

RESOURCE COMPETITION MODIFIES THE STRENGTH OF TRAIT-MEDIATED PREDATOR–PREY INTERACTIONS: A META-ANALYSIS

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Abstract. Only a fraction of the individuals in a given prey population are likely to be killed and consumed by predators. In contrast, nearly all individuals experience the chronic effects of predation risk. When threatened by predators, prey adopt defensive tactics whose costs can lead to reduced growth, maturation rates, survivorship, fecundity, or population density. This nonconsumptive impact of predation risk on prey is known as a “trait-mediated interaction” (TMI) because it results from changes in prey traits such as behavior or physiology. Ecological theory suggests that the strength of TMI effects will reflect a balance between the conflicting demands of reproduction vs. predator avoidance. Competitor density and resource availability are expected to alter the balance between these conflicting forces. We conducted a meta-analysis of experimental studies that measured TMI effect size while varying competitor and/or resource density. The threat of predation had an overall negative effect on prey performance, but the strength of this effect varied with the level of competition. High competition exacerbated the negative effect of intimidation on prey density but moderated the negative effect of intimidation on prey life history and growth. We discuss these results in light of previously published theoretical expectations. Our results highlight the variable and context-dependent nature of interspecific interactions.

Key words: behavioral modification; interaction modification; intimidation; intraspecific competition; predation; trait-mediated interaction.

INTRODUCTION

The mere threat of predation is often sufficient to modify prey behavior and phenotypes, affecting fitness and population dynamics (Abrams 1984, Werner and Peacor 2003). Prey respond to risk by adopting a repertoire of defensive strategies intended to minimize the threat of consumption. Predator avoidance can reduce prey population growth, as prey shift to less profitable microhabitats (Schmitz 1998, Downes 2001), reduce foraging (Morrison 1999) or mating effort (Ryan et al. 1981), or redirect resources from reproduction to chemical or structural defenses (Barry 1994). Predators thus affect prey populations both by consuming prey (density-mediated interactions; DMIs) and by inducing potentially costly defensive strategies (trait-mediated interactions; TMIs; Werner and Peacor 2003, Preisser et al. 2005). Following Preisser et al. (2005), we define TMIs as strategic changes in prey behavior, morphology, or physiology, in response to the presence of a predator. The strategic changes often have measurable developmental or demographic effects, which are the focus of this paper. These effects are often measured at the prey level, but may also cascade down to affect the prey's resources (trait-mediated indirect interac-

tions, or TMIs). In this paper, we focus exclusively on the effect of trait-mediated interactions between predators and their prey (i.e., two-level food chains).

There is a growing consensus that trait-mediated interactions are a major component of predator–prey dynamics (Werner and Peacor 2003, Schmitz et al. 2004). TMI effects can be measured by exposing prey to “non-lethal” predator treatments (e.g., caged predators or their chemical cues) and measuring the effect of perceived risk on prey growth, life history, and demography. Such methods have demonstrated significant effects of intimidation in a wide range of ecological communities. The effect of predator intimidation can be equal to or greater than that of direct consumption in governing predator–prey dynamics. A recent meta-analysis found that TMI effects were 63% as strong as the total net predator effect on prey demography across a range of systems (Preisser et al. 2005).

This large average TMI effect size suggests that trait-mediated interactions are an important facet of community dynamics; however, across-system averages may obscure ecologically significant variation. TMI effect sizes vary both across different species pairs and as a function of ecological context within a given predator–prey system. Understanding how and why TMIs vary should significantly advance our ability to understand and predict population-level interactions in ecological communities. For instance, theory predicts

Manuscript received 10 August 2004; revised 21 March 2005; accepted 22 March 2005. Corresponding Editor: D. K. Skelly.

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that prey foraging effort depends on an interaction between resource availability and predation risk (Abrams 1982, 1984, Mangel and Clark 1986, McNamara and Houston 1987, 1994, Houston and McNamara 1989, Abrams 1991, Luttbegg et al. 2003).

A number of models predict that prey will forage less (take fewer risks) as resources become more abundant (e.g., McNamara and Houston 1987, Mangel and Clark 1988, Ludwig and Rowe 1990, Werner and Anholt 1993, Luttbegg et al. 2003). At low resource levels, prey cannot afford to curtail their foraging because any defensive measures might lead to starvation. Foraging levels will therefore be similar in risk- and risk-free environments. TMI effects, calculated as the difference in performance between risk- and risk-free environments, are thus negligible when resources are scarce. In contrast, at high resource levels, risk-prone prey can dramatically reduce foraging and still satisfy their minimal energy needs. A given reduction in foraging time also forfeits more energy when resources are abundant. This leads to a large difference in growth between risk- and risk-free prey (a large TMI effect). The result is a positive relationship between TMI effect and resource levels (e.g., Fig. 2c in Luttbegg et al. 2003).

Using a different model, Peacor (2002) also predicted that predation risk reduces prey growth at high resource levels. However, unlike Luttbegg et al. (2003), he suggested that low resource levels can result in strong *positive* trait mediated effects in which predation risk actually increases prey growth rate. This effect depends on a nonlinear relationship between resource density and the per capita resource growth rate (e.g., a logistic growth curve). When resources are scarce, consumers compete strongly and have low growth rates, exploiting their resources beyond the maximum sustainable yield. Predation risk suppresses consumer foraging, but the resulting increase in resource density more than compensates for this loss, elevating consumer growth rates. At low resource density, predators thus inhibit the consumer population's negative effect on its own growth rate.

The contrast between the Luttbegg and Peacor models highlights an important issue in theoretical models of predation-foraging trade-offs: Model predictions are very sensitive to underlying assumptions (Abrams 1991, Křivan and Sirot 2004). Abrams (1991) showed that increased resource abundance can have diametrically opposite effects on foraging effort (and hence TMI effect size and direction) depending on: (1) whether consumers use foraging to avoid starvation and/or to subsidize reproduction, (2) whether reproduction is semelparous or iteroparous, (3) the time-scale of changes in resource levels, and (4) the exact shape of the functional responses relating foraging time to energy income, and energy income to reproduction. This context dependence might explain why the early empirical experiments of foraging-risk tradeoffs had yielded inconsistent results. Abrams (1991) concluded

that there was insufficient empirical data to evaluate which of the different model predictions fit most natural systems.

Over a decade later, there are now a substantial number of studies measuring TMI effects at different resource levels (Appendix). We performed a meta-analysis of these studies to test for general trends in how TMI effects vary with the strength of competition. In particular, we tested whether predation risk has a larger impact on prey as resources become more abundant (Luttbegg et al. 2003), and whether predation risk improves prey performance at low resource levels (Peacor 2002). We also considered the variance around these mean effect sizes, which may reflect the context dependence predicted by Abrams (1991).

METHODS

Literature survey

The effect of trait-mediated interactions can be measured by recording prey performance in the presence and absence of a perceived predator threat. Performance can include growth rates, life history traits such as instar duration or time to maturity, or changes in mortality or fecundity that affect prey population density. We surveyed the literature for studies that experimentally measured TMI effects, while simultaneously varying the level of resource competition either by varying the density of competitors or the density of the prey's resources. Comparing each threat treatment to its predator-free control provides an estimate of TMI effect, and these high- and low-resource TMI effects can be compared within each study to estimate the impact of competition on TMIs. To find papers measuring TMI strength at different levels of competition, we carried out key word searches on three online databases (BIOSIS, JSTOR, and Web of Knowledge Science Citation Index, described in detail in Preisser et al. 2005) and exhaustively searched the 1990–2004 editions of four journals (American Naturalist, Ecology, Oecologia, Oikos). We also examined citations within relevant papers, and used the Scientific Citation Index to find later studies that cited relevant papers.

Data collection

For each case, we recorded the sample size and the mean and standard error of the response variable in each of four treatments: low competition (LC) risk-free control, LC with predator threat, high competition (HC) risk-free control, and HC with predator threat. High competition treatments correspond to either high competitor density or low resource availability. Data were taken from the text, tables, or figures of the published papers. We determined values from figures by measuring them with digital calipers, and were accurate to $\pm 1\%$ of the actual value (based on measuring figures with known means).

We divided the type of response variable into three main categories: (1) effects on growth rate (e.g., change

in mass or size); (2) life history timing (e.g., instar duration, time to metamorphosis); and (3) population density (e.g., number of individuals, mortality, survivorship, fecundity, or emigration rates). All three measures are likely to have implications for prey fitness and population dynamics. We did not record shifts in prey behavior without clear demographic implications (e.g., Kohler and McPeck 1989). In many instances, we acquired data on multiple interactions from a single published report. We considered the interactions as independent data points when they involved different species pairs, environments, seasons, or ecological contexts (i.e., presence of a third species).

Data analysis

We measured the effect of predator threat on prey performance in each case using Hedges' d (Hedges and Olkin 1985): the difference between a treatment and control mean, standardized by the pooled standard deviation. The effect size was multiplied by a marker variable I to designate whether an increase in the response variable is detrimental ($I = -1$, e.g., mortality) or beneficial ($I = 1$, e.g., survivorship) for prey fitness.

To draw general conclusions about TMI effect magnitude and direction, we calculated the mean effect size (\bar{d}) using a random-effects model. Random effects were chosen to reflect our expectation that different study systems have variable TMI effects drawn from a distribution of effect sizes. We used MetaWin (Rosenberg et al. 2000) to calculate the mean of the effect size distribution. Because the data were non-normally distributed (judging by normal quantile plots), we calculated confidence intervals using the bootstrap routine implemented in MetaWin. Mean effect sizes were calculated separately for high- and low-competition levels, and we tested whether the mean effect size differed among the three classes of TMI response variable (growth rates, life history shifts, or population density effects). We then repeated these tests separately for studies that manipulated resource level and those that manipulated prey densities, in case these methods yield distinct patterns and did not represent a single "competition" variable.

We tested whether TMI effects varied with competition using a meta-analytic analogue of a paired t test. Within each experiment, we paired TMI estimates from high- and low-competition treatments (HC and LC, respectively). We then calculated a new effect size for each case, $\Delta|d|$, the difference in the absolute magnitude of the TMI effect between high and low competition treatments, where $\Delta|d| = |d_{\text{HC}}| - |d_{\text{LC}}|$. By taking the difference in absolute magnitudes, we highlight the change in effect magnitude and remove the confounding influence of effect direction. Qualitative results were similar whether we analyzed the difference in effect size (with direction) or absolute magnitude. We used standard meta-analytic techniques to estimate the mean across cases ($\bar{\Delta|d|}$), weighting the individual

cases using a pooled variance, $\text{Var}(\Delta d) = \text{Var}(d_{\text{HC}}) + \text{Var}(d_{\text{LC}})$. The null hypothesis that TMI effect sizes are identical at both resource levels corresponds to $\Delta|d| = 0$. Positive values of $\Delta|d|$ imply that resource competition leads to stronger TMI effects (regardless of effect direction); negative $\Delta|d|$ implies that competition decreases TMI effect magnitude. We tested whether the mean $\Delta|d|$ differed from zero or between TMI variables (growth, life history, or density).

We conducted three standard meta-analytic tests of possible bias arising from a "file-drawer effect" in which negative results remain unpublished. Such bias is expected to cause a negative correlation between effect size and sample size (Hedges and Olkin 1985) that can be detected by Spearman rank correlation. Rosenthal's and Orwin's fail-safe tests estimate the number of unpublished studies of zero effect ($\Delta|d| = 0$) that would be required to reduce our results to nonsignificant ($\alpha = 0.05$) or negligible ($\bar{\Delta|d|} < 0.2$) levels, respectively.

RESULTS

We found 40 papers measuring the effects of predator intimidation on prey performance under different levels of resource availability. Intimidation effects include reduced prey growth, delayed maturation, longer instar length, reduced fecundity or mating effort, or even starvation. Nineteen of the 40 papers manipulated the level of intraspecific competition by varying prey density, while the remainder varied resource density or the feeding regime. We combined both strategies to yield two treatments: low competition (LC; high resource or low prey density), and high competition (HC; low resource or high prey density). Many of the 40 papers contained results for multiple species pairs, or a given pair in different environmental contexts, yielding a total of 137 cases of paired HC and LC estimates of TMI strength (see Appendix).

Overall, prey were negatively affected by predation risk in both low- and high-competition treatments (for LC, $\bar{d} = -0.56$ [$-0.89, -0.24$]; mean with 95% confidence intervals [CI] in brackets; for HC, $\bar{d} = -0.55$ [$-0.85, -0.28$]; $P < 0.05$ in both cases). Pairing HC and LC TMI effects by study, TMIs were not significantly different when comparing high- and low-competition treatments ($\bar{\Delta|d|} = -0.11$ [$-0.40, 0.16$]). Because the overall mean effect size lumps together TMI effects measured on very different aspects of prey performance, this estimate obscures biologically important sources of variation. Separating out predator effects on prey growth, development rate, and density, we found that competition has a large but variable impact on the consequences of predator intimidation (Fig. 1). Prey subject to low levels of competition (high resource levels or low competitor density) experienced strong negative TMIs ($P < 0.05$) for all three aspects of prey performance, which did not differ significantly among each other ($Q = 1.19$, $P = 0.55$). At high levels of

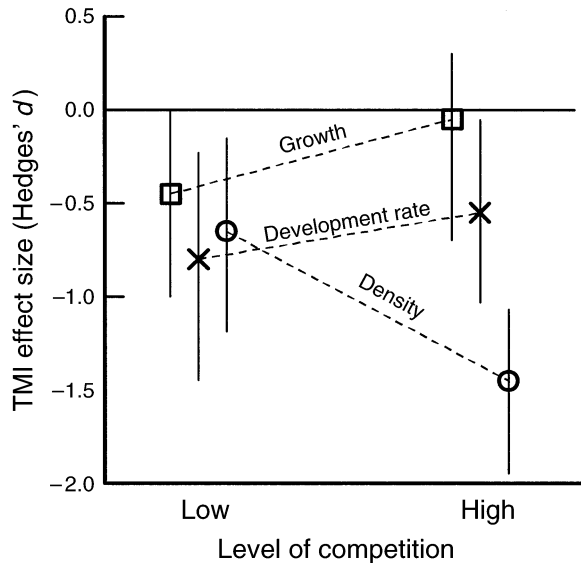


FIG. 1. The effect of predator intimidation of prey (trait-mediated interaction; TMI), as a function of competition strength and the response variable being measured: growth (squares); development rate (the inverse of the time to maturity; crosses); and prey population density (circles). Effect size is measured as the difference in prey performance between a threat and a risk-free treatment, standardized by the standard error. Symbols mark the mean effect size across cases; vertical lines represent the 95% confidence intervals for the mean effect. High competition corresponds to low resource or high competitor density.

competition, TMI effects on prey density and development rate remained negative ($P < 0.05$), whereas prey growth showed no significant trend in the effect of predator intimidation ($P > 0.05$). The three facets of prey performance thus responded differently to predator threat at high levels of competition ($Q = 23.35$, $P < 0.001$).

The nonsignificant mean TMI effect on prey growth does not imply that intimidation has no effect on prey growth, only that there is no consistent trend to TMI effects. Significant heterogeneity remains among studies even after accounting for differences in response variables and experimental approach ($Q_{119} = 210.8$, $P < 0.0001$). This heterogeneity is also reflected in the large pooled variance of the distribution of random effects ($\text{Var}_p = 4.34$). Consequently, the mean effect sizes reported here represent average trends in a highly variable distribution of effect sizes. Nonsignificant effects, such as mean TMI effects near zero at high competition, may simply imply that predation risk is equally likely to increase or decrease prey growth rates.

The variable impact of competition on different types of trait-mediated interaction is clearly illustrated by the paired contrast in effect magnitudes ($Q = 11.34$, $P = 0.0035$). Resource competition significantly magnified the (negative) effect of intimidation on prey density (e.g., changes in prey survivorship or fecundity), but

weakened the effect of intimidation on prey growth (Fig. 2). Effects on prey maturation rate tended to weaken with competition, though the trend was not significant. Because $\Delta|d|$ focuses on TMI magnitude alone, it obscures changes in TMI effect direction. Conducting an analogous contrast analysis on Δd (including effect direction), competition makes TMI effects on growth and development time less negative ($\bar{\Delta}d = 0.30$ and 0.34 , respectively, with confidence intervals: $[-0.06, 0.72]$ and $[-0.09, 0.83]$), but makes TMI effects on density still more negative ($\bar{\Delta}d = -1.41$ $[-2.82, -0.47]$; $Q = 23.99$, $P < 0.001$).

Competition had a fairly consistent impact on trait-mediated effects on prey population density. Of the 38 cases with prey density measurements, competition exacerbated negative TMI effects in 32 cases ($\chi^2 = 17.8$, $P < 0.001$). In contrast, life history and growth showed far more variation, and a simple sign test actually showed no consistent effect of competition (competition strengthened TMI effects in 13 out of 24 cases for life history; 36 out of 74 cases for growth). This further illustrates the substantial heterogeneity among systems in how prey growth and development respond to the interaction of resources and risk. In contrast to this vote-counting approach, meta-analysis reveals significant effects because it incorporates the magnitude of effects and their error terms. As a result, while competition increases TMI effects on growth and development about as often as it decreases TMI effects, the magnitude of decreasing effect strengths outweighs increasing strength, making $\bar{\Delta}|d|$ negative.

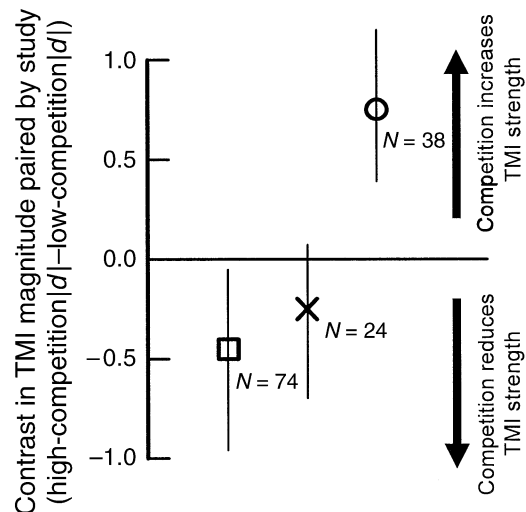


FIG. 2. The effect of resource limitation on the magnitude of the trait-mediated interaction (the effect of predator intimidation on prey performance). Symbols represent the mean contrast in effect magnitude, paired by study; vertical lines represent the 95% confidence intervals for the mean contrast. Numbers represent the number of cases (paired high- and low-resource treatments) contributing to a given mean. Response variables are growth (square) development rate (cross), and prey population density (circle).

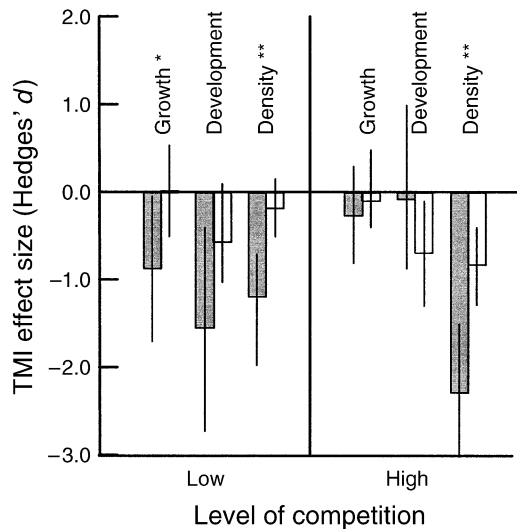


FIG. 3. The strength of trait-mediated interactions depends on whether experiments manipulated competitor density (shaded bars) or resource density (open bars). Mean effect sizes and 95% confidence intervals are given for each combination of manipulation strategy, prey response variable, and competition level. Asterisks (*) indicate when there is a statistically significant difference between effect sizes for prey-density and resource-density manipulation.

* $P < 0.05$; ** $P < 0.01$.

Although both prey and resource density can affect the level of resource competition, their relationships with competition intensity are neither equivalent nor necessarily straightforward. As a result, these two approaches did not have equivalent effects on TMI strength. Varying prey density generally resulted in stronger trait-mediated interactions than was observed in experiments manipulating resource density (Fig. 3). In experiments controlling resource levels, TMI effects were only consistently negative for prey density effects, not growth or maturation. This result argues against combining competitor- and resource-manipulation into a single analysis. However, analyzing these experimental designs separately resulted in qualitatively similar conclusions to those seen in Figs. 1 and 2. In both experimental approaches, competition exacerbated the negative TMI effects on prey density, and increased or had little effect on TMI effects on prey development rate and growth. These trends in $\bar{\Delta}|d|$ were significant when manipulating competitor density ($Q = 11.42$, $P = 0.003$) but not resource density ($Q = 3.68$, $P = 0.16$).

Tests of potential publication bias found no indication of a large file-drawer effect. There was no significant correlation between effect size and sample size for d_{HC} ($P = 0.654$, $r_s = -0.039$), d_{LC} ($P = 0.197$, $r_s = -0.111$), or $\bar{\Delta}|d|$ ($P = 0.318$, $r_s = 0.84$). Fail-safe tests suggest that our findings of a significant effect of competition on trait-mediated interactions is robust: 200 zero-effect cases (i.e., studies finding that com-

petition did not modify TMI effects) would be required to reduce competition's effect on prey density $\bar{\Delta}|d|$ to nonsignificance (Rosenthal's fail-safe test), or 75 such cases to reduce $\bar{\Delta}|d|$ to a value of 0.2 or less (Orwin's fail-safe test). For competition's effect on growth TMIs, Rosenthal's fail-safe test = 30 and Orwin's = 98; on maturation, Rosenthal's = 0, Orwin's = 9 (maturation $\bar{\Delta}|d|$ was nonsignificant to begin with).

DISCUSSION

Activities such as foraging and mating are crucial to an individual's fitness; however, they often entail an increased risk of predation (Lima and Dill 1990). Optimization theory suggests that organisms should modulate their behavior to maximize their expected fitness, trading a reduction in some fitness component for improved ability to evade consumption by a predator (Abrams 1984). This reduction in performance, survival, or fecundity constitutes a trait-mediated effect of the predator on its prey. Such trait-mediated interactions (TMIs) have been documented in a wide range of study systems, and a recent meta-analysis (Preisser et al. 2005) confirmed that TMIs are an important and general feature of predator-prey interactions.

The magnitude of predator-induced TMI effects is thought to depend on the balance struck between fitness lost due to direct consumption vs. that lost via defensive strategies. Variation in predator, competitor, or resource densities should change the strength of TMI effects by modifying the balance between the opposing demands of predator defense and growth or reproduction (Cerri and Fraser 1983, Abrams 1991). A number of models predict that TMI effect size should increase with resource availability, or, conversely, decrease with competition intensity (e.g., Luttbegg et al. 2003). Other models suggest that TMI effects may actually be positive when competition is intense (Peacor 2002). Our meta-analysis tested whether these theoretical predictions fit general trends in published experimental results. We conclude that competition has consistent effects on TMI strength, but that the strength and sign of this interaction depends on the response variable being measured. When competition is weak, predators have consistently negative TMI effects: They reduce prey growth, delay maturation, and decrease prey density. The effect of intimidation changes as competition increases or resources become more limiting: Intimidation has a consistently stronger negative effect on prey density, but a weaker (or more heterogeneous) net effect on prey growth and development time (Fig. 2). Note that the weak net effect can arise from a mixture of cases of strong positive and negative effects resulting from different biological contexts. We draw from both theory and individual case studies to discuss three consistent trends seen in our meta-analysis: (1) competition moderates TMI effects on prey growth and development, (2) competition exacerbates TMI effects on prey density, and (3) TMI effects were stronger in

cases that manipulated competitor density rather than resource density. We draw from both theory and empirical work to discuss possible explanations for these patterns.

*Competition reduces TMI effects
on growth and development*

Theory predicts that higher resource availability should lead to reduced risk-taking, and hence a greater difference in energy income between risk-prone prey and risk-free controls (Abrams 1984, 1991, Luttbegg et al. 2003). The simple explanation for this result is that prey can more readily “afford” the costs of predator avoidance under conditions of low competition/high resource density. Our meta-analysis supports these theoretical expectations for growth and developmental rate (Fig. 2). Specific examples of this pattern include tadpoles (Relyea 2004) and snails (Turner 2004). An exception occurs in *Daphnia*, where predator presence has a larger effect at low resource density (Walls et al. 1991). In this case, predator presence causes the induction of a spined morph regardless of resource levels.

Peacor (2002) also predicted a similar trend in TMI strength with competition, but for a very different reason (incorporating resource dynamics). Like the previous models, Peacor predicts that predators cause strong negative TMIs when competition is weak because prey reduce their foraging rate and hence lose energy income. Since resources are primarily self-limiting, reduced prey activity has a negligible impact on resource levels. On the other hand, if resources are limited primarily by consumption (i.e., top-down control), then reduced prey activity can lead to substantial increases in resource availability. This increase in resource density can more than offset the costs of low prey-foraging effort, so that predator intimidation actually boosts prey growth rates (Peacor 2002, Peacor and Werner 2004, but see Turner 2004). This model has been used to explain results for a number of studies in our data set (Peacor and Werner 2000, Resetarits et al. 2004) in which TMI effects on growth go from negative at low competition, to positive at high competition. Other studies (Anholt et al. 2000, Babbitt 2001, Barnett and Richardson 2002) have suggested that positive TMIs at high competition might instead result from resource subsidy by predator feces (but see Peacor 2002). Approximately half of the case studies in our data set found that predators improved prey growth and maturation rates under high competition, a result consistent with the Peacor model (2002). Nonetheless, the average trend was toward negative TMI effects on growth and development, suggesting that Peacor’s model is frequently not applicable. Some of the heterogeneity among studies may be due to different experimental designs, such as whether or not resource populations were allowed to vary dynamically or were held constant.

Competition increases TMI effects on prey density

The risk of predation significantly reduced prey density (including survivorship and fecundity) relative to risk-free controls. Competition (or resource limitation) exacerbated this effect, in direct contrast to competition’s mitigating effect on growth and life history TMIs, and to many theoretical predictions (e.g., Luttbegg et al. 2003). However, Abrams (1991) showed that the even the sign of the relationship between foraging effort and resource levels can depend on model assumptions. For instance, theory predicts that risk-prone consumers are more likely to decrease their foraging effort with higher competition if they are iteroparous and the changes in resource availability are short-lived ($\partial C_0/\partial R > 0$; Abrams 1991; TMI effects increase with stronger competition).

Competition could also amplify TMI effects if prey defensive strategies are insensitive to resource levels. While optimization theory suggests prey should dynamically vary their defensive strategy with resource level, prey may be unable to adopt optimal strategies due to limited plasticity. If prey adopt relatively constant defenses, these will be more costly when resources are scarce. Food-limited individuals can least afford these defenses, and may experience reduced fecundity or elevated mortality. For instance, *Daphnia* develop energetically costly spines regardless of resource level density (Walls et al. 1991).

One interesting possibility is that the density effects documented here can help explain our growth and life history results. Many experiments treat initial density levels as a categorical treatment effect (competition) when analyzing their results, regardless of whether density levels have changed during the course of the experiment due to mortality. We did not exclude such studies because it is not always possible to identify when survival and competition are confounded, and because this interaction may be both biologically realistic and contribute to the patterns emerging from our meta-analysis. Intense competition and risk may interact to place prey at risk of starvation and increased mortality (TMI on prey density, Fig. 2; Walls et al. 1991). If density is not properly controlled, elevated mortality could subsequently lessen the impact of competition. Ostensibly high-competition treatments could, in fact, end up experiencing lower competition late in the experiment. Surviving prey experience lower competition relative to their risk-free control, lessening or even reversing the observed TMI effect. This hypothesis predicts that TMI effects will follow a predictable time course at high competition: growth is initially depressed by predation risk, followed by an increase in prey mortality after which prey growth rates recover and are greater than in the risk-free controls still experiencing high competition. This model is consistent with the increased TMI effect on prey density under conditions of high competition and positive TMI

growth effects at high competition; however, not enough time course data is available to test this hypothesis.

Effect of manipulating prey vs. resource density

Experiments on the interaction between competition and predator intimidation can manipulate competition by varying prey (competitor) density, or resource density. TMI effects were consistently stronger in experiments that controlled prey density, as was the interaction between competition and TMIs (Fig. 3). We propose four nonexclusive hypotheses to explain this observation. First, TMI effects may coincidentally be more pronounced in study systems that are more amenable to controlling competition via competitor density. For example, prey density was manipulated in 45 out of 74 cases with amphibian prey and 10 out of 51 cases with arthropod prey ($\chi = 20.8$, $P < 0.001$). However, TMI effect strengths were not significantly different between amphibians and arthropods ($d = -0.67$, -0.53 , respectively) at low competition. Second, it is possible that resource- and prey-manipulation differ in their impact on the level of competition. Indeed, neither experimental design necessarily results in actual competition among prey. However, we see no a priori reason to believe that manipulating prey densities is consistently more effective, and this would not explain the consistent difference in TMI strength at both levels of competition. Third, resource availability may be more difficult to manipulate than prey density, due to feedbacks such as fertilization from predator feces.

Manipulations of prey density simultaneously affect resource competition, interference competition, and the per capita predation risk. The latter two mechanisms might produce the density-TMI interaction we observed. For instance, agonistic interactions among prey might increase the cost of predator avoidance. There are two reasons why these confounding effects might also explain reduced growth TMIs at high density: (1) predation risk might moderate agonistic interactions, improving growth or developmental rates; or (2) high density dilutes per capita predation risk, thereby reducing TMI effects on growth. We are not aware of any empirical or theoretical studies that have explicitly looked at these other effects of prey density (but see Grand 2002). The clear difference in how TMIs are affected by manipulations of competitor- vs. resource-density (Fig. 3) suggests that this will be a profitable avenue of research.

Context dependence

Meta-analysis is based on the analysis of mean effect sizes. Consequently, a $\bar{\Delta}|d|$ of 0 may not imply resources have no effect on TMI strength, since this result might also occur if there are significant positive and negative effects of roughly equal magnitude. In this study, we used a random-effects model for the meta-analysis, which assumes that there is a distribution of

true effect sizes. While we have focused on the mean of this distribution to look for general trends in effects, the variance is itself quite informative, reflecting the variation in effect size among study systems. The estimated pooled variance is quite large ($\text{Var}_p = 4.34$), indicating that there are cases of strong positive and negative effects, consistent with strong context dependence. Abrams (1991) showed that increasing resource levels can either increase or decrease a consumer's optimal foraging effort under risk. Theoretical predictions depend on the shape of functional response curves, the relative importance of starvation or reproduction in motivating foraging, and life history traits such as the speed of maturation and whether consumers are semelparous or iteroparous (Abrams 1991).

Of these possible sources of context dependence, we were only able to test whether the impact of competition on TMI effects varied between semelparous and iteroparous systems. Reproductive life history had no effect on this interaction for growth or developmental rate ($P = 0.934$, 0.281 , respectively), but did impact population density effects. Resource competition exacerbated TMI effects for semelparous ($N = 15$, $\bar{\Delta}|d| = 3.39$), but not for iteroparous taxa ($N = 25$, $\bar{\Delta}|d| = 0.20$, $P = 0.001$), in direct contrast to the prediction from Abram's (1991) model. Even after accounting for this source of context dependence, the large pooled variance for the random-effects distributions in our analysis suggests there is substantial heterogeneity among studies, a possible reflection of additional variables influencing the strength of the resource-risk interaction (Abrams 1991).

Publication bias

It is important to keep in mind that meta-analyses are subject to a number of possible sources of bias. First, researchers tend not to select study systems at random. Not all systems are equally amenable to experimental manipulation, while preliminary observations (anecdotal or experimental) may inspire (or discourage) a particular type of experiment. Our data set is strongly biased towards temperate amphibian and freshwater systems (half of the interactions involve amphibian prey), so our conclusions may not hold across a broader array of taxa. Given the context-dependent nature of risk-resource interactions (Abrams 1991), it is possible that our overall results reflect the predominance of a particular type of study system in our data set rather than truly general trends. This is a perennial headache for meta-analyses that will only be resolved when equivalent experiments are conducted on a wider array of systems.

Second, negative preliminary experiments may discourage a researcher from conducting a full experiment, and negative final results may be published in more obscure venues or not at all. This latter source of bias is of less concern in this study, as standard

meta-analytic techniques for detecting publication bias (Hedges and Olkin 1985) were uniformly negative.

Conclusions

A major goal of community ecology is to identify how species interact and estimate the strength of such interactions in order to predict the effects of perturbations. In principle, this information could be used to parameterize models of community interactions; in practice, reaching this goal has proved difficult. Leaving aside the considerable practical challenges to conducting experimental studies at appropriate spatial and temporal scales, our results highlight two major issues to consider when quantifying pairwise interactions. First, many studies fail to measure all facets of an interspecific interaction. Attack and consumption rates are important, but not necessarily sufficient measures of predator–prey interactions, as predators may also have significant chronic effects on prey resulting from intimidation (Werner and Peacor 2003, Preisser et al. 2005). Second, interaction strengths may vary greatly with changes in biotic and abiotic conditions. We have shown that the strength of trait-mediated predator–prey interactions can vary significantly as a function of competitor density and resource availability. This suggests that pairwise predator–prey interactions may often depend on the state of a third player, prey resources (Peacor and Werner 2004).

It is increasingly clear that an accurate description of predator–prey interactions must account for not only a single functional response curve with constant search and capture parameters, but also the ways in which resource availability, prey behavior, and predator density might modify those parameters (Abrams 1984, 1995). Interaction strengths measured under a particular ecological setting will therefore be inappropriate for predicting community dynamics under other conditions. On the other hand, our meta-analysis demonstrates that TMI effect strengths vary with competition in a fairly predictable way across a range of predator–prey systems. This suggests that the contingency inherent to interspecific interactions may be predictable. To address this issue, however, we need both theoretical predictions of what TMI response curves might look like, and empirical tests of these predictions. It is especially important that empirical tests move beyond categorical treatments like high/low food or predator presence and test more continuous axes that provide better resolution of the functional response curves (e.g., Relyea 2004).

ACKNOWLEDGMENTS

We thank M. Benard, B. Luttbegg, A. Sih, D. Skelly, B. Spitzer, K. B. Suttle, and an anonymous reviewer for constructive comments on this manuscript. The authors were supported by NSF grant DEB-00-89716 to M. Turelli (D. I. Bolnick), the University of Texas at Austin (D. I. Bolnick) and the University of California at Davis (E. L. Preisser).

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APPENDIX

A table of the data used in the meta-analysis for this paper, including the source of the data, identity of the predator and prey, how trait-mediated effects were measured, sample sizes, and effect sizes with full citation information for all papers contributing data to this meta-analysis is available in ESA's Electronic Data Archive: *Ecological Archives* E086-149-A1.