey densities (negative d), whereas trait-mediated interactions can increase or decrease prey densities, making the mean TMI effect appear smaller. A more appropriate comparison of their effect sizes involves the mean absolute value of d (thereby removing the confounding influence of effect direction). Analyzed this way, DMI magnitudes are still significantly stronger than TMI magnitudes (2.00 and 1.27, respectively; Table 1), though the difference is less striking than when effect directions are included. Note that these calculations exclude cases where DMI effects are inferred from the TMI and total effects using an additive model. This might explain the difference between the response ratio measures (which suggest

TABLE 1. Two measurements of the magnitude of trait- and density-mediated effects.

Effect	Two-level food chain			Three-level food chain			<i>P</i>
	Mean	95% CI	<i>N</i>	Mean	95% CI	<i>N</i>	
Response ratio							
TMI effect/total effect	0.58	(0.50, 0.67)	136	0.85	(0.71, 0.97)	30	0.0110
DMI effect/total effect	0.54	(0.47, 0.63)	133	0.33	(0.19, 0.49)	30	0.0133
Abs(Hedges' <i>d</i>)							
TMI effect	1.27	(1.07, 1.50)	131	1.24	(0.77, 1.75)	28	0.726
DMI effect	2.00	(1.69, 2.37)	87	0.54	(0.20, 1.10)	17	0.001
Total effect	1.95	(1.53, 2.45)	43	1.26	(0.81, 1.91)	15	0.120

Notes: The mean effect size, 95% confidence intervals, and number of case studies are given separately for two- and three-level food chains. The response ratios indicate the magnitude of trait-mediated interaction (TMI) or density-mediated interaction (DMI) effects relative to total predator effects (ignoring effect direction). Hedges' *d* measures the effect of an experimental treatment relative to a control, standardized by a pooled standard error, and is applied separately to TMI, DMI, and total effects. To remove the confounding influence of effect direction, we present the absolute (Abs) value of Hedges' *d*. In calculating DMI response ratios there were three data points for which the variance of the response ratio was undefined, so *N* = 133 instead of 136. Hedges' *d* was only calculated for studies that directly measured particular effects, excluding cases where we used an additive model to infer effects.

that TMIs are marginally stronger than DMIs) and the Hedges' *d* results.

The Hedges' *d* test confirms that the negative effect of predators on prey density cascades to affect resource density (Table 1). The effect of consumption (DMI) attenuated through the food chain, dropping from an absolute magnitude of 2.00 on prey to 0.54 on the prey's resource (*P* = 0.001). In contrast, the absolute magnitude of trait-mediated interactions was approximately constant (1.27 vs. 1.24). This is consistent with the response ratio results reported above: in trophic cascades, intimidation effects became stronger (relative to the total predator effect) while consumption effects became weaker. Consistent with previous studies of trophic cascades (Carpenter and Kitchell 1993, Schmitz et al. 2000, Halaj and Wise 2001), predators had an overall negative effect on their prey ($d_{\text{total}} = -1.65$) and positive effect on the prey's resources ($d_{\text{total}} = 0.48$).

The persistently strong TMI effect in trophic cascades may arise because intimidation can affect prey populations in two ways, reducing prey density and/or prey activity. By focusing exclusively on prey demographics, our measure of intimidation excludes a class of interactions that, while not affecting prey population dynamics, can have large effects on the prey's resources. For instance, in the presence of largemouth bass, bluegill sunfish retreated into sheltered vegetated habitats (Turner and Mittelbach 1990). While this environment was sub-optimal for foraging, there was no detectable trait-mediated effect, as all adult sunfish survived. Despite no detectable consumption or trait-mediated bluegill mortality, this habitat shift had a large beneficial effect on zooplankton densities as *Daphnia* living in open water were released from predation. Hence, trait-mediated effects can be greatly amplified through food chains, in contrast to the well-documented attenuation of density effects (Schmitz et al. 2000, Halaj and Wise 2001).

Trait-mediated effects were stronger in aquatic than in terrestrial ecosystems (Table 2). In two-level food chains, TMIs were 77% of the total effect in marine systems, 63% in freshwater, and 40% in terrestrial systems (*P* = 0.037). Density-mediated effects followed the opposite pattern, weakest in marine systems and progressively stronger in freshwater and terrestrial systems (22, 57, and 63%, respectively, *P* = 0.016). These differences were even more pronounced in cascading interactions (Table 2). TMIs were nearly equivalent to total predator effects on resource density in both marine and freshwater food chains (97% and 93%, respectively), while only half (57%) of predator effects in terrestrial ecosystems (*P* = 0.001). Again, DMI results were the inverse of this pattern, stronger in terrestrial systems (53%) than in aquatic systems (4% for marine, 31% for freshwater). While the two response ratio measures do not add to 100%, they consistently follow opposite trends. Because these trends are consistent, we focus on TMI effects for the remainder of this paper.

The generality of our conclusions is supported by a number of tests. First, combining data from both field and laboratory experiments did not bias our conclusions, as laboratory and field studies reported similar findings (Table 2). Second, our analyses of trait-mediated interactions were not affected by combining TMIs arising from different mechanisms. Out of 166 studies, 151 could be assigned to one of four general mechanisms: predator-predator facilitation (*n* = 42), reduced prey activity (*n* = 52), or emigration (*n* = 51), and spatial shifts (*n* = 6, only for three-level interactions). TMIs due to these mechanisms did not differ in magnitude in either two- or three-level food chains (Table 2). Third, there was no overall difference (*P* = 0.298) between studies reporting a total predator effect and those in which we inferred the total effect by adding TMI and DMI effects (see *Methods*). Fifty-eight out of 166 studies reported both the trait-mediated and total predator effect, allowing us to directly calculate

TABLE 2. The magnitude of trait-mediated interactions (TMIs) relative to the total predator effect in (A) two-level food chains and (B) three-level food chains, with 95% confidence intervals in parentheses.

Factor	Relative magnitude of TMI effects	No. studies	Model	df	Q^\dagger	P
A) Two-level food chains (predator effect on prey)						
Habitat						
Marine	0.77 (0.64, 0.91)	8	between	2	6.45	0.037
Freshwater	0.63 (0.52, 0.75)	105	within	133	102.45	0.977
Terrestrial	0.40 (0.27, 0.55)	23	total	135	108.90	0.952
Venue						
Laboratory	0.60 (0.47, 0.73)	60	between	1	0.16	0.686
Field	0.57 (0.45, 0.70)	76	within	134	111.43	0.923
			total	135	111.59	0.930
Mechanism						
Pred. facil.	0.54 (0.40, 0.70)	42	between	2	4.92	0.085
Red. act.	0.39 (0.24, 0.58)	32	within	118	99.96	0.884
Emigration	0.66 (0.51, 0.87)	47	total	120	104.89	0.836
B) Three-level food chains (predator effect on resource of prey)						
Habitat						
Marine	0.97 (0.96, 0.98)	2	between	2	13.77	0.001
Freshwater	0.93 (0.82, 1.01)	20	within	27	37.50	0.086
Terrestrial	0.57 (0.38, 0.78)	8	total	29	51.28	0.006
Venue						
Laboratory	0.81 (0.58, 0.95)	9	between	1	2.82	0.093
Field	0.94 (0.82, 1.02)	21	within	28	44.04	0.027
			total	29	46.87	0.019
Mechanism						
Sp. Shift	1.00 (1.00, 1.00)	6	between	2	5.17	0.075
Red. act.	0.83 (0.69, 0.96)	20	within	27	42.68	0.028
Emigration	0.99 (0.98, 1.05)	4	total	29	47.85	0.015

Note: Random-effects categorical models were used to test the influence of the following variables: habitat, experimental venue, and trait-mediated interaction mechanism (Pred facil, predator–predator facilitation; Red. act, reduced activity of prey; Sp. shift, spatial shift of prey affects resource).

† The homogeneity statistic Q is approximately a chi-square distribution, with degrees of freedom equal to the number of studies minus 1 (Hedges and Olkin 1985). Larger values of Q indicate that a large amount of between-study variation can be attributed to different categories of an explanatory variable.

the relative magnitude of TMI and total effects, yielding a mean of 56.8%. The remaining 108 studies measured TMI and DMI effects without reporting the total effect. Using our additive model to infer the total effect resulted in a similar mean size of TMI relative to total effect (66.2%). These groups did not significantly differ ($P = 0.31$), suggesting that the interaction between TMI and DMI effects is, on average, minimal. This does not mean there are no interactions, merely that interaction terms are fairly evenly balanced between amplifying and attenuating effects across the range of systems in our meta-analysis. Finally, it has been posited that the strength of TMI will vary with experimental duration, as density effects will tend to accumulate slowly relative to prey behavioral changes (Werner and Peacor 2003). Our data does not support this prediction: studies ranged in length from 15 min (Rahel and Stein 1988) to 2 yr (Rudgers et al. 2003), but there was no effect of experimental duration on the strength of TMI effects ($Q = 0.1597$, $P = 0.689$). It is possible that this result would change if we scaled

experimental duration in units of prey generations (P. A. Abrams, *personal communication*); however, the data necessary to perform such an advanced analysis was not available.

We are confident that our findings are not due to a bias toward publication of large-effect results. Publication bias should produce a significant correlation between effect size and sample size (Palmer 1999); we found no such pattern (Spearman rank correlation, $P = 0.109$). Orwin's fail-safe test indicated that 229 unpublished zero-effect studies would be necessary to reduce our TMI estimates to an arbitrarily chosen "negligible" effect size of 20% of the total effect (29 studies to reduce the mean to 50%). Rosenthal's fail-safe test estimated that 16 553 such studies were necessary to lower our estimate to the point where we cannot reject a null hypothesis of 0% TMI. Finally, a cumulative meta-analysis by year found that our estimated effect size does not change significantly as we add data points in chronological order. This indicates that our results are not driven primarily by one or a few publications

with large leverage due to multiple studies or large sample sizes.

DISCUSSION

Trait-mediated effects are generally as strong as or stronger than the effects of direct consumption. Most predator–prey and food web models, which focus on consumption, thus unwittingly ignore a dominant force structuring predator–prey interactions. While recent reviews have suggested that TMIs should be common and affect an array of ecological interactions (Werner and Peacor 2003, Schmitz et al. 2004), we did not expect them to play such a pivotal role.

Despite the surprisingly strong effect of intimidation, there are several reasons to believe that our estimate of TMI strength is conservative. First, we excluded TMI measures that did not have clear demographic effects. Second, predator intimidation can affect prey demographics in a number of ways (energy intake, survival, conversion of energy to offspring, etc.). Virtually all of the studies we analyzed measure only a single aspect of trait-mediated effects and may thus underestimate the total TM effect. For instance, studies partitioning predator effects on prey density into consumption and emigration components do not assess effects of intimidation on fecundity or starvation. Finally, there is no evidence for a publication bias towards larger TMI values. Such biases occur when low-power studies are selectively published, reporting large-effect results more often than small-effect results. The resulting negative correlation between sample size and effect size is not seen in our data set, and fail-safe tests indicated our results are robust. Nevertheless, meta-analyses must always be treated with caution, as they may be biased by selective choice of study systems, failure to publish negative results (Jennions and Moller 2002), and failure to find negative results that may be published in less prominent journals (Murtaugh 2002).

Strong trait-mediated effects are likely to complicate the empirical assessment of predator–prey interactions. It is not safe to assume that consumption rates (i.e., gut content data) are a good measure of predator's impact on prey numbers (Abrams 1993). Gut content data has been used to measure predator–prey interaction strength for community matrix models; however, such measures may fail to assess the predator's total effect (Yodzis 2000). Similarly, a reduction in prey density does not necessarily yield a corresponding increase in predator energy income. Enclosure experiments that preclude emigration may underestimate the total strength of the predator–prey interaction despite overestimating the effect of direct mortality, while unenclosed experiments make it difficult to distinguish between prey emigration and consumption. More appropriate experimental designs require simultaneous monitoring of emigration and consumption rates, a more difficult task than assessing prey densities pre- and post-predator addition. Experiments isolating a single

species of predator and prey to measure their pairwise interactions eliminate the possibility of predator–predator facilitation, a TMI that is approximately 54% of the total predator effect on prey survival when it has been measured. Reductions in prey activity can more easily be assessed in traditional predator–prey experiments; even so, experimental designs lacking a “non-lethal” predator treatment cannot easily separate the effect of intimidation and consumption. It may also be necessary to distinguish between strategic changes in prey traits and genetic changes in mean phenotype resulting from predator-induced natural selection.

The finding that TMIs amplify through food chains while DMIs attenuate provides quantitative support for the argument that behavioral effects should dominate many trophic cascades (Abrams 1992, 1995, Schmitz et al. 2004). Predators have large TM effects on both prey density and foraging rate. Only changes in density affect our assessment of two-level TM effects, but both types of TMIs may influence population density of the prey's food resources. While the classical formulation of trophic cascades depended on DMIs (Carpenter and Kitchell 1993), our work summarizes an accumulating array of experimental evidence (Beckerman et al. 1997, Schmitz 1998, Bernot and Turner 2001) indicating that TMIs strongly influence trophic cascades. Trophic cascades, where predators indirectly benefit plants by suppressing herbivores, may thus occur even when predators consume few prey. The relative paucity of work done on trait- vs. density-mediated effects in cascading trophic interactions, however, highlights the need for more empirical research on TMIs in three-level food chains. Until more of this research has been completed, the general assumption that TMIs drive trophic cascades should be treated with caution.

The large difference between TMIs and DMIs in aquatic and terrestrial systems may help explain ecosystem-level differences in cascading predator effects. Although several recent meta-analyses confirm that trophic cascades occur in terrestrial systems (Schmitz et al. 2000, Halaj and Wise 2001), a subsequent analysis found that cascading predator effects were stronger in aquatic than in terrestrial ecosystems (Shurin et al. 2002). Suggestions to explain this dichotomy (Strong 1992, Polis and Strong 1996) include different herbivore:plant body size ratios, fewer defensive compounds in aquatic producers, high levels of structural compounds in terrestrial producers, and greater food web complexity on land. Our results provide an alternate explanation: larger effects of TMIs in aquatic systems mean that trophic cascades there will be stronger even if terrestrial and aquatic predators consume equal prey biomass. Several factors might explain the stronger intimidation effects in aquatic than terrestrial systems. One possibility is that aquatic organisms are better able to assess their level of predation risk, perhaps through more effective transmission of visual or chemical cues indicating predator presence. Alternatively, the balance

of marginal benefits and costs of defensive tactics may differ in some consistent way between environments, so that for a given level of predator risk aquatic organisms adopt more costly defensive strategies.

Our meta-analysis indicates that trait-mediated interactions are a major component of predator-prey interactions. Such strong intimidation effects will have broad implications for general ecological theory. For instance, our study found that trait-mediated interactions greatly increase the strength of trophic cascades and are stronger in aquatic systems. This may help explain the results of a recent meta-analysis finding that trophic cascades are stronger in aquatic communities (Shurin et al. 2002). Several other important implications were not tested in this paper, but require serious empirical consideration. First, cascading predator effects due to behavioral shifts may cause systems to respond far more powerfully and quickly than consumption rates alone would predict (Schmitz et al. 1997, Schmitz 1998, Grabowski 2004). Second, strong TMI effects suggest that predator-prey coevolution may play a major role in structuring the strength of food web interactions (Werner and Peacor 2003). Introduced predators will have a relatively larger consumptive effect on naïve prey that have not yet evolved defensive behaviors. Finally, trait-mediated interactions may yield novel forms of ecological interactions; for instance, predators may indirectly “compete” by inducing defenses in another predator’s prey (Abrams 1984).

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LITERATURE CITED

- Abrams, P. A. 1984. Foraging time optimization and interactions in food webs. *American Naturalist* **124**:80–96.
- Abrams, P. A. 1991. Strengths of indirect effects generated by optimal foraging. *Oikos* **62**:167–176.
- Abrams, P. A. 1992. Predators that benefit prey and prey that harm predators: unusual effects of interacting foraging adaptations. *American Naturalist* **140**:573–600.
- Abrams, P. A. 1993. Why predation rate should not be proportional to predator density. *Ecology* **74**:726–733.
- Abrams, P. A. 1995. Implications of dynamically variable traits for identifying, classifying and measuring direct and indirect effects in ecological communities. *American Naturalist* **146**:112–134.
- Barry, M. 1994. The costs of crest induction for *Daphnia carinata*. *Oecologia* **97**:278–288.
- Beckerman, A., M. Uriarte, and O. Schmitz. 1997. Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. *Proceedings of the National Academy of Sciences, USA* **94**:10 735–10 738.
- Bernot, R., and A. Turner. 2001. Predator identity and trait-mediated indirect effects in a littoral food web. *Oecologia* **129**:139–146.
- Carpenter, S., and J. Kitchell, editors. 1993. *The trophic cascade in lakes*. Cambridge University Press, Cambridge, UK.
- Downes, S. 2001. Trading heat and food for safety: costs of predator avoidance in a lizard. *Ecology* **82**:2870–2881.
- Eklov, P., and T. Van Kooten. 2001. Facilitation among piscivorous predators: effects of prey habitat use. *Ecology* **82**:2486–2494.
- Forrester, G. 1994. Influences of predatory fish on the drift, dispersal, and local density of stream insects. *Ecology* **75**:1208–1218.
- Grabowski, J. H. 2004. Habitat complexity disrupts predator-prey interactions but not the trophic cascade on oyster reefs. *Ecology* **85**:995–1004.
- Halaj, J., and D. Wise. 2001. Terrestrial trophic cascades: how much do they trickle? *American Naturalist* **157**:262–281.
- Hedges, C., and I. Olkin. 1985. *Statistical techniques for meta-analysis*. Academic Press, New York, New York, USA.
- Huang, C., and A. Sih. 1991. Experimental studies on direct and indirect interactions in a three trophic-level stream system. *Oecologia* **85**:530–536.
- Hurd, L., and R. Eisenberg. 1984. Experimental density manipulations of the predator *Tenodera sinensis* (Orthoptera: Mantidae) in an old-field community. I. Mortality, development and dispersal of juvenile mantids. *Journal of Animal Ecology* **53**:269–281.
- Jennions, M. D., and A. P. Moller. 2002. Publication bias in ecology and evolution: an empirical assessment using the ‘trim and fill’ method. *Biological Reviews* **77**:211–222.
- Lima, S. 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Advances in the Study of Behavior* **27**:215–290.
- Lima, S., and L. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* **68**:619–640.
- Losey, J., and R. Denno. 1998. Positive predator-predator interactions: enhanced predation rates and synergistic suppression of aphid populations. *Ecology* **79**:2143–2152.
- Luttbeg, B., L. Rowe, and M. Mangel. 2003. Prey state and experimental design affect relative size of trait- and density-mediated indirect effects. *Ecology* **84**:1140–1150.
- Morrison, L. 1999. Indirect effects of phorid fly parasitoids on the mechanisms of interspecific competition among ants. *Oecologia* **121**:113–122.
- Murdoch, W., C. Briggs, and R. Nisbet. 2003. *Consumer-resource dynamics*. Princeton University Press, Princeton, New Jersey, USA.
- Murtaugh, P. A. 2002. Journal quality, effect size, and publication bias in meta-analysis. *Ecology* **83**:1162–1166.
- Paine, R. T. 1995. Preface. Pages ix–x in G. A. Polis and K. O. Winemiller, editors. *Food webs: integration of patterns and dynamics*. Kluwer Academic, Boston, Massachusetts, USA.
- Palmer, A. 1999. Detecting publication bias in meta-analyses: a case study of fluctuating asymmetry and sexual selection. *American Naturalist* **154**:220–233.
- Peacor, S., and E. Werner. 2001. The contribution of trait-mediated indirect effects to the net effects of a predator. *Proceedings of the National Academy of Sciences, USA* **98**:3904–3908.
- Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. *American Naturalist* **147**:813–846.

- Rahel, F., and R. Stein. 1988. Complex predator–prey interactions and predator intimidation among crayfish, piscivorous fish, and small benthic fish. *Oecologia* **75**:94–98.
- Rosenberg, M., D. Adams, and J. Gurevitch. 2000. *MetaWin*: statistical software for meta-analysis. Second edition. Sinauer, Sunderland, Massachusetts, USA.
- Rudgers, J., J. Hodgen, and J. White. 2003. Behavioral mechanisms underlie an ant–plant mutualism. *Oecologia* **135**: 51–59.
- Schmitz, O. 1998. Direct and indirect effects of predation and predation risk in old-field interaction webs. *American Naturalist* **151**:327–342.
- Schmitz, O. J., A. P. Beckerman, and K. M. O’Brien. 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology* **78**:1388–1399.
- Schmitz, O., P. Hamback, and A. Beckerman. 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *American Naturalist* **155**: 141–153.
- Schmitz, O., K. Krivan, and O. Ovadia. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters* **7**:153–163.
- Shurin, J. B., E. T. Borer, E. W. Seabloom, K. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2002. A cross-ecosystem comparison of the strength of trophic cascades. *Ecology Letters* **5**:785–791.
- Strong, D. R. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology* **73**:747–754.
- Turner, A., and G. Mittelbach. 1990. Predator avoidance and community structure: interactions among piscivores, planktivores, and plankton. *Ecology* **71**:2241–2254.
- Werner, E., and S. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology* **84**:1083–1100.
- Yodzis, P. 2000. Diffuse effects in food webs. *Ecology* **81**: 261–266.

APPENDIX A

A summary of the data gathered from papers used in the meta-analysis reported here is available in ESA’s Electronic Data Archive: *Ecological Archives* E086-026-A1.

APPENDIX B

Full reference information for all papers used in the meta-analysis reported here is available in ESA’s Electronic Data Archive: *Ecological Archives* E086-026-A2.