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PREY STATE AND EXPERIMENTAL DESIGN AFFECT RELATIVE SIZE OF TRAIT- AND DENSITY-MEDIATED INDIRECT EFFECTS

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Abstract. Indirect effects, in which one species affects another through an intermediate species, can occur by changes in either the density or the traits of the intermediate species. Ecologists have focused primarily on density-mediated indirect effects, but have become interested in quantifying the relative sizes of trait- and density-mediated indirect effects. We examined how state-dependent prey behavior and experimental protocols affect the sizes of measured trait- and density-mediated indirect effects in a three-species chain (predator, prey, and resource). We found that the size of trait-mediated indirect effects relative to the size of density-mediated indirect effects increases as the level of resources increases. We also found that the relative contributions of trait- and density-mediated indirect effects depend on the timing of manipulations in relation to the state of individuals and their vulnerability to predators. In addition, we found that trait-mediated indirect effects that have been measured during a portion of a season may diminish or disappear when measured across a whole season because of behavioral compensation. These results show that the relative contributions of trait- and density-mediated indirect effects in a system will be variable, and experiments need to be designed to account for dynamic systems.

Key words: *density-mediated indirect effects; predator–prey interactions; state-dependent behavior; trait-mediated indirect effects.*

Introduction

Indirect effects are transmitted from one species to another through one or more intervening species. For example, in a three-species chain, when predators reduce prey density (a direct effect), they indirectly affect prey resource supply. Early theory in community ecology assumed that per capita effects of one species on another were not determined by the traits or behaviors of the participants, and therefore all indirect interactions were density mediated (henceforth, density-mediated indirect interactions, DMII; sensu Abrams 1995). More recently, both theorists and empiricists have recognized that per capita effects are often altered through plastic or evolutionary adjustment of species' traits. In these cases, the effect of one species on another may be mediated by alteration of a behavioral, morphological, or physiological trait of an intervening species (trait-mediated indirect interaction, TMII; sensu Abrams 1995). For example, addition of predators may result in reduced prey foraging activity (the trait), which causes prey to consume fewer resources, leading to an increase in the resources. The list of individual traits that respond to the density or the presence–absence of other species is long (Schlichting and Pigliucci 1998, Tollrian and Harvell 1998). Therefore, the potential importance of TMIIs to the structure and dynamics of communities is large.

Empirical studies have demonstrated that TMIIs occur in natural and experimental systems (reviewed in Werner and Peacor 2003). Regarding the ''importance'' of TMIIs, a key question is whether they make up a substantial proportion, relative to DMIIs, of the indirect effects known to occur in nature (Kerfoot and Sih 1987, Schoener 1993, Wootton 1994). A large theoretical literature has demonstrated that TMII can make up a significant proportion of given indirect effects, and may even change the sign of those effects (e.g., Abrams 1991*a*, 1992, 1995; reviewed in Bolker et al. 2003). There is a growing base of empirical support for these conclusions. First, in some systems in which indirect effects have been measured, DMIIs could be ruled out because of a lack of density changes in the focal species, either as a result of natural processes or because of experimental intervention (Turner and Mittlebach 1990, McIntosh and Townsend 1996, Schmitz 1998). Second, a subset of studies has experimentally manipulated systems in such a way as to allow quantitative estimates of TMIIs and DMIIs, and these studies have demonstrated that TMIIs can be greater than DMIIs (Soluk and Collins 1988, Huang and Sih 1990, 1991, Wissinger and McGrady 1993, Schmitz 1998, Diehl et al. 2000, Peacor and Werner 2001).

In this paper, we focus on the common experimental protocol used to partition measures of DMIIs and

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TMIIs, and examine how background conditions may affect these measurements. Most of the experiments quantifying DMIIs and TMIIs have used linear three-trophic-level chains (predators, prey, and resources), with prey foraging behavior being the trait that affects interaction strengths. The common protocol used to isolate TMIIs and DMIIs, and the one that we will use, is composed of three treatments (Huang and Sih 1991, Wissinger and McGrady 1993, Beckerman et al. 1997, Schmitz 1998, Peacor and Werner 2001). The first treatment (no manipulation) provides a baseline measure of the amount of resources eaten by prey. The manipulation either can be composed of only the resource and the prey, or can include the predator. In the second treatment (risk manipulation), prey are manipulated to perceive a higher risk of predation, perhaps by the addition of caged predators or chemical signals of the presence of predators, but the actual level of predation risk is unchanged. In the third treatment (predator manipulation), additional predators are added to the system, so that both the prey's perception of risk and the actual level of predation risk are increased. Then, TMII and DMII are measured as the proportional reduction in the amount of resources eaten by prey between no manipulation and a risk manipulation, and between a risk manipulation and a predator manipulation, respectively.

Using this protocol and metrics, we first examine how the level of resources affects measurements of DMIIs and TMIIs. The behavioral ecology literature shows that how prey forage and react to changes in predation risk should be affected by the availability of resources. State-dependent foraging behavior (reviewed in Mangel and Clark 1988, Houston et al. 1993, Houston and McNamara 1999, Clark and Mangel 2000) is potentially important to our understanding of TMIIs, because the state of prey, such as their hunger and size, will vary considerably within an experimental system and across time. For example, when resources are abundant, prey may be less hungry or larger than under harsher conditions. Most existing theory predicts that these changes in prey state will cause a decrease in risk taking by prey as the resource supply increases (McNamara and Houston 1987, Mangel and Clark 1988, Ludwig and Rowe 1990, Werner and Anholt 1993, Abrams et al. 1996, Abrams and Rowe 1996). Thus, higher resource levels lead to lower predation on prey, with small or no increases in prey foraging success (McNamara and Houston 1987, Ludwig and Rowe 1990, Werner and Anholt 1993). However, in some circumstances with a different a model formulation, higher resource levels may cause an increase in risk taking by prey (Abrams 1991*a, b*, Van Buskirk 2000). Despite the apparent connections, we know of no case in which the effects of resource-level and state-dependent foraging behavior on the relative importance of TMIIs have been quantified.

Next, we examine how the timing of manipulations in the life cycle of prey affect measurements of TMIIs and DMIIs. The life history stage of prey may change over a season, and their need for resources and their risk of predation may depend upon their life history stage. Thus, we expect that, within a seasonal environment, prey risk taking and therefore TMIIs and DMIIs will depend upon the time in the season that prey are challenged by increased perceived or actual predation risk (Rowe and Ludwig 1991, Werner and Anholt 1993, Abrams et al. 1996). Recent empirical studies support this view (Johansson and Rowe 1999, Johansson et al. 2001).

Last, we examine how the length of observations affects measurements of TMIIs and DMIIs. Experimental manipulations to measure TMIIs and DMIIs typically last less than a season. It is not clear whether conclusions drawn from these short-term manipulations will be reflected in long-term dynamics. Theory suggests that they will, but empirical support is still lacking (e.g., Abrams 1987, 1995, Mangel and Roitberg 1992, McPeek and Peckarsky 1998, Schmitz 2000). Because prey can quickly reverse their behavioral responses and increase their foraging effort when predation risk subsides, we expect that TMIIs measured during a portion of a season may not accurately represent TMIIs for the whole season. In comparison, unless competition between prey for resources is strong, there will be less compensation in the amount of resources eaten when predators remove prey from the system.

METHODS

The model and its assumptions were inspired by a spider and grasshopper old-field system (Schmitz 1998). The system examined in the model is a linear three-species chain (predator, prey, and resource). Like grasshoppers, prey in the model experience a seasonal environment in which they start the season at a small size, grow during the season, and then reproduce at the end of the season. We assumed that the season is 39 days long, with 10 foraging bouts per day, and there is a fixed time horizon, with prey reproducing on day 40. This seasonal model matches many of the species that have been the subjects of TMII and DMII measurements (i.e., univoltine arthropods that die at the first frost and aquatic species that die or migrate when ponds dry up or freeze). Prey alter their foraging behavior in response to their body mass, perceived predation risk, and resource levels that determine the probability of finding food. Predation and starvation can reduce prey density during a season. Predator and resource species have fixed behavior, and their population densities or biomasses do not vary during the season unless manipulated.

Dynamic state variable model

At the beginning of each day, prey set their level of foraging effort, and that level of effort is used in each of the day's 10 foraging bouts. Foraging effort, $E(t)$, ranges from 0 (hiding) to 1 (maximum foraging) with intermediate foraging efforts at intervals of 0.25, and affects the probability that prey will find food and the probability of predation. During a foraging period, if $E(t) = e$, the probability of finding food is

$$\Pr_{\mathrm{f}}(e) = \min\left(1, \frac{e^{z}r}{r_{\max}}\right) \tag{1}$$

where r is the level of resources in the environment, z determines the shape of how foraging effort affects the probability of finding food, and $r_{\max} = 10$ is the level of resource at which the probability of finding food saturates. For our primary results, we used $z = 1$, but in sensitivity analyses, we varied z (0.2, 0.75, 1.5, and 2). A prey's daily foraging success, $S(t)$, is binomially distributed, which we write as $\Pr\{S(t) = s|E(t) = e\} = \mathrm{Bin}(10, \Pr_{\mathrm{f}}(e), s)$. At the end of a day in which s resource units are consumed, prey mass is changed by $s - 2$, thus accounting for a daily metabolic cost. We choose this size of metabolic cost to create a situation in which individuals need to forage to avoid eventual starvation, but they can expect to increase their mass if they use a large foraging effort, except when resources are very scarce. Sensitivity analyses showed that the size of metabolic costs did not qualitatively affect our results. Prey mass ranges from 0, where starvation occurs, to 200.

The probability of being killed by a predator during a single day is

$$\Pr_{\mathrm{m}}(e, p, x) = \min\left[1, pe\left(m_0 + m_1x + \frac{m_2}{x}\right)\right] \tag{2}$$

where p is the number of predators, m_0 is the size-independent mortality rate, m_1 is the size-dependent mortality rate, and m_2 is the size-inverse mortality rate. As foraging effort increases, the probability of predation increases. For grasshoppers, the probability of predation by spiders decreases as they grow (Beckerman et al. 1997, Schmitz et al. 1997); thus, we used negative size-dependent predation ($m_0 = 0.0001$, $m_1 = 0$, and $m_2 = 0.3$) for our primary results. In our sensitivity analyses, we also used size-independent predation ($m_0 = 0.01$, $m_1 = 0$, and $m_2 = 0$) and positive size-dependent predation ($m_0 = 0$, $m_1 = 0.0002$, and $m_2 = 0$).

We found optimal prey foraging efforts using a dynamic state variable model (Clark and Mangel 2000). We assumed that, as for grasshoppers, all reproduction occurs at the end of the foraging season (day 40) and is a function of the prey's mass. Prey fitness at the end of the season is

$$F(x, r, p, T) = \left(\frac{x}{x_{\max}}\right)^{v} \tag{3}$$

with $x = X(T)$ being the prey's mass at the terminal day T, $x_{\max} = 200$ being the maximum possible prey mass, and v setting the shape of the fitness function. For our primary results, we assumed that prey fitness increases with a prey mass, but at a decelerating rate ($v = 0.2$). In our sensitivity analyses, we varied the shape of the fitness function ($v = 0.2$, 0.75, 1.0, 1.25, and 2.0). For time steps prior to the end of the season,

$$\begin{aligned} &F(x, r, p, t) \\ &\quad = \max_{e}\, [1 - \Pr_{\mathrm{m}}(e, p, x)] \sum_{s=0}^{10} \mathrm{Bin}[10, \Pr_{\mathrm{f}}(e), s] \\ &\qquad \times F(x + s - 2, r, p, t + 1) \end{aligned} \tag{4}$$

with $F(0, r, p, t + 1) = 0$ (prey starvation). We assume that prey know p, the signal of how many predators are present, and that they behave as if p will not vary for the rest of the season. We solved Eqs. 3 and 4 using backward iteration. The foraging effort producing the maximum expected fitness was recorded as the prey's behavior for that combination of mass, resources, predators, and time.

Forward iteration

The model provides prey behavioral rules in response to their mass, resources, predators, and time. We used forward iterations to predict the resulting prey behavior and its consequences for the three trophic levels.

We are ultimately interested in the relative magnitudes of the TMII and DMII of predators on resources. In the forward simulations, we used the same set of three manipulations used in common empirical experiments (i.e., no manipulation, a risk manipulation, and a predator manipulation). We isolated the TMII of predators on resources by comparing treatments with a risk manipulation to treatments with no manipulation. Matching previous analyses (e.g., Huang and Sih 1991, Wissinger and McGrady 1993), we measured TMII as the proportional reduction in resources eaten when the risk manipulation altered prey behavior:

$$\mathrm{TMII} = 1 - \frac{\text{resource eaten (risk manipulation)}}{\text{resource eaten (no manipulation)}}. \tag{5}$$

We isolated the DMII of predators on resources by comparing treatments with a predator manipulation to treatments with a risk manipulation. We measured DMII as the proportional reduction in resources eaten when the predator manipulation reduced prey density:

$$\mathrm{DMII} = 1 - \frac{\text{resource eaten (predator manipulation)}}{\text{resource eaten (risk manipulation)}}. \tag{6}$$

We measured prey behavior as the daily average foraging effort of all living prey. We measured predation as the percentage of prey eaten by predators over a season.

The initial condition for the forward iterations was 100 prey, starting with a mass ($x(1)$) of 4 and two

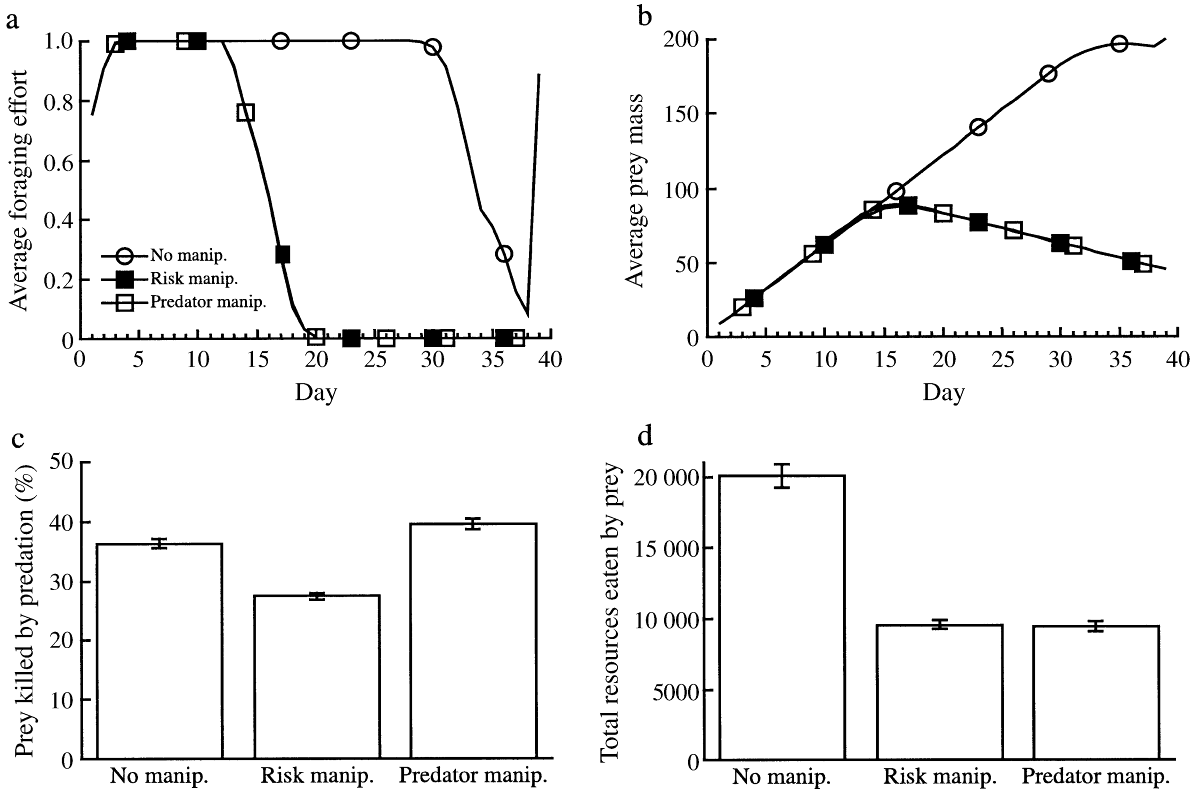

FIG. 1. (a) The average foraging effort of prey and (b) the average prey mass over the days of a season from 30 replicates, each starting with 100 prey. (c) The percentage of prey killed by predators (mean ± 1 SE) over a complete season for the three manipulations (ANOVA, $F_{2,87} = 66.7$, $P < 0.05$; Tukey test, all pairwise comparisons, $P < 0.05$). (d) The total resources eaten by prey (mean ± 1 SE) over a complete season for the three manipulations (ANOVA, $F_{2,87} = 638.4$, $P < 0.05$; Tukey test, no manipulation vs. risk and predator manipulations, $P < 0.05$, risk manipulation vs. predator manipulation, $P > 0.05$). Prey mass ranges from 0 (starvation) to 200 (maximum mass). Foraging effort ranges from 0 (hiding) to 1 (maximum foraging). Resource levels are set at a moderately high level of 8 on a scale of 0 to 10.

predators ($p = 2$). Because prey are not depleting or competing for resources, the initial number of prey was simply the sample size and had no effect on the model results. Initial prey mass only significantly affected prey behavior at the beginning of the season. We first investigated the general patterns of prey behavior, prey foraging success, and predation using a resource level (r) of 8. Then we studied the effects of resource levels on TMIIs and DMIIs by varying the level of resources (r) from 2.5 to 10. The perceived number of predators for the risk manipulation and the actual number of predators for the predator manipulation were increased to $p = 8$ on day 10 and remained at that level for the rest of the season. For the no manipulation treatment, the number of predators remained at two for the whole season. Varying the size of manipulations (i.e., the numbers of predators) did not alter our general findings. For each of the manipulations, we ran 30 replicates of the forward iteration.

The timing of manipulations and the length of observations are often chosen by researchers and constrained by the logistics and life histories of prey and predators. To investigate how these choices affect measured TMII and DMII, we conducted risk and predator manipulations that lasted 10 days and started on day 1, 11, 21, or 31. We measured prey behavior, predation, and their effects on resources eaten either during the 10-day manipulation or across the whole season.

RESULTS

Prey behavior and its effects

With the baseline level of predation risk (two predators present), prey initially used moderate foraging efforts, but quickly switched to using the maximum foraging effort (Fig. 1a). Negative size-dependent predation risk caused the initial restraint in prey foraging effort (i.e., high foraging effort was too risky for the small prey). Late in the season, prey used lower foraging efforts as they approached the maximum prey mass, and on the last day they used a higher effort in an attempt to achieve the maximum prey mass. When a signal of additional predators or actual predators were added on day 10, prey reduced their foraging efforts

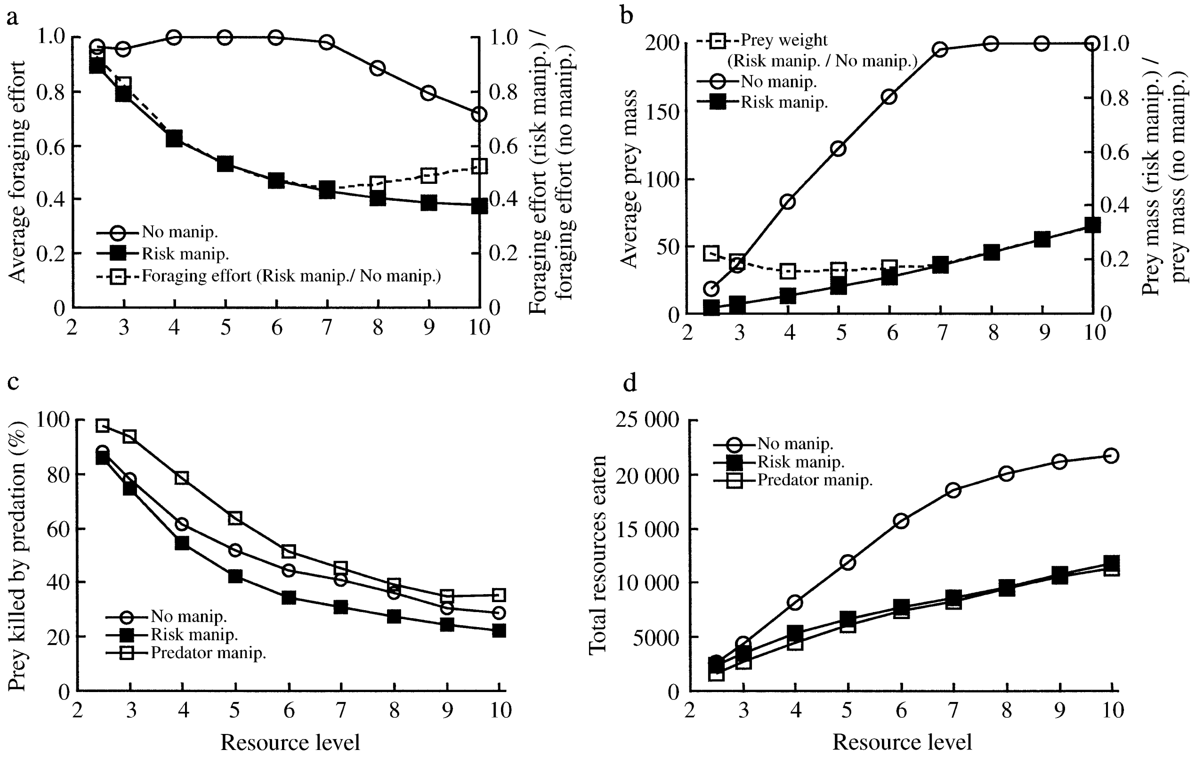

FIG. 2. (a) Prey foraging effort averaged over the season vs. resource levels for no manipulation and a risk manipulation with 30 replicates. The right-hand *y*-axis gives the proportion of the average prey foraging effort with a risk manipulation relative to with no manipulation. (b) Average prey mass at the end of the season vs. resource levels for no manipulation and a risk manipulation. The right-hand *y*-axis gives the proportion of the average final prey mass with a risk manipulation relative to with no manipulation. (c) The percentage of prey killed by predators and (d) the total resources eaten by prey over a complete season vs. resource level for the three manipulations. Because SE bars are not distinguishable from the means, they are not shown. Prey mass ranges from 0 (starvation) to 200 (maximum mass). Foraging effort ranges from 0 (hiding) to 1 (maximum foraging). Resource levels range from 2 (low) to 10 (high).

eventually to the point that they ceased foraging. The reduction in foraging effort did not occur until three days after the manipulation. To an observer, this three-day lag between the manipulation and prey's response might be interpreted as a delay in prey detecting the change in predation risk. However, no delay in detection occurred in this model. In the solution to this model, prey indirectly set an optimal final mass that balances the benefits of increased mass and the associated predation risk of achieving that mass. When predation risk changes, that optimal final mass changes, but prey may continue to forage to achieve their optimal final mass.

Changes in prey behavior in response to the risk and predator manipulations affected prey mass, rates of predation, and the amount of resources eaten. The risk and predator manipulations lowered average prey mass in comparison to no manipulation (Fig. 1b). The risk manipulation reduced the number of prey eaten by predators in comparison to no manipulation (Fig. 1c), because it caused prey to use less risky foraging behavior. The predator manipulation increased the number of prey eaten by predators in comparison to no manipulation. The total amount of resources eaten by prey is a function of the density and foraging effort of prey. The risk manipulation lowered the amount of resources eaten by prey compared to no manipulation (Fig. 1d). This difference was because the risk manipulation caused a reduction in prey foraging effort, and it occurs despite the fact that the risk manipulation lowered rates of predation. The risk manipulation caused a 52.2% reduction in resources eaten compared to no manipulation (a TMII of 0.522 as measured by Eq. 5). The predator manipulation caused a 1.2% reduction in resources eaten compared to the risk manipulation (a DMII of 0.012). Given our baseline parameters, the measured TMII was much larger than the measured DMII.

Resource effects

Using the same baseline parameters while varying resource levels, we explored how resource levels affected measured TMIIs and DMIIs. With abundant resources, prey reacted quickly to risk and predator manipulations. With a resource level (r) of 10, prey reduced their foraging effort from the maximum foraging

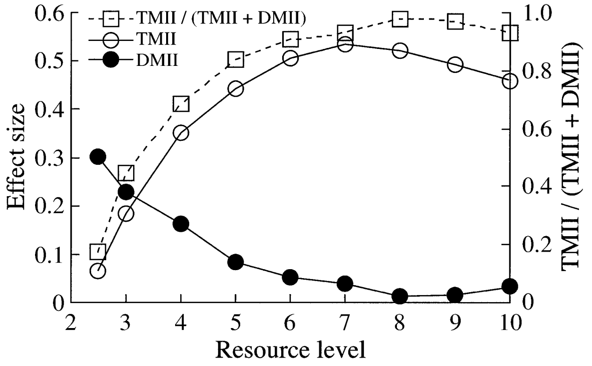

FIG. 3. The size of trait- and density-mediated indirect effects (TMII and DMII) of predators on resources vs. resource levels for the three manipulations with 30 replicates. The right-hand *y*-axis gives the proportion of the indirect effect caused by a trait-mediated effect.

effort to an average foraging effort below 0.95 on day 12 (two days after the manipulation). However, with $r = 2.5$, prey lowered their average foraging effort below 0.95 on day 26 (16 days after the manipulation). Thus, detecting the behavioral responses of prey to changing predation risk may require longer observations when resources are scarce. Even if the behavioral change is detected, the time difference between the manipulation and the response will make it hard to attribute the behavioral change to the changed level of predation risk.

As resource levels increased, seasonally averaged foraging effort declined (Fig. 2a) regardless of the manipulation. However, with more abundant resources, there was a greater proportional reduction in foraging effort, in comparison to behavior with no manipulation and with a risk manipulation. Average prey mass increased with increasing resource level for all of the manipulations (Fig. 2b). The absolute difference in final prey mass with no manipulation and with a risk manipulation increased steadily as the level of resources increased, until prey began to achieve the maximum prey mass. The percentage of prey eaten by predators decreased for each of the manipulations as the level of resources increased (Fig. 2c). This is caused by the lower prey foraging efforts and larger prey mass, which reduces the probability of predation, given negatively size-dependent predation risk.

As resource levels increased, the absolute difference in the total amount of resources eaten by prey with no manipulation and with a risk manipulation increased, while the absolute difference in resources eaten between the risk manipulation and predator manipulation decreased slightly (Fig. 2d). Thus, as resources increased, TMIIs increased and DMIIs decreased (Fig. 3). There was a slight decrease in the size of TMIIs at high resource levels, caused by the reduction in foraging effort associated with prey reaching their maximum mass. Thus, the sizes of TMII and DMII depend on resource levels, with TMII dominating when resources are moderate to abundant and DMII dominating when resources are scarce. This occurs because when resources are abundant, prey can quickly and reliably gather resources, and therefore can afford to respond to increased predation risk by lowering their foraging effort (Fig. 2a). In contrast, when resources are scarce, prey have to commit more foraging effort to gain and maintain mass. In this circumstance, even if prey perceive increased predation risk, they may not be able to afford lowering their foraging effort and are left exposed to higher predation risk (McNamara and Houston 1987). Thus, the level of resources chosen by the researcher in experiments will affect the measurements of TMII and DMII. We also predict that prey behavioral responses to predation risk will be more obvious and will more significantly shape community dynamics when resources are abundant, and that significant TMII will not occur in harsh environments.

Sensitivity analyses

To test the robustness of the result that TMIIs increase and DMIIs decrease with increasing resource levels, we varied the shapes of the fitness, predation risk, and foraging success functions (Appendix). First, we varied the shape of the fitness function (Eq. 3), and found the result to be sensitive to the shape of the fitness function. With a linear or a convex fitness function, DMIIs continue to decrease as resource levels increase, but TMIIs do not increase (Fig. 4a). As fitness functions becomes less concave, prey lose greater potential fitness when they reduce their foraging effort in response to increased predation risk, and thus the prey tend to respond less behaviorally and TMIIs become smaller.

Next, we varied the shape of the predation risk function (Eq. 2). We found that the result was weakest when predation risk was negatively size dependent (our baseline assumption). We found that with a linear fitness function ($v = 1$), which previously caused no response in TMIIs to changing r, TMII increased with r if the predation risk function was size independent or positively size dependent (Fig. 4b). When predation risk increased as prey got larger, large prey showed stronger behavioral responses to increased predators, and this caused larger TMIIs that responded to r.

Finally, we varied how the foraging effort of prey affects their foraging success. We varied the shape of the foraging success function (Eq. 1). With $z < 1$, increases in foraging effort when foraging efforts are low have a large effect on foraging success. With $z > 1$, increases in foraging effort when foraging efforts are high have a large effect on foraging success. The only observed effect of varying z was small TMIIs when z was small (Fig. 4c). With a small z, prey used low foraging efforts, because little further foraging success could be gained by increasing foraging effort. However, increases in predation risk did not solicit further reductions in foraging effort, because when z is low,

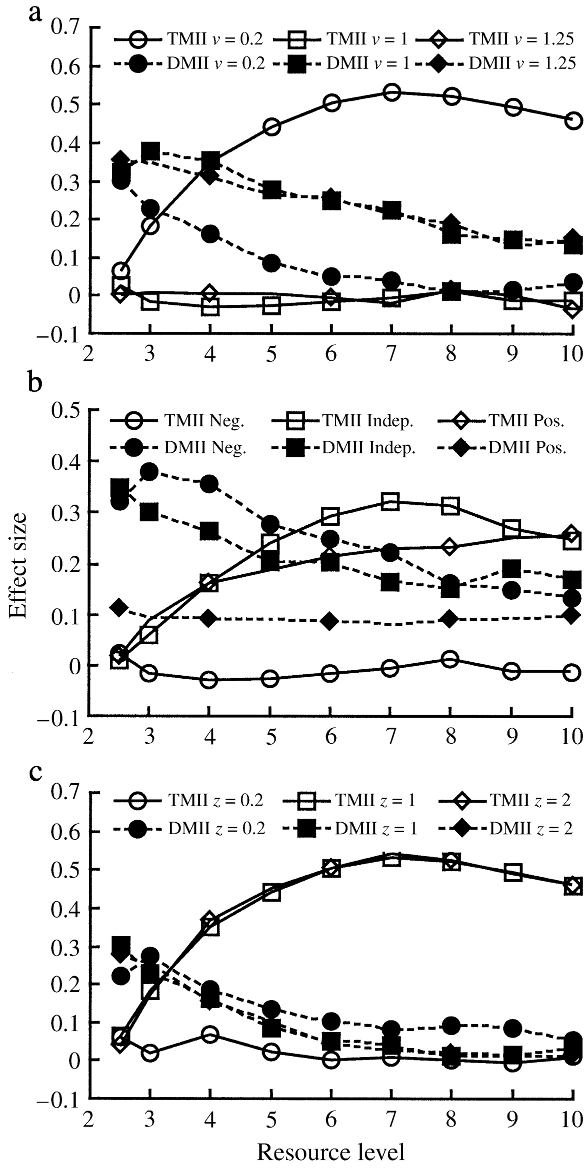

FIG. 4. The size of trait- and density-mediated indirect effects (TMII and DMII) of predators on resources vs. resource levels with (a) different prey fitness functions (concave, $v = 0.2$; linear, $v = 1$; and convex, $v = 1.25$); (b) different predation risk functions (negative size-dependent, $m_0 = 0.0001$, $m_1 = 0$, and $m_2 = 0.3$; size-independent, $m_0 = 0.01$, $m_1 = 0$, and $m_2 = 0$ with $v = 1$; and positive size-dependent, $m_0 = 0$, $m_1 = 0.0002$, and $m_2 = 0$) with $v = 1$; and (c) different foraging success functions (foraging success increases quickly with increasing foraging effort when efforts are low [$z = 0.2$], when efforts are high [$z = 2$], or when effects increase at the same rate for all foraging efforts [$z = 1$] with $v = 0.2$ and negative size-dependent predation. Each point is an average from 30 replicates.

further reductions in foraging effort cause a large loss in foraging success. Thus, prey did not behaviorally respond to increased predators and TMIIs were small.

Our sensitivity analyses have shown that, in many circumstances, TMIIs increase in size relative to DMIIs with increasing resource levels, and we never observed the opposite pattern. However, the pattern is sensitive and points out the need to know the functional forms of fitness, predation risk, and foraging success.

Timing of manipulations and the length of observation

Using the baseline parameters, we varied the timing of risk and predator manipulations and the length of observations to test the robustness of measured TMIIs and DMIIs. How prey behaviorally responded to a risk manipulation (the response to predator manipulations was identical) depended on the timing of the manipulation. When the manipulations were done early in the season, the behavioral reactions of the prey were small or delayed (Fig. 5a, b). In contrast, when the manipulations were done late in the season, the behavioral reactions were an immediate cessation of foraging (Fig. 5c, d).

However, when we measured average prey foraging effort across the complete season, rather than just during the manipulation, the risk manipulation had a small impact on average prey foraging effort. With no manipulation, average prey foraging effort across a complete season was 0.88. With a 10-day risk manipulation, average prey foraging effort was 0.88, 0.87, 0.75, and 0.78 for manipulations started on day 1, 11, 21, and 31, respectively. When risk manipulations were done early in the season (day 1 or 11), no significant effect on the average prey foraging effort occurred because prey compensated for reductions in foraging effort early in the season with increases in foraging effort late in the season. When risk manipulations were done late in the season, there was some reduction in average prey foraging effort, because prey drastically reduced their foraging effort during the manipulations and less time remained for behavioral compensation. Thus, if changes in predation risk are episodic, measuring behavioral responses during portions of the season may not accurately measure the impact of prey behavior on the community because of behavioral compensation.

The timing of manipulations and the length of observations affected the amount of resources eaten by prey and, thus, our measurements of TMIIs and DMIIs (Fig. 6). When observations were only conducted during the manipulations and the manipulations were started on day 1, we measured a large DMII and a small TMII. Early in the season, prey are close to starvation, and thus do not show a strong behavioral response to increased predation risk. This leads to the small TMII. Prey suffering higher predation risk because of their small size causes the large DMII. Later in the season when prey have increased their mass, they can better afford to behaviorally respond to increased predation risk by lowering their foraging effort. Thus, when the manipulations were started on day 11, 21, or 31, we measured large TMIIs and small DMIIs.

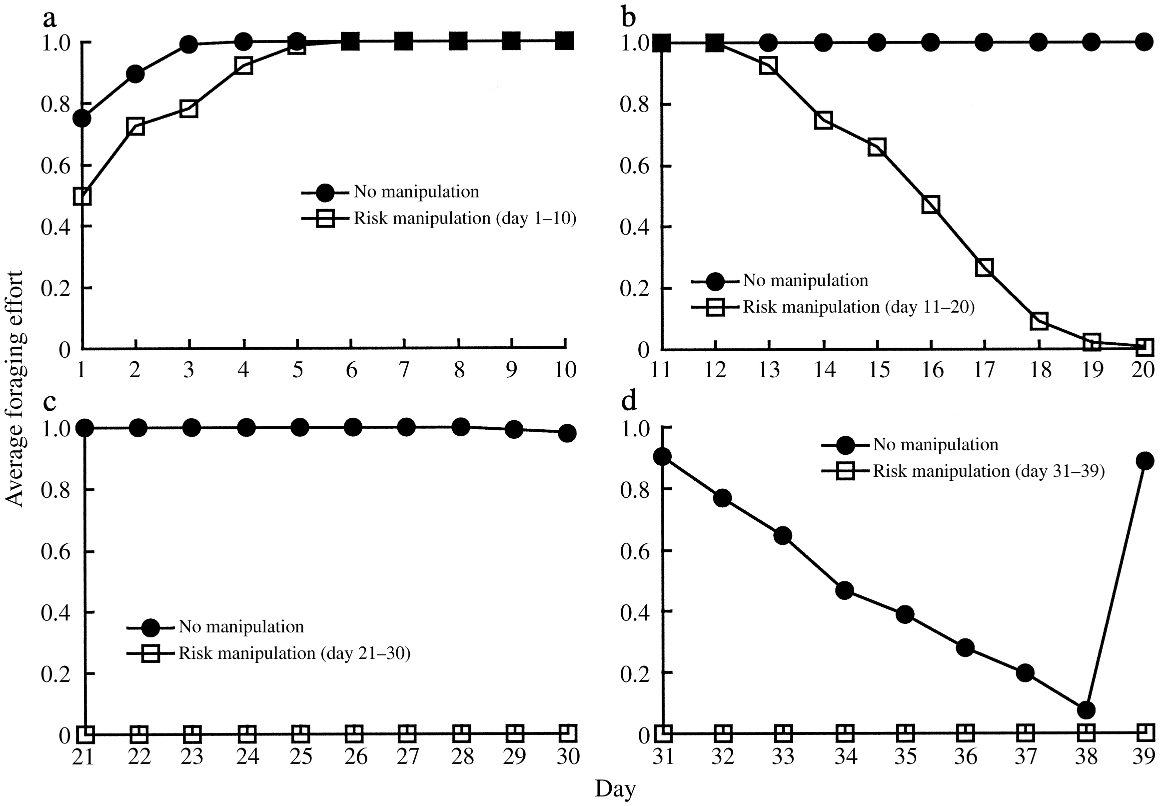

FIG. 5. The average foraging efforts of prey during no manipulation and during a 10-day risk manipulation started on (a) day 1, (b) day 11, (c) day 21, and (d) day 31. Data are from a single replicate that started with 100 prey. Foraging effort ranges from 0 (hiding) to 1 (maximum foraging). Resource levels are set at a moderately high level of 8 on a scale of 0 to 10.

Our measurements of TMII and DMII were very different when observations spanned the complete season rather than just the duration of the manipulations. When the amount of resources eaten by prey was measured across the complete season, the only large measured indirect effect was the DMII if the manipulations were done at the beginning of the season (Fig. 6). This large DMII occurs because prey are most vulnerable early in the season, and because the earlier a prey is killed by a predator, the longer the effects of reduced prey density accrue. The lack of DMIIs when the manipulations were conducted later in the season shows that when conducting experiments, it is critical to know the natural relative timing of changes in predation risk and periods of prey vulnerability. The large TMIIs that were measured during the manipulations disappeared when measured over the whole season because of behavioral compensation. Prey compensated for their periods of low foraging effort during the manipulations by increasing their foraging effort after the manipulations. Therefore, showing that periods of high predation risk affect prey behavior and thus indirectly affect resources should not be interpreted as evidence that these effects will have season-level consequences.

These results should only be viewed as warning of how measurements of TMII and DMII can depend on the timing of manipulations and the length of observations. The results are very sensitive to assumptions about resource levels, fitness functions, and predation risk. For example, if, at baseline levels of predation risk, prey use the maximum level of foraging effort for

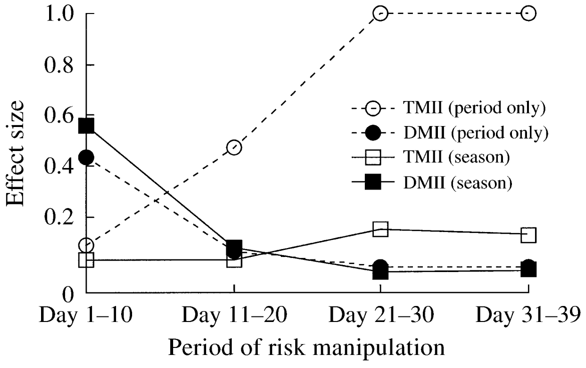

FIG. 6. The size of trait- and density-mediated indirect effects (TMII and DMII) of predators on resources measured either during manipulations or over a complete season vs. the start date of 10-day manipulations for three manipulations with 30 replicates.

the whole season, then there is no opportunity for prey to behaviorally compensate for periods of low foraging effort by increasing their effort during other periods. Thus, TMII measured only during a portion of the season might accurately reflect season-level consequences. The shape of the predation risk function also has large effects on when DMII will be largest and when prey will most strongly respond behaviorally to risk and predator manipulations.

Discussion

We have shown that the importance of TMIIs relative to DMIIs depends upon resource levels, with TMIIs being larger when resources are abundant. In our particular formulation, this effect can be dramatic: a doubling of resources (from 2.5 to 5) completely reversed the sign of the difference between the DMIIs and TMIIs (Fig. 3). This means that an experiment conducted at the lower resource level would lead to the conclusion that TMIIs were unimportant in the system, whereas at the high resources, one would conclude that almost the entire indirect effect resulted from a TMII. This fits the prediction from behavioral ecology that as resource levels decrease, foragers will take more risks and thus will suffer higher rates of predation (McNamara and Houston 1987, Mangel and Clark 1988, Ludwig and Rowe 1990, Werner and Anholt 1993). It has been argued that foraging effort might increase with increasing resource levels because reduced foraging effort causes a greater loss of foraging success when resources are abundant (Van Buskirk 2000), and therefore TMIIs should be reduced when resources are abundant. This argument, however, focuses on the amount of per capita resources eaten by prey and not on the state-dependent fitness effects of eating those resources. Empirical support for the opposing predictions is equivocal. For some species, foraging effort does increase as resource levels increase, despite predation risk (Dill and Fraser 1997). However, other empirical studies suggest that DMIIs decrease with increasing resource levels. Anholt and Werner (1995) showed that the rate of predation on bullfrog larvae was reduced when resources were increased. Similarly, an increase in competition, presumably leading to reduced resource supply, increased the rate of predation on another anuran (Peacor and Werner 1997).

The result that TMIIs will increase and DMIIs will decrease with increasing resource levels should be true for systems in which prey foraging effort decreases with resource levels. However, we have made several assumptions that may affect the relative impact of resources on indirect effects, and thus deserve further theoretical and empirical testing. Whether and how strongly resource levels affect TMIIs and DMIIs depends on whether and how strongly prey react to changes in predation risk. Our sensitivity analyses suggest that how prey react to predation risk should depend on their fitness function (i.e., how their foraging success affects their reproductive success) and how predation risk changes with the size of the prey. In addition, the reliability of information that prey receive about current predation risk should affect their behavioral reactions to changes in predation risk, with behavioral reactions being strongest when prey have reliable information (Luttbeg and Schmitz 2000). We assumed that prey had perfect information about the level of predation risk, which may have increased the size of observed TMIIs and changes in TMIIs as resources varied. Behavioral reactions to changing predation risk also depend on the patterns and predictability of predation risk. Lima and Bednekoff (1999) showed that how prey should behaviorally react to periods of increased predation risk depends on how long that period is expected to last, with behavioral reactions being strongest when periods of high predation risk are expected to be brief or rare. We assumed that prey behaved as if the period of high predation risk were going to persist for the rest of the season, which may have decreased the size of observed TMIIs and changes in TMIIs as resources varied. In addition, this assumption is also responsible for the observed delay in behavioral reactions to increases in predation risk. If prey expected the increase in predation risk to be only a pulse, then their reaction during the period of higher predation risk would be quicker and stronger. Finally, we assumed that there was no competition between prey for resources, but the existence and form of competition may have large impacts on how prey react to changing predation risk. For example, if interference competition is high, prey in some cases might benefit from increasing their foraging effort when predation risk is high and interference competition is low.

We also showed that the timing of experiments had a strong effect on the relative contribution of TMIIs to the total indirect effect. Similar to the resource-level effect, the timing of an experiment can dramatically change the conclusion that would be drawn about the relative contributions of TMIIs and DMIIs. One general result of the integration of foraging and life history theories has been that optimal decisions of foragers depend upon the time in their life cycle when the decision is being made (Mangel and Clark 1986, 1988, Rowe and Ludwig 1991, Clark 1993, Houston et al. 1993, Abrams et al. 1996). If trait values depend not only on densities of adjoining species, but also on the life history stage of the prey, then TMIIs should likewise depend upon prey life history. This effect is shown in our simulations. Early and late in the life history, prey behavior was fairly insensitive to predation risk. Early stages were near their starvation boundary and, hence, in need of accumulating energy; as a result, predators had little effect on foraging rate. On the other hand, midway through the life history, starvation was not an issue and foragers were therefore sensitive to predators. Consequently, experiments conducted early in this season would conclude that TMIIs were of little importance, but the opposite would be concluded from experiments conducted midseason. A pair of empirical studies supports this prediction. Schmitz et al. (1997) found significant TMIIs and DMIIs when they measured the effects of predatory spiders on grasshoppers (early- to mid-instar nymphs) and their resources early in the season. However, when the measurements were done later in the season, with late-instar and adult grasshoppers, only significant TMIIs were found (Beckerman et al. 1997).

Finally, we also showed that measuring DMIIs and TMIIs over a portion of a season might give inaccurate measures of season-level effects. In particular, TMIIs that were considerable during manipulations were less important when measured across a whole season. When predation risk is variable, prey can alter their behavior to match current conditions and temporal variation in predation risk (Lima and Bednekoff 1999). Therefore, during periods of low predation risk, prey can behaviorally compensate for periods of high predation risk by increasing their foraging effort. Peacor and Werner (2001) argue that trait-mediated effects of predators may be large because reductions in prey foraging are immediate and occur over the whole period considered, in contrast to density effects that are slow to accumulate and only occur after predation occurs. However, when predation risk is variable, these same arguments may be reasons why trait-mediated effects of predators are small compared to density-mediated effects. Rapid changes in prey foraging effort can compensate for periods of high predation risk, and the effects of trait changes are not as permanent as the effects of density changes.

There have been several calls for ecologists to incorporate individual behavior into their thinking and experiments in population and community ecology (e.g., Partridge and Green 1985, Anholt 1997, Fryxell and Lundberg 1998). There is now a body of theoretical and empirical research to make the case that behaviors can be important to population and community dynamics, such as stability (Ives and Dobson 1987, Luttbeg and Schmitz 2000). There is less evidence from direct comparisons of the strength of trait- and density-mediated effects (Soluk and Collins 1988, Huang and Sih 1990, 1991, Wissinger and McGrady 1993, Diehl et al. 2000, Peacor and Werner 2001). A more quantitative goal such as this one will require more careful experiments and interpretation. While doing these tests, we should look to the large theoretical and empirical studies of foraging behavior to guide our experiments. This body of research is a rich source of ideas and data that can aid empiricists in designing and interpreting their experiments. For example, the foraging literature suggests that prey behavior should depend on the temporal pattern and predictability of predation risk (Lima and Bednekoff 1999), and the clarity of information that prey have about current predation risk (Luttbeg and Schmitz 2000). This suggests that we will not find a single ratio of TMII : DMIIs in any one system. Instead, this ratio will depend upon the state of the members of that system. Recent empirical results (Peacor and Werner 2001) demonstrate that the relative importance TMIIs transmitted through a prey species depends upon the density of predators. To this, we add that they also depend upon the density of resources, the timing of the manipulation, and the state of the prey.

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APPENDIX

Figures showing sensitivity analyses of how functional forms affect the sizes of trait- and density-mediated indirect effects vs. resource levels are available in ESA's Electronic Data Archive: *Ecological Archive* E084-024-A1.