SCALING FROM INDIVIDUALS TO FOOD WEBS: THE ROLE OF SIZE-DEPENDENT RESPONSES OF PREY TO PREDATION RISK

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ABSTRACT

Ecologists strive to build a theory to predict reliably population and community dynamics across taxa and systems. This ability is often hampered by an incomplete empirical understanding of the functional way different components fit together to determine dynamics. We show here how to overcome this critical hurdle. We describe a research program whose aim is to understand the implications of body size-dependent responses of herbivores to predation risk for food web interactions. We illustrate how to introduce body sizedependent risk response rules into a modeling framework that can scale from individual detail to community-level phenomena. We then show how to use the model to predict the attendant effects of such size-dependent responses of herbivores to predation risk on trophic interactions and food web structure, and explain how to evaluate the net food web effects of variation in herbivore body size using field experimentation that emulates the modeling. Our focus is on effects of predation risk and resource quality on size-dependent risk responses of grasshoppers in a New England old-field ecosystem. We show qualitative congruence between results of the simulation and field experiments, specifically, that grasshopper behavior can have a profound effect on the character of trophic interactions and the plant composition of the food web. We find, however, that herbivore body size had no significant effect on the net abundance of different plant resources. We therefore conclude that it would be reasonable to abstract considerable complexity associated with sizedependent responses of grasshoppers to predation risk and represent behavior more simply as their mean risk response in order to predict reliably the strength of plant herbivore interactions in this food web.

INTRODUCTION

How different organizational levels (e.g., individual, population, community) combine to govern species interactions in ecological systems remains a fundamental research question in ecology (Rosenzweig, 1991; Abrams, 1995; Werner and Anholt, 1996; Peckarsky et al., 1997; Agrawal, 2001; Schmitz, 2001; Ovadia and Schmitz, 2002). This

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question is motivated by the need to understand how much mechanistic complexity must be included in theory and how much can be abstracted safely while still achieving biologically faithful and quantitatively accurate generalizations of community structure and function.

Classical theory in food web ecology (e.g., Rosenzweig, 1973; Oksanen et al., 1981; Carpenter et al., 1985; Menge and Sutherland, 1987) has resolved this question by assuming that it is sufficient to abstract individual-scale details and characterize species interactions simply in terms of net changes in population densities of the different species making up the community. Abstracting individual-scale details is reasonable if their effects attenuate on the timescale of changes in population density. If they do not, then one must keep track of individual-scale detail in order to describe dynamics sufficiently (Abrams, 1992, 1995; de Roos, 1997; Peckarsky et al., 1997; Agrawal, 2001; Schmitz, 2001).

Empirical evidence is increasingly showing that mechanisms operating at the individual level such as behavior ought to be included in models describing communitylevel interactions (Rosenzweig and Abramsky, 1997; Lima, 1998; Sih et al., 1998; Lima, 2002; Werner and Peacor, 2003). For example, anti-predator behavior of prey, through either a reduction in overall foraging activity or selection of habitat to decrease contact with predators, can cause strong direct effects of predators on prey abundance and consequently lead to strong indirect effects of the predators on the prey's resources and its competitors (Sih et al., 1998; Schmitz et al., 2000; Agrawal, 2001; Peacor and Werner, 2001; Lima, 2002).

Recent food web theory has explicitly formalized this trade-off between foraging gains and avoiding contact with predators to decrease predation risk, but it has done so by characterizing interactions in terms of a typical or average behavioral response of an individual in the population (Abrams, 1992, 1995). Populations, however, are effectively ensembles of individuals that differ in the magnitude of traits such as age, size, and physiological condition. Furthermore, theory predicts that these trait differences may uniquely determine how individuals trade-off foraging gains against predator avoidance (Ludwig and Rowe, 1990; Abrams and Rowe, 1996; Clark and Mangel, 2000). This, therefore, raises the following key question: To what extent can intraspecific trait variation be abstracted safely while still achieving an accurate generalization of food web interactions?

One key trait is consumer body size because it determines the kind and amount of resources individuals can exploit and their vulnerability to predation. Body size-dependent responses to food and predators may be especially important for organisms in populations with non-overlapping generations that live in seasonal environments (Rowe and Ludwig, 1991; Abrams and Rowe, 1996). Basic allometric rules suggest that consumer body size should be positively correlated with its food intake rate, resulting in increased net negative effect on the consumer's resources. Alternatively, state-dependent models predict that individuals, who are initially smaller and thus require more time to mature, may have lower fitness than individuals who mature more rapidly because of an initial size advantage (Rowe and Ludwig, 1991; Abrams and Rowe, 1996). Moreover,

these differences in initial size may influence the way individuals in the population trade-off avoiding predators and growth rate/foraging gains (Clark and Mangel, 2000). For instance, if the cost of avoiding predators in small individuals is a complete failure to mature by the end of the season, then initially smaller individuals may feed more frequently than larger individuals despite the existence of some nonzero level of predation risk (Abrams and Rowe, 1996; Clark and Mangel, 2000). Over the course of a season, such size-dependent trade-off behavior could result in differential direct effects of predators on the abundance of a given-sized prey, and indirect effects of the predators on the abundance of the resources used by prey of a given size. To this end, comparatively few theoretical and empirical studies have investigated how these opposing effects of allometry and state-dependence at the individual-level interact to determine the nature and strength of the indirect effect of predators on the consumer's resources that emerge at the community level.

We present here an overview of our research program aimed at developing a theoretical and empirical understanding of the implications of body size-dependent responses of herbivores to predation risk for food web interactions in a typical New England old-field community. We describe our theoretical component by introducing how body size effects are examined in an individual-based model, Gecko (Booth, 1997), which has been calibrated to the natural field system (Schmitz, 2000). We then show how the model is used to predict the attendant effects of such size-dependent responses of herbivores to predation risk on trophic interactions and food web structure. We then describe experimental research used to test these predictions in the field. We conclude by identifying the relevant degree of abstraction that will allow development of an analytical theory whose aim is to predict community dynamics in this particular system.

NATURAL HISTORY

Our insight about the natural field system is based on ten years of empirical research conducted in old-fields located at the Yale-Myers Research Forest in northeastern Connecticut. The herbs Solidago rugosa, Daucus carota, Aster novaeangliae, and Trifolium pratense, and the grass Poa pratensis typically dominate these meadows. We have consistently found that, in the absence of Pisaurina mira spiders, Melanoplus *femurrubrum* grasshoppers preferentially exploit and reduce the abundance of grass (Beckerman et al., 1997; Schmitz et al., 1997; Schmitz and Suttle, 2001; Schmitz and Sokol-Hessner, 2002). P. mira presence causes grasshoppers to forego feeding on grass and to seek refuge in leafy herbs, resulting in decreased abundance of herbs (Beckerman et al., 1997; Schmitz et al., 1997; Schmitz and Suttle, 2001; Schmitz and Sokol-Hessner, 2002). This shift in resource use by grasshoppers results in a positive indirect effect of the spider on grass and a detrimental indirect effect on herbs. Moreover, this interaction chain seems to be the primary determinant of community structure in this system. A recent longterm study shows that the above shift in resource use by grasshoppers explains how the abundance of a competitively dominant herb species, Solidago rugosa, is altered leading to shifts in both plant species diversity and plant productivity (Schmitz, 2003).

We find substantial variation in *M. femurrubrum* body size within early development stages (i.e., 2nd instar grasshopper nymphs; Fig. 1). Such variation has important implications for several reasons. First, basic allometric rules dictate that body size should be positively correlated with resource exploitation ability (Fig. 2a). Second, body size of *P. mira* predators determines their ability to capture and subdue *M. femurrubrum* prey (Schmitz et al., 1997; Schmitz and Suttle, 2001). This then leads to a body-size threshold beyond which prey are no longer vulnerable to predation (Ovadia and Schmitz, 2002) resulting in size-selective predation by spiders (Fig. 2b). The combined effect of these two size-dependent modalities might be carried over to the level of plant abundance in the food web (Fig. 2c), but it is uncertain exactly how this will occur because there are several contingent ways that trophic-level effects can emerge from individual behavior.

First, large grasshoppers, experiencing relatively low predation risk, may feed more frequently on the risky but highly nutritious grass, while small ones, seeking refuge from predators, may spend more time foraging on the safe but less nutritious herbs (Fig. 2c).



Fig. 1. Frequency distribution of grasshopper body length (2nd instar grasshopper nymphs). This distribution was used to designate three size classes: large individuals—the uppermost 5% of the frequency distribution (body length > 12 mm); small individuals—the lowest 5% of the frequency distribution (body length < 9 mm); and average individuals—the middle portion of the frequency distribution (9–12 mm).



a. Body size may confer different exploitation competitive ability for the best resources.

Fig. 2. Predicted effects of (a) grasshopper body size-dependent resource exploitation ability, (b) size-selective predation by spiders, and (c) both a and b in combination on abundances of grass and herb plants. (a) Basic allometric rules dictate that body size should be positively correlated with resource exploitation ability. (b) Body size of spider predators determines their ability to capture and subdue grasshopper prey. In other words, there is a body size threshold beyond which prey are no longer vulnerable to predation, leading to size-selective predation by spiders. (c) The combined effect of these two size-dependent modalities might be carried over to the level of plant abundance in the food web, but it is uncertain exactly how this will occur because there are several contingent ways that trophic-level effects can emerge from individual behavior. For instance, large grasshoppers, experiencing relatively low predation risk, may cause strong net negative effect on the risky but highly nutritious grass, while small ones, seeking refuge from predators, should cause stronger net negative effects to the less nutritious but safe herbs.

Such body size-dependent risk responses may result in differential net effects on the biomass of grasses and herbs (Fig. 2c). This scenario, however, ignores the opposing effects of state-dependent responses of prey to predation risk in seasonal environments (Rowe and Ludwig, 1991; Abrams and Rowe, 1996; Clark and Mangel, 2000). In order to reproduce, individual *M. femurrubrum* must complete their lifecycle before the end of the season (Fig. 3). Thus, small individuals may compensate for their initially smaller body size by increasing total feeding activity or by spending more time feeding in the risky but more nutritious grass (Fig. 3). In contrast, large individuals are less likely to have difficulties completing their lifecycle, and thus should take less risk (Fig. 3). However, these idiosyncratic size effects could attenuate at the food web scale, implying that it is sufficient to abstract the effects of individual variation in prey body size in terms of a population average. Because it is not clear a priori which contingencies operate in this system, it will be difficult to specify a priori an analytical model that makes reliable predictions about food web structure and dynamics. To understand the interplay between these three body size-dependent modalities and their combined effects on population processes, we used a computational approach, which makes no assumptions about population-level effects (i.e., degree of density-dependence, shape of predator functional response, etc.). Instead, population processes emerge as a consequence of individual-scale physiology, behavior, and interactions.



The trade-off between predation risk and growth rate in a seasonal environment

Fig. 3. Predicted state-dependent responses of grasshoppers to predation risk in a seasonal environment.

COMPUTATIONAL SIMULATOR

We modeled the food web using Gecko, a spatially explicit individual-based model (IBM), which has been designed using the framework of Complex Adaptive Systems (CAS) to capture the natural history of this old-field community (Booth, 1997; Schmitz, 2000). The CAS framework explicitly addresses the traits of individuals and how these traits produce system responses (Railsback, 2001). The simplicity of the agents used in most CAS research, compared to real organisms, makes it more likely that basic characteristics and themes of the studied system can be sorted out (Railsback, 2001). Thus, the CAS framework can help us overcome the system-level biases of ecology and the apparently overwhelming complexity of ecosystems, enabling a focus on fundamental aspects of modeling population-level phenomena as the emergent properties of individuals (Railsback, 2001). In other words, this new generation of IBMs can avoid many serious conceptual problems (e.g., inappropriate assumptions, mixing individual- and population-level parameters) typically characterizing older IBMs (Railsback, 2001).

Earlier versions of Gecko use rules that generate two out of the three body sizedependent patterns mentioned above, i.e., a positive correlation between resource exploitation ability and body size, and negative correlation between predation risk and body size. We introduce here an additional rule that allows for body size-dependent behavioral responses, i.e., variation in risk responses as a function of body condition and growth trajectory. We then explore the dynamics of a food web consisting of two groups of plants, three different size-classes of herbivores that select between the two plant groups providing different levels of nutrition and safety from predators, and a predator that preys on the herbivores.

GENERAL RULES

Simulations are driven not by functions but by assigning rule sets to individuals in the simulator at a very fundamental level i.e., physiology and behavior (Booth, 1997; Schmitz and Booth, 1997; Schmitz, 2000). These rules change as a function of body size and they are literal translations of the behavior of organisms under field conditions. Individuals undergo un-gridded movement on a finite plane (i.e., a free-floating topology). Moreover, individuals are represented by spheres with their centers lying on this plane and they are free to move in two dimensions. An individual has a radius r, and accordingly a virtual volume $4/3\pi r^3$ and area πr^2 . An individual's radius is proportional to biomass^{1/3}. An individual's volume increases as resources are consumed, assimilated, and stored. The rate at which an individual gathers resources is proportional to its area and, correspondingly, biomass^{2/3}. To stay alive, individuals must consume enough resources to meet metabolic requirements. Metabolic rate is proportional to biomass^{3/4}. Because metabolic cost increases faster with individual biomass than resource intake rate, there are upper constraints on maximum volume that an individual can reach. Individuals can overlap in space, allowing competition for local resources if the individuals belong to the same species or same trophic category, or consumer-resource interactions if individuals belong to different trophic categories.

PLANT RULES

Plants absorb nutrients directly from the plane and compete for nutrients. Local resource uptake is proportional to an individual's resource gathering capabilities, i.e., its area. Large individuals have a competitive advantage because they can deplete the resource pool at a faster rate than smaller individuals. Competition causes anything from reductions in individual body-size growth to death, depending on an individual's physiological state (size of resource stores and metabolic costs) relative to local resource intake. The ultimate net effect of competition is a reduction in reproductive output or even an outright failure to reproduce owing to chronic shortages in resource intake.

Plants undergo asexual reproduction when their size exceeds a minimum breeding volume. Offspring are endowed with a supply of resources that determines their body size radius. The size of the endowment depends on the extent to which a parent's resource pool exceeds the parent's breeding radius. Offspring are placed at a random distance outside their parent's radius according to the function: distance = (parent radius + offspring radius) × $e^{random[0....1]}$. This guarantees that parent and offspring never overlap in space immediately after reproduction. Offspring are also placed in a random direction away from their parent.

The two plant species representing the primary producers in our food chain are identical in terms of all parameters used to estimate their resource intake rate, growth rate, reproduction rate, etc. They differ only in terms of the herbivore's perspective. One plant species is highly nutritious and thus termed "preferred" plant. The second, "safe" plant is less nutritious but it represents a refuge from predation. By creating this type of community structure we introduced a trade-off between food and safety for the herbivores.

HERBIVORE RULES

Herbivores have perception, and an intent that stimulates movement on the landscape, which is effectively a biased random walk with reflecting boundary conditions. They actively search for resources (plants) within a designated search path width that scales to their body size radius. The distance that herbivores move each time-step is equal to their body size radius. Directional movement is steered by a "veer" function, i.e., they move forward in the general direction they face plus or minus a random veer of no more $\pi/2$ radians (90 degrees) left or right of their current heading. When feeding, herbivores select the individual plant within that search path that yields the highest rate of resource intake to maximize the chance of meeting demands for maintenance, growth, and reproduction. The herbivore takes a discrete "bite" out of the plant. The size of the bite taken is proportional to the herbivore's radius (i.e., size-dependent resource exploitation ability). Herbivores add consumed resources to their own body stores (thus increasing their own volume). Plants lose that amount of resource, causing their volume to shrink. Plants, however, are not killed directly by herbivores. Even when herbivory reduces plant volume to zero, depending on local resource availability the plants will have a chance to re-grow.

Herbivores have a predator detection radius that is a multiple of their body size radius. Since both herbivore movement and predator detection radius are positively correlated with body size, large individuals should be better at detecting and evading predators than small ones (i.e., size-selective predation). When a predator enters the herbivore's detection radius predation threat is signaled and the herbivore freezes for one time-step. If in the next time-step the predator is detected again, the herbivore uses a state-dependent probabilistic rule to choose between moving away from the oncoming predator in a direction of a safe or risky plant. The probability that an individual herbivore will retreat to a safe plant is positively correlated with its body condition and growth trajectory. In other words, an individual with a good body condition, or one having a high chance of completing the lifecycle before the end of the season, is more likely to move away from the oncoming predator in a direction of the safe but less nutritious plant and vice versa. Because these state-dependent behavioral responses take into account the entire life history development of an individual herbivore, rather than maximizing its instantaneous net energy gain or its instantaneous survival, they maximize the expected probability that it will survive and grow to reproductive size (e.g., Railsback, 2001). Herbivores on safe plants will continue to eat safe plant biomass until the predator moves beyond their detection radius. At this point, the herbivores deem it safe to leave the safe plant and resume feeding on the preferred plant.

Herbivores undergo asexual reproduction when their size exceeds a minimum breeding volume. Because we assume non-overlapping generations, we keep the offspring non-active (eggs) until the end of the season, i.e., offspring have no effect on interaction strength. Furthermore, our focus here is the strength of plant herbivore interactions rather than the long-term community dynamics and we thus simulate only one growing season (i.e., year) and do not present reproduction data.

To allow for consistent differences in body sizes and growth trajectories among individual herbivores, as observed in our field system (Ovadia and Schmitz, 2002), we created three size classes: (1) average, which contained individuals who had growth rate/nutrient consumed ratios identical to that used in earlier Gecko prototypes; (2) small, which contained individuals who had an 8% lower than average growth rate for each unit of nutrient consumed; and (3) large, which contained individuals who had an 8% higher than average growth rate for each unit of nutrient consumed; who had an 8% higher than average growth rate for each unit of nutrient consumed. We chose 8% because this was the maximum level of variation that allowed small individuals to persist in the simulator.

PREDATOR RULES

Predators have an attack radius that enables them to detect and then actively hunt prey. This attack radius is a multiple of their body size radius. They search randomly until a prey item is detected within the attack radius and they then move directly toward that prey item. A predation event occurs when there is a contact (or an overlap) between the prey and the predator. Here the biased random walk of the predator is driven simply by prey detection and opportunity for capture. For simplicity, we assumed that predators do not undergo population dynamics nor exhibit flexible adaptive behavior. Rather, they are treated as an environmental component of the plant-herbivore interaction by simply keeping the number of predators constant throughout the entire season. Future research should relax these simplifying assumptions and allow for adaptive behavioral and population-level responses, which would turn Gecko into a predatorprey game model.

TIME AND SEASONALITY

In Gecko, the focus of time is on feeding, so a time-step is equal to the portion of a day equivalent to a feeding period (e.g., one to several hours). In our simulations, a day is comprised of ten feeding periods. The landscape produces resources incrementally each time-step. Within each time-step, resources are consumed in discrete units by plants and animals.

We incorporated seasonality into the computational model by dividing the season into a growing period of 1900 time-steps (i.e., 10 "hours" per day \times 190 days) and a dormant period of one time-step. In the simulations, all plants initiate growth at the beginning of the growing season. At the end of the growing season, surplus resources are allocated to seed production and living plants then whither back to the center point of their location. Any seeds that were produced during the 190-day growing season germinate and grow; seeds produced at the end of the season remain dormant and thus cannot influence interaction strength.

Herbivores and predators are introduced into the environment after 100 days (1000 time-steps) of the season to emulate the emergence times in the study field. In the simulations, herbivores must accrue enough resources to grow and can only reproduce as adults (i.e., they must reach a critical body size before they can reproduce). Reproduction depends upon the size of resource stores accrued by adults, which, in turn, depends upon resource intake rate and food conversion efficiency. As a consequence of local variation in resource availability coupled with the restricted season length, and depending on their food conversion efficiency, some individuals are able to reproduce several times in a growing season, whereas others may not reproduce at all. Such variability in potential reproductive success among individual herbivores, combined with the new state-dependent behavioral rules that we incorporated into Gecko, allows us to investigate how allometry and adaptive behavioral response of herbivores to predation risk interact to influence the strength of food web interactions.

ENERGY FLOW AND NUTRIENT RECYCLING

Following Hairston and Hairston (1993) we assume that 10% of abiotic resources taken up by plants are converted into plant tissue, 33% of plant tissue is converted into herbivore biomass, and 85% of herbivore biomass is converted into predator biomass.

Organisms die when they cannot pay metabolic costs. Dead organisms are recycled back into the nutrient pool of the landscape. Hence, this is not a completely open system.

STOCHASTICITY

Stochasticity enters the simulations in several ways. First, it arises from the initial random seeding of organisms onto the landscape. Second, although movement of organisms in space is qualitatively directional, there is a random component due to the veer function. The degree of stochasticity varies positively with the veer angle. Third, the strengths of local species interactions are emergent properties of the number of individuals that occur locally in space and the size of the resource pool at a given location. The exact local interactions are not reproducible among runs of the simulator. Fourth, the risk response of herbivores is driven by a state-dependent stochastic rule. Finally, reproduction is stochastic because it depends entirely on local resource uptake over consecutive time periods.

FROM SIMULATIONS TO PREDICTIONS

We simulated only one growing season (i.e., year) using the following seven combinations: a control with only plants and treatments combining plants with small, average, or large herbivores in the absence and presence of predators. Because Gecko is a stochastic simulator, we obtained ten realizations for each treatment combination and calculated the mean and standard error for each simulation outcome. It is important to note that, in each run of the model, individual herbivores of the same size class had equal initial body size. However, because of the stochastic nature of Gecko we quickly observed an emergent variation in body size within in each size class. In natural populations, such variation in body size may result in differential success of individuals within the population and consequent evolutionary response or changes in population dynamics.

We found that across all size classes, predators caused a small but significant (ANOVA, $F_{1,54} = 258$, p < 0.001) reduction of about 12% in herbivore survival (Fig. 4). Additionally, there was a significant predator × body size treatment interaction (ANOVA, $F_{2.54} = 6.37$, p = 0.003), indicating size-selective predation at the population level. Specifically, in the absence of predators, there was a weak effect of herbivore body size on herbivore survival, however, the addition of predators caused a relative increase of up to 11% in survival of large herbivores compared with that of small ones (Fig. 4).

At the food web-level, we observed cascading effects that are consistent with a traitmediated mechanism (Fig. 5). Specifically, in the absence of predators, there was a significant reduction in the biomass of preferred plant relative to predator present treatment (ANOVA, $F_{2.61} = 2764$, p < 0.001; Fig. 5a). The opposite pattern was observed for the safe plants (Fig. 5b). In the presence of predators, there was a small but significant reduction in the biomass of safe plant relative to predator absent treatment (ANOVA, $F_{2.61} = 217$, p < 0.001). In the case of a density-mediated mechanism, the presence of predators should result in lowered net negative effects of herbivores on both preferred and safe plants. Finally, there was a significant number of trophic level × body size treatment interactions for both preferred and safe plants (ANOVAs, $F_{4.61} = 10.42$,



Fig. 4. Effects of herbivore body size class and predators on herbivore survival, at the end of a simulated season in the Gecko simulator. Across all size classes, predators caused a small but significant reduction of about 12% in herbivore survival. There was a significant predator × body size treatment interaction, indicating size-selective predation at the population level. In the absence of predators, there was a weak effect of herbivore body size on herbivore survival; however, the addition of predators caused a relative increase of up to 11% in the survival of large herbivores compared with that of small ones. Data are means and standard errors, n = 10 realizations of each treatment.

p < 0.001 and $F_{4,61} = 12.34$, p < 0.001, respectively). In the absence of predators, we could not detect significant differences in the net negative effects of herbivores on the biomass of both preferred and safe plants among size classes (Figs. 5a and 5b, respectively). The addition of predators brought about a significant reduction in the net negative effects of herbivores of the small size class on both preferred and safe plants relative to food webs containing average and large size class herbivores (Figs. 5a and 5b, respectively).

The emergent insight from the simulation analysis is that it would be reasonable to abstract body size-dependent risk responses as a typical or mean response when predicting net food web effects only for large and average size herbivores. Small herbivores experience higher predation mortality that is carried over to the population scale, resulting in lowered net negative effects of herbivores on plant biomass. Additionally, they exhibit weaker responses to a shift away from preferred plants in the face of direct predation risk because of their need to complete development before the mating season begins. The combined effect of these numerical and behavioral responses may result in the loss of the trait-mediated signal for safe plants in food webs containing small grasshoppers. To test if the simulation results reflect interactions in the field, we conducted an experiment that replicated the factorial design used in the simulations and measured the consequences of grasshopper body size on trophic abundances and interactions in an old-field community.



Fig. 5. Net negative effects of herbivores on the biomass of (a) preferred and (b) safe plants in food webs of a varying number of trophic levels, at the end of a simulated season in the Gecko simulator. The results show cascading effects that are consistent with a trait-mediated mechanism. In the absence of predators, there was a significant increase in the net negative effect of herbivores on preferred plant biomass relative to predator present treatment. Additionally, predators caused a small but significant increase in the net negative effect of herbivores on safe plant biomass. In the case of a density-mediated mechanism, the presence of predators should result in lowered net negative effects of herbivores on both preferred and safe plants. There was a significant number of trophic level \times body size treatment interactions for both preferred and safe plants. In the absence of predators, there were no detectable differences in the net negative effects of herbivores on the biomass of both preferred and safe plants among size classes. The addition of predators caused a significant decrease in the net negative effects of herbivores of the small size class on both preferred and safe plants relative to food webs containing average and large size class herbivores. Data are means and standard errors, n = 10 realizations of each treatment.

EMPIRICAL STUDY

STUDY DESIGN

The empirical study was undertaken in an old-field located at the Yale–Myers Research Forest in northeastern Connecticut USA (Schmitz and Suttle, 2001), and comprised of two complementary experiments. First, we conducted a bench-top experiment under semi-field conditions to quantify the potential for size-selective predation of grasshoppers by the spiders. Second, we conducted an enclosure experiment in the field to quantify the direct and indirect effects of spiders on size-based grasshopper populations and the indirect effects of the predator on grass and herb resources, mediated by different-sized grasshoppers.

In early July 2001, we sampled grasshoppers using sweep nets and measured the length (head to end of abdomen) of individual grasshoppers. Previous research (Schmitz et al., 1997; Schmitz and Suttle, 2001) indicated that body length in *M. femurrubrum* grasshoppers is inversely related to vulnerability to predation by *P. mira* spiders. Using the frequency distribution of grasshopper body length (Fig. 1), we designated three size classes: large individuals were those in the uppermost 5% of the frequency distribution (body length > 12 mm); small individuals were those in the lowest 5% of the frequency distribution (body length < 9 mm); and average individuals were those from the middle portion of the frequency distribution (9–12 mm). The average size class represented a benchmark to evaluate consistency between this and previous studies that also used a random sample of similar-sized individuals (Schmitz et al., 1997; Schmitz and Suttle, 2001).

The bench-top experiment was conducted in July 2001 in 0.5 m² × 1 m high screen terraria affixed to small benches. The benches were arrayed outdoors in a grid at the Yale–Myers research station such that each terrarium received similar exposure to natural sunlight and moisture. Each terrarium was filled with pieces of sod cut from the same fields in which we conducted the enclosure experiment. Each piece of sod was selected to ensure an approximately equally representation of grass and herbs. The terraria were small enough to observe grasshoppers feeding, yet large enough to permit grasshopper movement to avoid contact with predators. The experiment was designed to measure short-term prey size selection by spiders. We stocked the terraria with three individual *P. mira* spiders and four small and four large *M. femurrubrum* grasshoppers. After 24 hours, we collected all grasshoppers in the terraria that remained alive and measured their body length.

We conducted an enclosure experiment in the field to test for direct effects of spiders on experimental populations of grasshoppers and indirect effects of spiders on grass and herb resources. A positive indirect effect of predators on plants can be detected whenever predator addition to food webs results in a lowered net negative effect of herbivores on the biomass of plants relative to food webs containing only herbivores and plants. A negative indirect effect occurs whenever predator addition to food webs brings about an increase in the net negative effect of herbivores on plants biomass relative to food webs containing only herbivores and plants.

The enclosure experiment in the field was conducted in standard aluminum screening

enclosure cages measuring 0.25 m² (basal area) \times 1 m (height). The protocol for cage construction and placement in the field has been presented elsewhere (Schmitz et al., 1997). The cages were arrayed in a randomized-block design separated by 1.5 m and placed over natural vegetation in the field. This method of cage placement does not introduce bias in initial grass and herb composition in the cages (Schmitz and Suttle, 2001). We removed all animals within the cages by carefully hand-sorting through the vegetation and litter in each cage. We removed all the large insects and spiders from the cages. Small spider species could not be removed: although their size and habitat use prevented capture, it also precluded their ability to prey upon the grasshoppers or the treatment spiders.

The enclosure experiment consisted of six treatments and a control randomly assigned to each of 15 blocks. We assembled, in enclosure cages, experimental food webs composed of plants only (1-trophic level control), plants and grasshoppers assigned by size class (three, 2-trophic level treatments), and plants, grasshoppers assigned by size class, and a spider predator (three, 3-trophic level treatments). In early July 2001, we collected grasshoppers for the enclosure experiments using sweep nets. Individual grasshoppers were sorted into one of the three size classes (Fig. 1). At the same time, we collected *P. mira* spiders in the field using sweep nets. We stocked each 2-level and 3-level treatment cage with six early instar (2nd) grasshopper nymphs, which was about 1.5 times natural field densities at the time of stocking. Grasshoppers were intentionally stocked this way to produce a pulse perturbation that allowed their densities to decline toward levels set by local limiting factors in each cage (e.g., food resources, predators, etc.). In some cases, these local levels may be higher than the average density for the whole field (Schmitz et al., 1997; Schmitz and Suttle, 2001). At this time, we also stocked one spider predator to the 3-level treatment cages.

We conducted censuses of enclosure densities of grasshoppers and spiders over the course of the entire experiment. After initial stocking, the first three censuses were performed at intervals of two days to ensure that grasshopper populations did not go extinct due to artifacts of initial conditions (none went extinct). Thereafter, enclosures were monitored every five days until termination of the experiment in early September. Ten days before terminating the experiment, we used calipers to measure grasshopper body length during the course of a routine census. In such censuses, grasshoppers typically rise up on the screening and remain immobile long enough to measure body length. Length measurements were used to estimate growth rate and test whether the relative differences in size among classes remained consistent during the season.

The enclosure experiment was run for the full generation time of the grasshoppers. It was terminated in early fall just before the seasonal onset of frosts that kill the arthropod community and cause the herbaceous plant community to senesce. At this time, all plants in the enclosures were clipped to the soil surface, sorted by class (grass and herb), dried at 60 °C for 48 h, and weighed.

DATA ANALYSIS

We tested for direct effects of *P. mira* on *M. femurrubrum* grasshoppers in field enclosures in two different ways. We first conducted a survival analysis to compare the

mortality rates of different size classes of grasshoppers in the presence and absence of spiders using the Cox Proportional Hazard Model (Hosmer and Lemeshow, 1999). This is a commonly used survival analysis method, which allows evaluating effects of different predictors (i.e., covariates) on mortality rate independent of the time varying background mortality rate (Hosmer and Lemeshow, 1999). To control for repeated measurements on a subject, which in our case were individual cages that were repeatedly censused throughout the season, we used a robust jackknife variance estimator grouped by observations per cage (Lin and Wei, 1989). Second, we compared the end-of-season survival (percent surviving) in size-structured 2-level webs (plants and grasshoppers) and size-structured 3-level webs (plants, grasshoppers, and spiders) using a randomized block ANOVA on arcsine-square root transformed data. This was followed by Bonferroni-corrected *t*-tests to identify treatments that differed.

We measured the body length of grasshoppers before stocking and again after 30 days of experimentation (i.e., ten days before the enclosure experiment was terminated). Per capita body growth rate in an experimental cage was calculated as:

final body length – initial body length

30 d

We tested for treatment effects on the per capita body growth rate of grasshoppers using randomized block ANOVA that was followed by Bonferroni-corrected *t*-tests to identify treatments that differed. It is important to note that an exponential body size growth model generated almost identical patterns. For simplicity, we present here only the results for the above linear model.

Net negative effect of herbivores on plant biomass in each experimental cage was calculated as:

$100 \times (block control plant biomass - treatment plant biomass)$

block control plant biomass

We tested for indirect effects of *P. mira* on plants by comparing the net negative effects of herbivores on plants in size-structured 2-level webs (plants and grasshoppers) with effects in size-structured 3-level webs (plants, grasshoppers, and spiders) using randomized block ANOVAs on arcsine-square root transformed data for grass and herbs separately. We used Bonferroni-corrected *t*-tests to identify treatments that were significantly different.

RESULTS

The prey size-selection trials revealed that approximately three of every four grasshoppers consumed by *P. mira* were in the small size class (Fig. 6a). Such size-based differences in mortality are also reflected in survival probability estimates from caged populations in the field (Cox Proportional Hazard Model, likelihood ratio test = 50, DF = 3, p < 0.001; Figs. 6c and 6d). Specifically, survival of large and average



trials demonstrating that spider predators can capture and subdue grasshoppers and that grasshoppers assigned to small size classes suffer significantly higher mortality than larger grasshoppers. (b) Field experiment data showing that mean grasshopper survival at the end of season varies significantly with grasshopper size-class but not with predator treatment (data are means and standard errors). (c, d) Survival curves of grasshoppers within each of Fig. 6. The effect of initial body size-class and predator treatment on survival and population demography of grasshoppers. (a) Results of behavioral the size classes estimated by using the Kaplan-Meier method (Kalbfleisch and Prentice, 1980), in the (c) absence and (d) presence of spider predators, indicating that survival probability of large and average grasshoppers is significantly higher than that of small grasshoppers. grasshoppers was 2× higher than that of small grasshoppers (Cox Proportional Hazard Model, z = -8.22, p < 0.001). Furthermore, this difference in survival probability between the small and larger size classes was consistent between the no predator and predator treatments (Cox Proportional Hazard Model, predation × size treatment interaction, z = 0.67, p = 0.5, Figs. 6c and 6d). The majority of predation effects occurred within the first ten days of the experiment. By the end of the season, survival within each size class in the no predator treatment was similar to survival in the predator treatment (Cox Proportional Hazard Model, z = 0.004, p = 1).

Similarly, the percent of surviving grasshoppers at the end of the experiment (Fig. 6b) varied significantly with grasshopper size class (ANOVA, $F_{2,70} = 61.16$, p < 0.001), but not with predator treatment (ANOVA, $F_{1,70} = 0.24$, p > 0.63). There was no significant size × predator treatment interaction (ANOVA, $F_{2,70} = 1.07$, p > 0.35), nor a significant block effect (ANOVA, $F_{14,70} = 1.42$, p > 0.17). Bonferroni comparisons revealed that the percent of surviving grasshoppers among the large and average size classes was not significantly different, irrespective of predator presence or absence (Fig. 6b). However, among the small size classes, the percent of surviving grasshoppers was significantly lower than that of the other two size classes (Fig. 6b).

Per capita body growth rate of grasshoppers remained significantly different among size classes over the course of the season (ANOVA, $F_{2,45} = 12.29$, p < 0.001; Fig. 7). Bonferroni comparisons revealed that per capita body growth rate in the small and average size classes was significantly higher than that of the large size class (Fig. 7). There was no significant predator effect (ANOVA, $F_{1,45} = 0.002$, p = 0.96; Fig. 7). Additionally, we could not detect a significant size × predator interaction (ANOVA, $F_{2,45} = 0.51$, p > 0.603; Fig. 7), nor a significant block effect (ANOVA, $F_{14,45} = 1.524$, p > 0.141).



Fig. 7. The effect of initial body size-class and predator treatment on per capita body growth rates of grasshoppers over the course of the season. Per capita body growth rate of individuals in the small and average size classes were significantly higher than that of the large size class. Data are means and standard errors.

At the food web level (Fig. 8), there was a significant effect of the number of trophic levels on the net negative effect of herbivores on grass (ANOVA, $F_{2,82} = 35.07$, p < 0.001) and herbs (ANOVA, $F_{2,82} = 38.93$, p < 0.001). Block effects were not significant in either analysis (ANOVAs, $F_{14,82} = 0.85$, p = 0.62 for grass; and $F_{14,82} = 0.95$, p = 0.52 for herbs).



Fig. 8. Net negative effects of grasshoppers on the biomass of (a) grass and (b) herbs in food webs of a varying number of trophic levels. (a) In the absence of predators (2-trophic level treatment), grasshoppers had a significantly stronger net negative effect on grass biomass, relative to the plant-only control (1-trophic level treatment). The addition of predators (3-trophic level treatment) brought about a decrease in the net negative effect of grasshoppers on grass biomass to the extent that there was no detectable difference between the 3-level and 1-level treatments. There were no significant differences in the net negative effects of grasshoppers on grass biomass among the three size classes. (b) In the absence of predators, all three size classes of grasshoppers had marginal net negative effect of all three size classes of grasshoppers on herb biomass. There were no significant differences in the net negative effects of grasshoppers on herb biomass. There were no significant differences in the net negative effects of grasshoppers on herb biomass. There were no significant differences in the net negative effects of grasshoppers on herb biomass. There were no significant differences in the net negative effects of grasshoppers on herb biomass. There were no significant differences in the net negative effects of grasshoppers on herb biomass. There were no significant differences in the net negative effects of grasshoppers on herb biomass. There were no significant differences in the net negative effects of grasshoppers on herb biomass among the three size classes. Data are means and standard errors.

Bonferroni comparisons revealed that in the absence of spider predators, the net negative effect of grasshoppers on grass biomass was significantly stronger than that observed in the presence of predators (Fig. 8a). We could not detect any effect of grasshopper size class (ANOVA, $F_{2,82} = 2.49$, p = 0.09), nor a significant size × number of trophic level treatment interactions (ANOVA, $F_{4,82} = 0.72$, p = 0.58).

The presence of predators brought about a significant increase in the net negative effect of grasshoppers on herbs relative to the predator absent treatment (Fig 8b). There were no significant differences in the net negative effects of grasshoppers on herb biomass among the three size classes (ANOVA, $F_{2,82} = 0.61$, p = 0.55), nor a significant size × number of trophic level treatment interactions (ANOVA, $F_{4,82} = 0.72$, p = 0.58).

Our conclusion from the empirical work—that prey size-dependent risk responses to predators can be abstracted as an average body size response when predicting trophic level interactions—is subject to two interpretations. Either it is a true effect, or we were not able to detect the effect due to low replication. To discern which contingency applied, we conducted power analyses for all non-significant results assuming a body size effect of up to 20%. This revealed that the chance of committing a Type II error with respect to the effect of size class (i.e., concluding that there was no body size effect when there really was) was on the order of 1-5%. Thus, the results cannot be attributed to a statistical artifact of low replication.

GENERAL IMPLICATIONS

One of the central difficulties in developing generalizable theory in community ecology is deciding on the appropriate structure of a theoretical model that is intended to make reliable predictions about community-level processes. This is not an easy task because one must recognize that communities are comprised of many populations, which are themselves made up of many individuals. The challenge here is to decide how much finer-scale detail must be included to arrive at mechanistically reliable predictions about community structure and function. In most cases, such detailed insight is absent, and so theorists are often forced to guess what degree of abstraction is appropriate. This is not a trivial decision because the ensuing predictions from theory ultimately can steer the development of entire research programs.

We present here an overview of our research program aimed at developing a theoretical and empirical understanding of the implications of body size-dependent responses of herbivores to predation risk for food web interactions in a typical New England old-field community. Rather than build a set of competing analytical models of community dynamics that embody a host of contingent assumptions about functionality between body size and population- and community-level processes, we instead used a single, complex but biologically faithful model of whole community function driven by basic physiological and behavioral rules assigned to individuals. We made no assumptions about the nature and functionality of population-scale processes. Instead, we let population processes emerge as a consequence of individual-scale behavior. If behavior is important at the population-scale, we should be able to trace the causal chain from field.

individuals to populations; if behavior attenuates at the scale of population dynamics, we can abstract behavioral-scale details. The further advantage is that we could conduct field experiments that precisely match the experimental design used in simulation experiments to evaluate congruence between model predictions and processes in the

We found good qualitative congruence between results of the simulation and field experiments. Our field experiment indicated that, at the food web level, the presence of P. mira spiders had a significant positive indirect effect on grass resources and a significant negative indirect effect on herbs, despite having little or no net direct effect on grasshopper survival in any of the size classes by the end of the experiment. This outcome was consistent with our Gecko simulations and with expectations for indirect effects of predators on plants that are mediated entirely by changes in grasshopper foraging behavior to decrease predation risk (Schmitz, 1998). In the absence of predators, grasshoppers appear to preferentially exploit and reduce the abundance of the nutritionally superior grass. P. mira presence caused grasshoppers to forego feeding on grass and to seek refuge in leafy herbs, resulting in decreased abundance of herbs. The indirect effect of predators on the preferred plant in Gecko was almost identical to that observed for grass in the field. However, the negative indirect effect of predators on the safe plant was substantially weaker than that observed for herbs in the field. This is because in Gecko herbivores feed most of the time on the preferred plant and may switch to the safe plant only when detecting a predator, while in the field the existence of some non-zero background predation risk causes grasshoppers to feed on herbs even when there is no imminent risk of mortality due to predator encounter.

Models are conceptual abstractions based on processes that modelers deem important to overall structure and function. Thus, despite good *qualitative* congruence between modeling and field experimentation, there will always be *quantitative* differences owing to an inability to specify exactly the strength and mechanism of individual interactions. However, such quantitative discrepancies allow the simulator to be a useful benchmark for refining our understanding of mechanisms operating in natural systems.

For example, Gecko simulations indicated that there should be a weak (5%–11%) effect of grasshopper body size on grasshopper survival. Our field experiment, however, demonstrated a strong (40%–50%) net effect of grasshopper size on survival over the full course of the experimentation, irrespective of predator presence or absence. Grasshoppers assigned to the small size classes suffered higher mortality rates than grasshoppers assigned to larger size classes even in the absence of spider predators. One possible cause of such a size effect is that small grasshoppers have a lower capacity to digest and assimilate much of the vegetation in the fields (Belovsky, 1986). Thus, smaller grasshoppers must spend considerable effort seeking high quality plant resources that tend to be comparatively rare (Belovsky, 1986; Beckerman, 2002). Experiments have revealed that this can lead to heightened starvation mortality of individuals in small size classes owing to greater intraspecific competition for food resources (Belovsky and Slade, 1995; Beckerman, 2002). Such a size-dependent digestive constraint was not built into Gecko. Including this constraint would require smaller grasshoppers to search harder for

highly nutritious, highly rare forage, which would in turn increase the strength of intraspecific competition among individuals in this size class.

Gecko predicted weak numerical effects of predators on herbivores (~12%); however, in our field experiment even such weak numerical effects were not detected. Similarly, Gecko indicated a negative correlation between predation mortality of herbivores and their body size. Such size-selective predation was observed in our bench-top experiment but not in the enclosure experiment. We interpret this to mean that, in the field, the differential effects of predation attenuated over the course of the season, i.e., the net effects of predation were largely compensatory to natural mortality in the grasshopper population. This outcome is consistent with a series of independent studies using the same species at our study site (Schmitz et al., 1997; Schmitz and Suttle, 2001; Schmitz and Sokol-Hessner, 2002), as well as in independent studies with grasshopper species at other geographic locations (Belovsky and Slade, 1995; Oedekoven and Joern, 2000). Thus, although there might be a strong link between herbivore body size and its population demography, as our field experiment indicated, body size-dependent responses of herbivores to predation risk can be abstracted to an average or typical risk response when we examine its population dynamics.

The conclusion that effects of individual body size variation can be abstracted was further corroborated by our field experiment, but was supported only partially by Gecko. Our simulations show a weak but significant negative correlation between herbivore body size and the final abundance of both preferred and safe plant. Furthermore, these differential effects of herbivore body size on plant abundances were stronger in the presence of predators, to the extent that the signal of trait-mediated trophic cascades was not detected for safe plants in food webs containing herbivores of the small size class. In contrast, our field experiment indicated that, despite the differences in survival between small grasshoppers and the two other size classes, herbivore body size had no significant effect on the net abundance of nutritious (grass) and safe (herb) plants. The grasshopper growth rate data provide some clue about the mechanism producing this outcome. Grasshoppers in the small and average size classes exhibited higher growth rates over the course of the season, than grasshoppers in the large size class. Such higher growth rates are probably sustained by higher foraging effort. Indeed, we estimated the expected net negative effect of grasshoppers of the different size classes on plants based on calculations of their cumulative effect over the season. We calculated the cumulative daily density of each size class in each cage for the entire season and, based on a conservative assumption that each individual in each size class has an equal per capita daily consumption rate, estimated the expected net negative effects of all individuals in the different size classes on the plants. We estimated that the net negative effect of grasshoppers of the small size class on plant biomass should be at least 40% weaker than that of the large size class. The observed absence of such a difference supports the assertion that individuals in the small size class fed more than individuals in larger size classes. As a consequence, the effect of lower density of smaller grasshoppers appeared to be compensated by the greater per capita foraging effort of the surviving individuals.

Such size-based differences in effort are expected whenever there is a high risk that small individuals with an annual lifecycle will fail to complete their development by the end of the season (Ludwig and Rowe, 1990; Rowe and Ludwig, 1991). Our field results are consistent with theoretical predictions (Abrams and Rowe, 1996) that initially smaller individuals may feed more frequently than larger individuals to sustain higher growth rates despite the existence of some nonzero level of starvation or predation risk. Such compensatory responses were not included in Gecko.

Clearly, using Gecko as a benchmark enabled us to identify additional mechanisms that may need to be included in the simulator in order to obtain more biologically accurate descriptions of the interplay among individuals. These mechanisms can be embodied into Gecko and another round of simulation modeling can be conducted to see if we obtain closer quantitative agreement between modeling and field experimentation. Nevertheless, we feel that we have already obtained sufficient qualitative insight from the modeling-validation process to also suggest the kind of analytical framework needed to predict the dynamics in this old-field community.

This study shows that accurately predicting trophic interactions in this system (and possibly other similar field systems) requires including behavioral details related to the predation risk-growth rate trade-off made by the prey. In other words, a formal model of trophic interactions requires specifying the dynamics of two classes of plant resource (nutritious but risky grass: safe but less nutritious herbs), a herbivore that switches adaptively between the resources in response to predation risk, and a predator that causes prey risk responses but no additive prey mortality. However, we found that grasshopper body size had little or no net effect in mediating the strength of the indirect effect of P. mira spiders on the grass and herbs. Thus, for this particular system, it would be sufficient to abstract the details associated with size-dependent risk responses and simply represent the predation risk-growth rate trade-off displayed by individuals as a typical or average response in models of trophic interactions (e.g., Abrams, 1992, 1995). Moreover, most of the density-dependent processes occur within a season, not among seasons, so the modeling framework must account for within as well as between year interactions. Ecologists have rarely used analytical frameworks that include this kind of structure when exploring adaptive consumer behavior and food web interactions (Bolker et al., 2003). We suggest that this may be a profitable, new route for theory development in our endeavor to make ecological theory more congruent with biological reality.

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