HOW DEPENDENT ARE SPECIES-PAIR INTERACTION STRENGTHS ON OTHER SPECIES IN THE FOOD WEB?

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Abstract. In ecological theory species interaction strengths are typically described by constants or functions that depend on the densities of the two interacting species. However, if species' traits (phenotypes) are plastic, then modifications in these traits (induced by the presence of another species) could affect interaction strengths of the focal species with a number of other species in the system. The magnitudes of such higher-order effects on interaction strengths have not been reported and are not straightforward to measure. We present a methodology to quantify changes in consumer–resource interaction coefficients (a metric of interaction strength) due to effects of predators on consumer (i.e., the prey of the predator) phenotype (e.g., nonlethal or trait-mediated effects). Application of this method to studies in diverse systems indicates that predators can strongly reduce consumer–resource interaction coefficients, often in the range of 20–80%. We use analytic and simulation models to show that effects on interaction coefficients of this magnitude can lead to trait-mediated effects that contribute more strongly than density-mediated effects to the net effects of predators on consumers and their resources, and even qualitatively change model predictions. Our results strengthen previous claims that trait-mediated effects strongly influence species interactions and suggest that recent calls to quantify interaction strengths must be broadened to include examination of the variation in interaction strengths due to their dependence on densities of other species (most notably predators) in food webs.

Key words: food web; higher-order interaction; indirect interaction; interaction coefficient; interaction strength; nonlethal; phenotypic plasticity; trait-mediated.

INTRODUCTION

Interactions among species are one of the principal processes generating patterns in ecological communities. Accordingly, much of the theory of community ecology relies on equations describing species population growth rates as a function of coefficients representing the strength of species-pair interactions. Clearly, any predictions of community properties based on this foundation must rest on an appropriate description of the direct interactions between species.

Due to the fundamental role of the interaction coefficient in theoretical conceptualizations of communities, there have been renewed calls for empirical measurement of the strength of species interactions (Paine 1992, Osenberg et al. 1997, Wootton 1997, Laska and Wootton 1998, McCann et al. 1998, Berlow et al 1999, Abrams 2001). Laska and Wootton (1998), for example, argue that interaction coefficients (which they denote as ''per capita interaction strengths'') are the most useful empirical metric quantifying the impact of one species on another. This metric underlies various other measures of interaction strength used in theory (e.g., elements of the community matrix, the Jacobian matrix,

or the inverse Jacobian matrix) to quantify the direct and indirect effects of species on each other (Bender et al. 1984). Correspondingly, many empirical studies have estimated interaction coefficients by directly measuring consumption rates (Goldwasser and Roughgarden 1993, Wootton 1997), or from time series of population densities (Pfister 1995, Ives et al. 1999).

A fundamental assumption that underlies both the majority of community theory and the empirical measurement of interaction strengths is that species-pair interactions are independent of other species in the system. However, if a target species responds to another species by modifying its phenotype (reviewed in Lima and Dill 1990, Kats and Dill 1998, Lima 1998, Tollrian and Harvell 1999), this modification can potentially affect the interaction strength of the target species with a number of other species in the food web (reviewed in Werner and Peacor 2003). Thus, interaction coefficients may vary dynamically as a function of the density of other species in the food web (Abrams 1987, Werner 1992, Wootton 1993), which can strongly affect species population dynamics (reviewed in Bolker et al. 2003). Theoretically, this variation represents a higher-order interaction (sensu Vandermeer 1969) because terms in population growth rate equations are composed of three or more species densities.

It is therefore of considerable importance to quantify the magnitude of higher-order effects on interaction coefficients. Are these effects large enough to warrant inclusion in ecological theory? Although empirical evidence strongly suggests that a third species can affect the interaction coefficient between two other species (e.g., Werner and Peacor 2003), there have been no explicit measurements of the magnitude of this effect. To address this issue, we present a method quantifying the effects of a predator on consumer–resource interaction coefficients in a three-species food chain. Based on this method, estimates derived from the literature indicate that phenotypic responses of consumers to predators often strongly affect the consumer–resource interaction coefficient magnitude. We further present theoretical analyses indicating that the estimated effects are large enough to contribute substantially to the net effect of the predator on both the consumer population and the consumer's resources. Although we focus on how predators affect consumer–resource interactions, analogous methods likely would provide similar results in other three-species configurations in which higher-order interactions have been reported (Werner and Peacor 2003). When viewed in concert with their nonlinear nature, our estimates of the variation in interaction coefficient magnitude underscore the potential importance of higher-order effects arising from phenotypic plasticity on the structural and dynamical properties of food webs.

METHODS TO ESTIMATE PREDATOR EFFECTS ON CONSUMER–RESOURCE INTERACTION COEFFICIENTS

Consider a three-species food chain, in which a predator, P, preys on a consumer, C, which preys on a resource, R. The population growth rates of the three species can be expressed in general form as

$$\frac{dR}{dt} = f(R) - i_{RC}RC$$

$$\frac{dC}{dt} = i_{CR}RC - i_{CP}CP - d_{C}C$$

$$\frac{dP}{dt} = i_{PC}CP - d_{p}P \qquad (1)$$

where d_C and d_P are per capita mortality rates of the consumer and predator, respectively, due to external factors. The interaction coefficients, i_{RC} and i_{CR}, are functions that define the per capita effect of the consumer on resource population growth rate and resource on consumer population growth rate, respectively, and i_{CP} and i_{PC} describe analogous functions for the predator-consumer interaction.

In the absence of phenotypic responses to the predator, i_{RC} is a constant, as in the Lotka-Volterra equations, or a function of resource and/or consumer density (i.e., $i_{RC} = i_{RC}(R,C)$). For example, if handling time constrains intake of the resource, a Holling Type II functional response can be used to describe i_{RC}. However, if predator-induced changes in consumer phenotype affect the consumer–resource interaction, then in contrast to traditional models, i_{RC} also will be a function of predator density. We represent the interaction coefficient in predator presence relative to predator absence as

$$i_{RC} = (1 - \Delta_{RC})i'_{RC}. \qquad (2)$$

The prime designates the parameter value in absence of the predator. Δ_{RC} is the fractional amount that presence of the predator affects i_{RC}. For example, a Δ_{RC} of 0.6 indicates that predator presence reduces the consumer–resource interaction coefficient by 60%. Here we evaluate the predator effect at a particular predator density, though the method can be extended to incorporate the functional dependence of Δ_{RC} on predator density, $\Delta_{RC}(P)$.

We can estimate Δ_{RC} empirically by measuring the effect of the consumer on the resource in the presence and absence of the predator. Let ρ be the reduction in resource level due to the consumer (which is the initial minus the final level if resources do not grow). For small time intervals, t, ρ is approximately equal to the product of t and the removal rate by the consumer in Eq. 1:

$$\rho \approx i_{RC}RCt. \qquad (3)$$

Here we abstract the interaction coefficient, which often aggregates interactions over the entire life history of a species, to describe short-term effects that result from interactions occurring during specific life history stages. The ratio of the resource reduction in predator presence and absence is then

$$\frac{\rho}{\rho'} \approx \frac{i_{RC}RC}{i'_{RC}RC}. \qquad (4)$$

The resource and consumer density are assumed to be equivalent when the predator is absent and present, i.e., we are analyzing the effect of changes in consumer phenotype in otherwise equivalent systems. Employing Eqs. 2 and 4, we arrive at an equation that can be used to estimate Δ_{RC}:

$$1 - \Delta_{RC} \approx \frac{\rho}{\rho'}. \qquad (5)$$

The effect of predator presence on the mean individual consumer growth rate can be used to estimate the effect of the predator on the interaction coefficient i_{CR}. We represent the predator effect on i_{CR} in a similar manner as on i_{RC}:

$$i_{CR} = (1 - \Delta_{CR}). \qquad (6)$$

Δ_{CR} defines the fractional amount that predator presence reduces i_{CR}. For small time periods, t, the mean growth of an individual consumer, g, will be equal to the product of t and the gain due to resource consumption, and therefore, we obtain the following:

$$g \approx i_{CR}RCt. \tag{7}$$

Using Eqs. 6 and 7, and performing a similar operation as in the derivation of Eq. 5, we arrive at

$$1 - \Delta_{CR} \approx \frac{g}{g'}. \tag{8}$$

Predator presence can affect i_{CR} through effects on the traits that affect consumer foraging rate (as in the previous case for i_{RC}), and also through effects on the efficiency of converting resources into consumer growth (Loose and Dawidowicz 1994, McPeek et al. 2001).

We made several assumptions in deriving Eqs. 5 and 8 that must be considered if these equations are applied to experimental data. First, we assumed that resource level was equivalent in predator presence and absence. However, if resource reduction is lower in presence of the predator (due to reduced consumer foraging rates) this will result in underestimates of Δ_{RC} and Δ_{CR} using Eqs. 5 and 8. Second, effects of the predator on consumer density, and therefore on ρ and g and the estimates of Δ_{RC} and $\Delta_{CR,}$ were also assumed to be negligible. This assumption clearly will be satisfied in many experiments using ''nonlethal'' predators to examine trait-mediated effects of predators, e.g., by providing chemical cues of predators (Huang and Sih 1991, Turner 1997) or incapacitating predators (Wissinger and McGrady 1993, Beckerman et al. 1997). Finally, we assumed that differences in consumer foraging rates due to differences in consumer size in predator presence and absence are small. If consumers grow to larger sizes in absence of the predator, Eq. 8 will overestimate the predator effect.

ESTIMATES OF PREDATOR EFFECTS ON CONSUMER– RESOURCE INTERACTION COEFFICIENTS

We identified studies in the literature that isolated the nonlethal effect of predators on consumer growth or resource density and that satisfied the requirements in the previous section. We then estimated Δ (e.g., Δ_{RC} or Δ_{CR}) by applying Eqs. 5 or 8. In some cases we suspected that changes in resource levels were large enough to reduce estimates of Δ, but we include them because they provide a conservative estimate. In order to avoid overestimating the magnitude of the predator effect when individual consumer growth was large, we assumed consumer growth rate was exponential and proportional to size, and computed Δ_{CR} for small changes in growth (i.e., using growth rate rather than growth in Eq. 8). This procedure provides a conservative estimate of the predator effect. We also present the estimates of Δ_{CR} without this correction to provide an upper boundary on the estimate of Δ_{CR}. We highlight the cases in Tables 1 and 2 where we suspect that these two factors may influence the estimates.

We found 17 studies that permitted estimates of Δ. Table 1 presents estimates of Δ_{RC} derived from predator effects on resource level using Eq. 5, and Table 2 presents estimates of Δ_{CR} derived from predator effects on consumer growth using Eq. 8. These estimates of Δ ranged from 0.95 (i.e., a 95% reduction in interaction coefficient magnitude) to negligible, with the majority of estimates falling between 0.2 and 0.8 (median value of 0.45, Tables 1 and 2). Six of the studies, representing four distinct species interactions, were performed in the field with representative predator density. Values of Δ from field studies were similar to the laboratory and mesocosm studies, suggesting that the tabulated values are indicative of those in natural systems. In one study (Beckerman et al. 1997), Δ_{RC} was negative, indicating that presence of the predator increased the magnitude of the consumer–resource interaction, which Beckerman et al. attribute to an induced habitat shift in the consumer. Unfortunately, there are not yet enough studies to make any rigorous comparisons of the magnitude of Δ between habitats or species. However, the values of Δ indicate that the predator effect can be quite large in diverse taxa, including those found in freshwater, marine, and terrestrial systems.

MODEL ANALYSIS

In this section, we use two models to examine whether the estimated magnitude of Δ is large enough to strongly influence the net effect of the predator in a three-species food chain. In the first model, we examine the predator effect on equilibrium densities of the consumer and its resource; in the second, we examine the short-term predator effects on consumer growth rate and resource level.

Consider the three species food chain in which predator presence causes a reduction in the consumer–resource interaction coefficients. We assume that resource growth rate in absence of the consumer follows a convex curve that can be approximated by the logistic growth equation. In the simplest form, the species population growth rates in a system with constant predator density then are

$$\frac{dR}{dt} = rR\left(1 - \frac{R}{K}\right) - (1 - \Delta)i'_{RC}RC$$

$$\frac{dC}{dt} = (1 - \Delta)i'_{CR}RC - i_{CP}CP - d_cC$$

$$\frac{dP}{dt} = 0 \qquad (P = P_0) \tag{9}$$

where i'_{RC} and i'_{CR} are now constants. The intrinsic growth rate of resources is represented with r, and K is the carrying capacity. P_0 is the (constant) density of the predator, and other symbols are as in Eqs. 1 and 2. We assume that the predator effect on i'_{CR} and i'_{RC} are equivalent (as in, e.g., Abrams 1987). Note that the magnitude of i_{CP} will likely be affected by phenotypic responses of the consumer to predator presence, and therefore is also a function of predator density. It would

be necessary to include this functional dependence in a system in which predator densities change (Abrams 1987). Here, however, we simply examine the predator effect on R and C as a function of i_{CP} at a constant predator density.

A simple manipulation of the consumer growth rate in Eq. 9 indicates that the values of Δ derived from empirical studies are of sufficient magnitude to influence the net effect of the predator on consumer density. If we divide by the population growth rate of the consumer in the absence of the predator and any background mortality, $i'_{CR}RC$, then,

$$\frac{dC/dt}{i'_{CR}CR} = (1 - \Delta) - \frac{i_{CP}CP}{i'_{CR}CR} - \frac{d_C C}{i'_{CR}CR}. \quad (10)$$

Consider a nonlethal predator effect leading to $\Delta = 0.5$, which is near the modal value we estimated (Tables 1 and 2). Then consumer population growth will be negative if the loss due to predation and background mortality exceed 0.5 (i.e., the third and fourth terms in Eq. 10). Therefore, assuming that the consumer population growth rate is positive or near zero, the negative effect of the predator-induced reduction in $i'_{CR}RC$ will be equal to or greater than the negative effect due to direct predation on consumer growth rate. For values of Δ from the upper range of those derived (i.e., $\Delta > 0.5$), the importance of the nonlethal effect relative to direct predation (i.e., density effects) will be even larger. For values from the lower range, the contribution of the nonlethal effect will be smaller but still considerable. Thus, based on our estimates of Δ, the nonlethal effect of the predator on consumer population growth rate is predicted to be on the same order of magnitude as the lethal effect. A similar argument can be made to demonstrate that the nonlethal (trait-mediated) indirect effect on the resource is of the same order of magnitude as the density-mediated indirect effects due to predation.

These predictions are supported by analysis of resource and consumer densities at equilibrium, which are

$$R = \frac{i_{CP}P_0 + d_c}{(1 - \Delta)i'_{RC}}$$

$$C = \frac{(1 - \Delta)i'_{CR}r - \frac{r}{K}(i_{CP}P_0 + d_c)}{(1 - \Delta)^2 i'_{RC}i'_{CR}}. \quad (11)$$

In Fig. 1 we plot resource and consumer density at equilibrium as a function of the lethal (density) and nonlethal effect of the predator on the consumer–resource interaction coefficients. The isopleths indicate the combination of lethal and nonlethel effects which lead to the specified resource or consumer densities. This representation, which we denote the ''predator-effect phase space'' (Peacor and Werner 2001), is designed to clarify and make explicit the two components of the predator's effect on system responses.
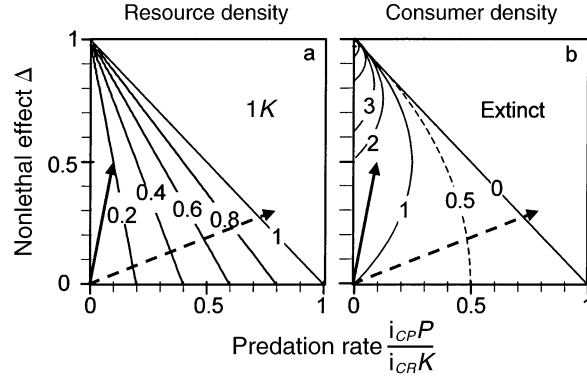

FIG. 1. Results of the analytical model (Eq. 9) presented in the predator-effect phase space; i.e., as a function of predation rate (x-axis) and reduction of the consumer–resource interaction coefficient (Δ, y-axis). Isopleths indicate the (a) resource and (b) consumer equilibrium densities. To make this representation general, the predation rate is expressed in the unitless metric of $i_{CP}P_0$ normalized to the maximum per capita consumer growth rate, $i_{CR}K$. Also for generality, the resource density is normalized to the carrying capacity K, and the consumer density is normalized to the density in predator absence (i.e., the ordinate value). The dashed and solid arrows exemplify the effect of a predator with a high predation rate and low Δ, and the effect of a predator with low predation rate and intermediate Δ, respectively (see *Model analysis*). The background mortality of the consumer, d_C, is zero.

Results indicate that at both low and high predation rates, nonlethal effects of the predator in the range of those estimated from empirical studies (Tables 1 and 2) have a large impact on consumer and resource density at equilibrium. Consider, for example, the effect of a predator which removes consumers at a high rate, i.e., $i_{CP}P/i_{CR}K = 0.8$, and has a relatively small nonlethal effect with $\Delta = 0.3$ (illustrated by dashed arrows in Fig. 1). In the absence of any nonlethal effect, the predator will decrease consumer density from 1 to 0.2, and increase resource density from 0 to $0.8K$ (this can be seen in Fig. 1 by evaluating the consumer and resource density on the x-axes where $\Delta = 0$). However, the addition of the nonlethal effect with $\Delta = 0.3$ dramatically alters the predator effect: the predator will drive an extant consumer population extinct, and resources will increase to K. Next consider a predator with lower density effects, $i_{CP}P/i_{CR}K = 0.1$, but an intermediate nonlethal effect, $\Delta = 0.5$. The lethal effect alone will reduce consumer density to 0.8 and increase resource density to $0.1K$. However, the addition of a nonlethal effect of $\Delta = 0.5$ leads to a doubling of the resource level, and consumer density increases from 0.8 to nearly 2. In fact, the nonlethal effect *reverses* the net predator effect on consumer density from negative to strongly positive.

The mechanism responsible for the net positive effect on consumer density is straightforward. At high consumer foraging rates and consequently low resource levels, a predator-induced reduction in foraging rate can cause a proportionately larger increase in resource
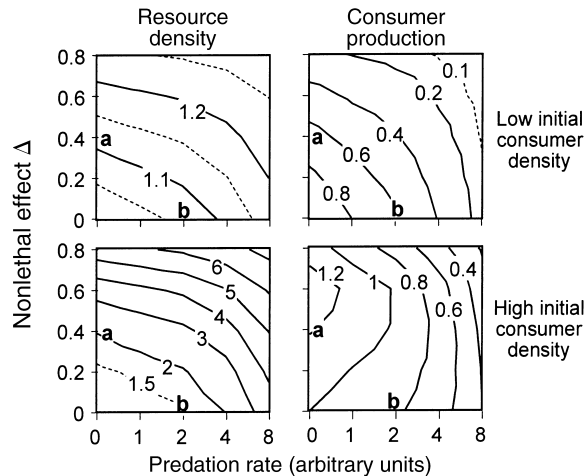
FIG. 2. Results of the simulation model presented in the predator-effect phase space. The isopleths indicate the combination of predation rates (x-axis) and induced reduction in the consumer–resource interaction coefficients (Δ; y-axis) that lead to the indicated resource density (left panels) and consumer production (total biomass gain of all surviving individuals; right panels). The values are presented relative to their value at the ordinate where there is no predator effect. Results are shown for low (upper figures) and high (lower figures) initial consumer densities. The geometrically increasing predation rates of 1, 2, 4, and 8 led to a total reduction in consumer density of 22%, 40%, 64%, and 88%, respectively. The letter **a** indicates the position in predator-effect phase space where there is a 40% reduction in the consumer–resource interaction coefficient but no density effect, and the letter **b** represents a 40% reduction in consumer density, but no nonlethal effect.

renewal rates due to the nonlinear relationship between resource level and resource growth rate (Abrams 1987, Abrams and Rowe 1996, Peacor 2002). The predator's presence effectively acts to oppose the consumer population's propensity to overexploit the resources. Thus, though every individual forages at a reduced rate, each individual acquires more resources due to the increased resource levels.

We next use a simulation model to examine the non-lethal predator effect on the average individual consumer growth rate and resource levels. This model, which does not assume equilibrium, more closely parallels most empirical work performed within the generation time of at least some of the interacting species. Further, species densities in natural and experimental systems often deviate strongly from the equilibrium condition used in the previous analysis. In the simulation model, resource level, mean consumer size, and consumer density, were updated at discrete time steps. Mean consumer growth was proportional to resource consumption, which was equal to the product of the consumer–resource interaction coefficient, i_{RC}, and resource level. Growth was thus size independent, but including size-dependent growth did not affect the qualitative nature of the results. As in the previous model, the logistic equation was used to describe re-

source growth. A fraction of the resources (one-tenth the carrying capacity) was not accessible for consumption, i.e., served as a refuge. Predation rate was constant (as in the previous model) and independent of consumer size, and therefore a constant fraction of consumer density was removed at each time step. Here we present results performed at two (low and high) initial consumer densities. The response variables measured were consumer production (product of mean individual growth and final density) and resource density. Simulations were performed over a large range of nonlethal effects (Δ) and predation rates, i.e., over a broad range of the predator-effect phase space.

The simulation model results indicate that the nonlethal effect of the predator can strongly influence the net effect of the predator on short-term consumer production over a wide range of parameter values (Fig. 2). At low consumer densities, a predator-induced reduction in the consumer–resource interaction coefficient had a negative effect on consumer production approximately equal to an equivalent reduction in consumer density. For example, a reduction in i_{RC} of $\Delta = 0.4$ and a predation rate that reduced consumer density by 40% both reduced consumer production by ~40% (compare points a and b on the upper right panel of Fig. 2). In contrast, at high initial consumer densities, a reduction in the consumer–resource interaction coefficient opposed the negative effect of predation on consumer production, especially at lower predation rates. As in the equilibrium model, there were combinations of lethal and nonlethal magnitudes that led to a net positive effect on the consumer. This positive effect was larger and spanned a larger region of the predator-effect phase space when initial consumer density was even higher than that illustrated.

Finally, consider the positive indirect effect of the predator on resource density (Fig. 2). The nonlethal effect of the predator had a stronger impact on resource density than a proportionately equivalent reduction in consumer density. For example, a 40% reduction in the consumer–resource interaction coefficient had a stronger positive effect on resource level than a 40% reduction in consumer density regardless of whether initial consumer density was low or high (compare points a and b on the left panels in Fig. 2). The reasons behind this result are straightforward. The total impact of the consumer on the resource is a function of the density of the consumer and the attack rate of each individual. Predator presence causes reductions in both, which then are transmitted to the resource. Over a finite period of time, the foraging reduction is immediate, affects the entire population, and occurs over the entire interval. Thus the cumulative indirect effect of the predator-induced foraging reduction over the cohort lifetime can be very significant. The density reduction, on the other hand, occurs gradually over time and is transmitted only in proportion to the individuals removed and not the entire population. Thus, we can expect nonlethal

TABLE 1. Estimates of Δ_{RC} derived from consumer effect on resources in the presence and absence of predation risk (Eq. 5).

Predator cue	Consumer (prey)	Resource	Δ_{RC}	Error (1 SE)	Venue	Experiment duration	Source
Fish	isopod	leaves	0.40	0.11	lab	7 d	Short and Holomuzki (1992)
Fish	salamander larvae	isopod	0.59†‡	0.05	lab	1 h	Huang and Sih (1991)
Fish	stonefly larvae	mayfly larvae	0.72‡	0.06	lab	24 h	Soluk and Collins (1988)
Spider	grasshopper	grass	0.73†	0.22	field	2 mo	Beckerman et al. (1997)
		herb§	−0.84†	0.55			
Spider	grasshopper				field	2 mo	Schmitz (1998)
	Chorthippus curtipennis	grass	NS				
		herb	NS				
	Melanoplus feurrubrum	grass	0.61‖	0.39			
		herb§	NS				
Stonefly larvae¶	mayfly larvae	periphyton			lab	24 h	Peckarsky et al. (1993)
Kogotus 1989			0.26	0.08			
modestus 1990			0.54	0.08			
Megarcys 1989			0.33	0.07			
Signata 1990			0.49	0.08			
Fish karimone	damselfly:	*Daphnia pulex*			lab	4 d	McPeek et al. (2001)
	Ischnura verticalis		0.54	0.20			
	Enallagma laterale		0.48	0.14			
	E. divagans		0.74	0.15			

Notes: Assumptions that may have been violated are indicated (see *Methods to estimate predator effects on consumer–resource interaction coefficients*). The standard error of Δ_{RC} was calculated by error propagation. Unless indicated with NS, Δ_{RC} was derived from data in which the predator effect on consumer phenotype significantly affected resource level.

† Resource differences in predator presence and absence may cause a conservative estimate of Δ_{RC} (regarded as potentially important if resources were reduced by >20% in the herbivore–no predator treatment).

‡ The magnitude of Δ_{RC} may be affected by a phenotypic change of the resource in addition to that of the consumer.

§ Heterogeneous resource base of grass and herbs. Effects on grass and herbs were measured independently.

‖ The significant effect observed for *M. femurrubrum* was not observed in a separate treatment where enclosures only contained grass.

¶ The experiment was performed for two species in two different years.

effects (i.e., trait-mediated effects) of the predator to contribute strongly to its net indirect effects, even when predator effects on consumer density are quite large.

DISCUSSION

This study indicates that phenotypic responses of consumers to presence of predators can strongly affect consumer–resource interaction coefficients across diverse taxa and systems (Tables 1 and 2). Estimates of Δ fall primarily in the range 0.2–0.8, indicating a 20–80% reduction in consumer–resource interaction coefficients in predator presence. The large magnitude of the nonlethal predator effects therefore provides direct quantitative evidence that interaction strengths may vary strongly over space and time as species' densities or community composition vary.

Model results show that reductions of the magnitude estimated from experiments will contribute strongly to the net direct and indirect effects of a predator in a food chain. In fact, values from the middle to higher end of this range in a simple model had larger effects on consumer and resource growth rate than density effects. Further, both an analytical model evaluating

species' equilibria, and a simulation model evaluating short-term dynamics, showed that the estimated predator-induced reduction in interaction coefficients can strongly affect consumer production, consumer density and resource density. In the simulation model, predator-induced reductions in consumer–resource interaction coefficients had larger indirect effects on resource level than proportionately equivalent reductions in consumer density due to predation, and were not overwhelmed by density effects even at high predation rates. In addition, these trait-mediated effects can either reinforce or counter the lethal effects of the predator depending on circumstances.

The magnitude of the predator effect on the consumer–resource interaction strength estimated here is likely representative of many other species interactions. For example, there are numerous studies reporting substantial predator effects on species traits associated with foraging. Lima (1998) reviews over 100 recent studies demonstrating behavioral responses (decrease in activity, increased refuge use, and habitat shifts) of a wide range of taxa on exposure to predators (see also reviews by Lima and Dill 1990, Kats and Dill 1998,

TABLE 2. Estimates of Δ_{CR} derived from consumer growth in the presence and absence of predation risk.

Predator cue	Consumer (prey)	Resource	Δ_{CR} if exponential growth	1 SE
Crayfish	snail	periphyton	0.29†‡	0.004
Crab	snail	green alga	0.82§	0.03
Crushed snail	snail	periphyton		
¼/d			0.18† NS	0.38
1/d			0.21† NS	0.59
4/d			0.34†	0.59
Whelk:	clam	suspension		
Caged			0.53	0.06
Lethal			0.65	0.08
Fish	*Chironomus*	artificial food‖		
	midge	low	0.40‡	0.26
	larvae	medium	0.32‡	0.13
		high	0.28‡	0.10
Fish	Damselfly:	*Daphnia pulex*		
	Ischnura verticalis		0.44	0.11
	Enallagma laterale		0.66	0.15
	E. divagans		0.95	0.12
Salamander larvae	grey tree frog larvae	plankton and detritus	0.16†‡	0.13
Natural pond background¶	green frog larvae	periphyton and detritus	0.32†‡	0.03
Dragonfly larvae	wood frog larvae	rabbit chow, periphyton, and detritus	0.14‡	0.04
Dragonfly larvae	green frog larvae	periphyton and detritus	0.19‡	0.02
Fish karimone concentration	*Daphnia magna*	green algae *Scenedesmus acutus*		
0.0002			−0.03 NS	0.03
0.001			0.03 NS	0.05
0.002			−0.02 NS	0.03
0.01			0.31	0.04
0.02			0.43	0.04
0.1			0.58	0.03
0.2			0.62	0.02

Notes: A conservative estimate is provided by assuming exponential growth proportional to size (see *Methods to estimate predator effects on consumer–resource interaction coefficients*). The SE of Δ_{CR} was calculated by error propagation. Δ_{CR} was also calculated with the assumption that growth was independent of size (Eq. 8). Assumptions that may have been violated are indicated (see text). Unless indicated with NS, Δ_{CR} was derived from data in which the predator had a significant effect on consumer growth.

† Resource differences in predator presence and absence may cause a conservative estimate of Δ_{RC} (regarded potentially important if resources were reduced by >20% in the herbivore–no predator treatment).

‡ Consumer size-dependent growth can affect estimates (see text).

§ No predator effect was observed for a nonfeeding crab.

‖ Predator effect was examined at three resource levels.

¶ The effect of natural levels of predator cue in pond water was determined with in situ experiments performed open to pond water. Aged pond water, in which predator cues have degraded, was used as a control.

Tollrian and Harvell 1999, Werner and Peacor 2003). Although it is not possible to calculate effects on species interaction strengths from most of these studies, there is no reason to believe that these effects are less than those estimated from the studies examined here. Further, while we have focused on a food chain in our analyses, in principal, our results should be general to other food web configurations in which one species affects the interaction between two others (reviewed in Werner and Peacor 2003). For example, if resource density affects consumer phenotype (Abrams 1991, Werner and Anholt 1993, Anholt and Werner 1995, Grand and Dill 1999), then the predator–consumer in-

teraction coefficients (i_{CP} and i_{PC} in Eq. 1) would deviate from conventional theory and be a function of resource density.

Theoretical studies predict that the dynamic nature of interaction coefficients introduced by phenotypic plasticity can either stabilize or destabilize population dynamics of species in simple three- and four-species model systems (Bolker et al. 2003). However, these analyses do not present the variation in interaction coefficient magnitude responsible for the results. Thus it is difficult to infer how our estimated values of Δ will influence the general stability and diversity properties of multi-species food webs. In addition, the functional

TABLE 2. Extended.

Fraction size increase	Δ_{CR} if linear growth	Venue	Time (d)	Source
4.78	0.33	lab	43	Lewis (2001)
1.55	0.85	lab	34	Yamada et al. (1998)
		mesocosm	14	Turner (1997)
1.21	0.19			
	0.23			
	0.36			
		field		
<1.1	0.54		36	Nakoaka (2000)
	0.67			
		lab	25	Ball and Baker (1996)
12.3	0.57			
8.6	0.55			
4.3	0.55			
		lab	4	McPeek et al. (2001)
1.11	0.45			
1.04	0.66			
1.10	0.95			
16.0	0.38	field	14	Skelly (1992)
4.3	0.49	field	5	S. D. Peacor, M. Fraker, and E. E. Werner, *unpublished data*
2.56	0.21	mesocosm	5	S. D. Peacor, *unpublished data*
18.9	0.44	mesocosm	12	S. D. Peacor and E. E. Werner, *unpublished data*
		lab	4	Loose and Dawidowicz (1994)
8.9	−0.07			
7.8	0.08			
8.7	−0.04			
4.3	0.56			
3.3	0.69			
2.4	0.81			
2.3	0.83			

relationship between predator density and interaction coefficient magnitude will strongly affect model predictions, and therefore there is a need for empirical measurements of this functional relationship (Abrams 2001, Bolker et al. 2003). To our knowledge, only the study of Loose and Dawidowicz (1994), who measured the effect of fish karimone on *Daphnia* growth rate, provides this functional relationship, and indeed it is strongly nonlinear (Table 2). Presenting theoretical and empirical results in terms of the magnitude of the change of the interaction coefficients would help to bridge the gap between theoretical and empirical studies of the role of phenotypic plasticity in ecological communities.

Only the data of McPeek et al. (2001) allowed an estimate of both Δ_{CR} and Δ_{RC}. In two of the three damselfly species examined, Δ_{CR} was considerably larger than Δ_{RC} (Tables 1 and 2). This difference could be a result of physiological responses to predator presence that affect metabolic rates or factors affecting conversion of resources into consumer biomass, i.e., factors that would affect Δ_{CR} but not Δ_{RC} (McPeek et al. 2001). The difference may also arise if a large amount of resources are used for maintenance rather than growth (in both predator presence and absence). Any predator-induced reduction in resource acquisition then would have a proportionally larger negative effect on consumer growth than on the quantity of resources removed, and therefore Δ_{CR} would be greater than Δ_{RC}. While such differences will unlikely affect the qualitative nature of the model results presented here (where we assumed Δ_{CR} and Δ_{RC} were equivalent), these results highlight the fact that predator-induced changes in consumer phenotype can have different effects on i_{CR} and i_{RC}.

The method proposed here enables an estimate of the predator effect on interaction coefficients that would be difficult to derive directly from consumer trait changes. The relationship between traits and interaction strength is difficult to quantify, there are likely a suite of consumer traits that combine in complex ways to determine interaction strength, and these traits may vary strongly as a function of environmental factors (e.g., time of day). The method developed here, however, resolves this problem by quantifying a response (i.e., change in consumer effect on resource density or

on consumer growth) that effectively aggregates the effects of all of consumer trait changes integrated over time.

The accuracy of the protocol presented here to estimate Δ depends critically on the duration of the experiment. Parameters describing rates must be derived from experiments that are brief relative to feedbacks in the system (Billick and Case 1994, Osenberg et al. 1997). Specifically in the case addressed here, as duration of the experiment increases, factors such as diminishing returns and indirect effects through other species in the system have increasingly pronounced effects on the consumer and resource. For example, the effect on growth rate of equivalent predator-induced reductions in consumer foraging rate can vary strongly, and even differ in sign, depending on consumer density, competitor density, resource dynamics, and the duration of the interactions (Peacor and Werner 2004). These effects will obscure the impact of the predator on the consumer–resource interaction coefficient. Therefore, experiments must be short enough to minimize such confounding factors. One also must be aware, however, that phenotypic responses to predators occurring over short exposure periods may deviate from those occurring over longer exposure periods for two reasons. First, the need to feed may cause animals to decrease phenotypic responses to predator presence as they become more frequent or lengthy (Lima and Bednekoff 1999) and second, the expression of some phenotypic changes may take longer than others (e.g., morphological responses may be slower than behavioral responses). This problem can be addressed empirically by using short-term experiments with organisms that have been exposed to predators prior to introduction into a system.

A goal of community theory is to understand how species interactions influence properties such as diversity and stability. Theory plays a vital role in this because it is not possible to empirically address long-term dynamics in many systems given the relatively long generation times of organisms in these systems. Clearly such theory must capture the essential characteristics of species interactions that ultimately dictate the manner in which species affect one another's abundance and dynamics. Our preliminary survey of the literature indicates that higher-order interactions due to phenotypic plasticity may often be an important influence on interaction strengths and strongly affect species abundances and dynamics. Our results therefore strengthen previous claims that trait-mediated effects strongly influence species interactions, and extend the calls to quantify and determine the distribution of interaction strengths in food webs (Paine 1992, Laska and Wootton 1998, Berlow et al. 1999) to also quantify how these interaction strengths vary as a function of species densities in the food web.

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