TOP PREDATORS CONSTRAIN THE HABITAT SELECTION GAMES PLAYED BY INTERMEDIATE PREDATORS AND THEIR PREY

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ABSTRACT

Effects of predators on prey habitat selection, and reciprocal effects of prey on predator habitat selection, have been analyzed using game theory. In the absence of predators, models predict that prey (e.g., herbivores) will aggregate strongly in habitats where their resources (e.g., plants) are abundant. However, game theoretic models predict that in the presence of predators, prey use of resource-rich habitats declines. Paradoxically, it is instead predators that are predicted to be mostly strongly aggregated in areas where the prey's resources (plants) are abundant, even though the predators themselves do not utilize these resources. This striking result has been dubbed the "leapfrog effect" by Sih (1998, 2004). Here I explore the possibility that predictions for predator and prey habitat selection are sensitive to the assumption that predators forage free from any predation risk of their own. I contrast the predictions of a 3-trophic level model with those of a 4-trophic level model, and show that incorporating the constraint imposed on "intermediate predator" foraging behavior by the risk of attack from "top predators" can produce substantial changes in model predictions. Most importantly, the leapfrog effect is largely eliminated. Top predators impose important constraints on foraging decisions made by intermediate predators, opening up new solutions for herbivores.

INTRODUCTION

It is now well established that prey may detect the presence of their predators and respond by changing their behavior, morphology, physiology, or development to reduce their risk of predation (Agrawal, 2001; Relyea, 2003). Predators, in turn, may respond to this adaptive plasticity in their prey, changing their foraging behavior and potentially evoking further responses from their prey (Lima, 2002). Such reciprocal interactions between predators and prey have been analyzed using game theory (Iwasa, 1982; van Baalen and Sabelis, 1993; Hugie and Dill, 1994; Bouskila et al., 1998; Sih, 1998; Kotler et al., 2002). These game theoretic models generally represent the focal interaction as a 3-species module (e.g., carnivore-herbivore-plant), isolated from the rest of the

community (but see Heithaus, 2001). Predator behavior is predicted to maximize the capture of prey under the key constraint of inducing potentially effective prey defenses.

In some communities, however, predators (which I will now call "intermediate predators") may forage under the risk of attack from their own assemblage of predators ("top predators"). This additional constraint could fundamentally change the outcome of the interaction of the original prey with the intermediate predator, opening up "solutions" for the prey organism that were previously unavailable because of the broad range of foraging options available to the intermediate predator.

How commonly do predators forage under risk from their own predators? Dynamically important predator–predator interactions, which may take the form of intraguild predation (Polis et al., 1989), appear to be widespread in a diverse array of well-studied systems, including freshwater, marine, and above- and belowground terrestrial communities (Polis, 1991; Polis and Strong, 1996; Rosenheim, 1998; Woodward and Hildrew, 2001, 2002; Wardle, 2002). Thus, predators, like their prey, may often need to balance enhanced food intake against increased risk of their own predation when foraging.

My goal here is to explore how the predictions of a habitat selection game played by an intermediate predator and its prey (see reviews by Lima, 2002; Sih, 2004) might change under the influence of a top predator.

A HABITAT SELECTION GAME

A 3-TROPHIC LEVEL IDEAL FREE DISTRIBUTION

To provide a point of comparison, I begin by describing a habitat selection game played across three trophic levels: an immobile basal primary producer resource (density R), which is consumed by an herbivore (density H), which in turn is consumed by a predator (density P) (Fig. 1A). The model is identical to the "more realistic predator–prey game" analyzed by Sih (1998), but assuming a linear functional response for predators. Sih (1998) analyzed how herbivores and predators might distribute them-

A   B

Predator, P Top predator, T

↑   ↑

Herbivore, H Intermediate predator, P

↑   ↑

Plant, R Herbivore, H
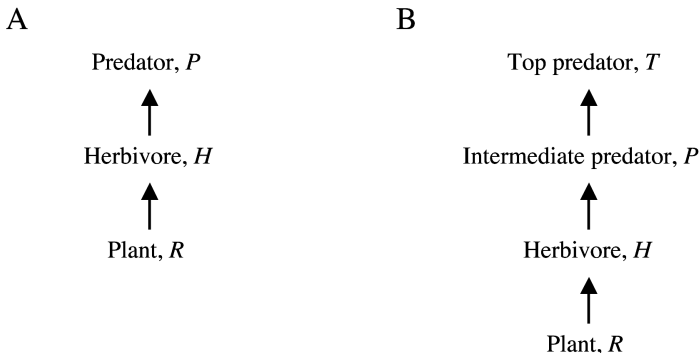
↑

Plant, R

Fig. 1. Trophic interactions modeled in a habitat selection game. (A) The 3-trophic level food chain. (B) The 4-trophic level food chain.

selves in an environment made up of two patches, *a* and *b*, within which resource availability (e.g., plant quality or density) may vary. The model makes the following assumptions: (1) the fitness of the predator is proportional to its feeding rate (f_P), whereas the fitness of the herbivore is proportional to the ratio of its feeding and predation rates (f_H/μ_H); (2) herbivores and predators compete intraspecifically, such that $f_H = R/H^x$, where *x* is the herbivore competition coefficient ($0 \leq x \leq 1$), and $f_P = c_P H/P^y$, where *y* is the predator competition coefficient ($0 \leq y \leq 1$) and c_P is a constant describing the proportion of prey killed per unit time by one predator; (3) the herbivore experiences a predation rate, μ_H = (individual predator feeding rate)(predator density)/ (prey density) = $(c_P H/P^y) \cdot P/H = c_P P^{1-y}$; and (4) the two patches do not differ in their inherent riskiness (i.e., predators capture the same proportion of available prey per unit time in each patch). The simultaneous evolutionarily stable strategy (ESS) (a double ideal free distribution) for predators and herbivores occurs when neither player can increase its fitness by moving between patches. At the ESS, Sih (1998) shows that the herbivore and predator ratios across the two patches are

$$\frac{H_a}{H_b} = \left(\frac{R_a}{R_b}\right)^{\frac{y}{1-y(1-x)}} \tag{1}$$

$$\frac{P_a}{P_b} = \left(\frac{R_a}{R_b}\right)^{\frac{1}{1-y(1-x)}} \tag{2}$$

Following Sih (1998), I use the model to explore three scenarios that provide an overview of the model's predictions.

Scenario 1. The herbivores exhibit "ideal" competition ($x = 1$) while predation is strictly prey-dependent ($y = 0$). Under this scenario, the herbivores are predicted to be distributed uniformly across the two patches ($H_a/H_b = 1$), while the predators match the distribution of the herbivore's food (i.e., the host plant) perfectly ($P_a/P_b = R_a/R_b$). This striking and somewhat counterintuitive "leapfrog effect" is perhaps the most important and consistently observed prediction emerging from game theoretic analyses of predator–prey habitat selection (Iwasa, 1982; van Baalen and Sabelis, 1993; Hugie and Dill, 1994; Sih, 1998; Heithaus, 2001).

Scenario 2. The herbivores exhibit ideal competition ($x = 1$) while predation is ratio-dependent ($y = 1$). Under this scenario, both the herbivores and the predators are predicted to match the distribution of host plant resources perfectly ($H_a/H_b = P_a/P_b = R_a/R_b$).

Scenario 3. Herbivores and predators both exhibit intermediate levels of intraspecific competition. This is likely to be the most realistic of the three scenarios. If we let $x = y$ and allow both to vary between 0 and 1, we can see that herbivore distributions are consistently predicted to undermatch the distribution of their host plants (i.e.,

$H_a/H_b < R_a/R_b$; herbivores aggregate in areas of rich host plant resources, but their degree of aggregation is less than that of their host plants), whereas predators consistently overmatch the distribution of host plant resources ($P_a/P_b > R_a/R_b$; Fig. 2).

The most salient feature of these predictions is that predators often reduce the extent to which herbivores aggregate in areas where their host plant resources are richest. In the absence of predators, herbivores are predicted to aggregate strongly in habitat patches with richer host plant resources: under the strongest intraspecific herbivore competition ("ideal" competition, $x = 1$), herbivores are predicted to match plant resource density, with progressively weaker forms of intraspecific competition leading to progressively stronger overmatching of plant resources. However, predators can block this response. Predators aggregate in plant-rich habitats themselves, producing an elevated risk of predation for herbivores, and essentially preempting their greater use by herbivores. Herbivores are thus relegated to habitat patches with lower resource availability.
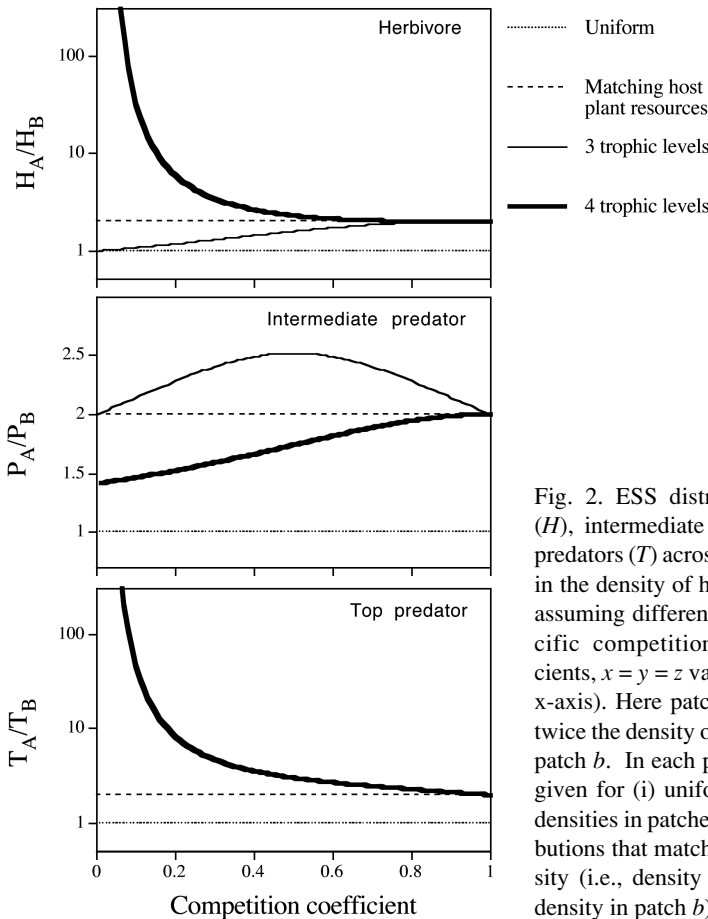

Fig. 2. ESS distributions of herbivores (*H*), intermediate predators (*P*), and top predators (*T*) across two patches that differ in the density of host plant resources, and assuming different intensities of intraspecific competition (competition coefficients, $x = y = z$ vary from 0 to 1 along the x-axis). Here patch *a* is assumed to have twice the density of host plant resources as patch *b*. In each panel reference lines are given for (i) uniform distributions (equal densities in patches *a* and *b*) and (ii) distributions that match the ratios of plant density (i.e., density in patch *a* = twice the density in patch *b*).

A 4-TROPHIC LEVEL IDEAL FREE DISTRIBUTION

Here I extend Sih's (1998) model to explore a habitat selection game played by predators and prey across four trophic levels. For example, we can think of the system as including a top predator (density T) that consumes an intermediate predator (density P), which in turn consumes an herbivore (density H) that feeds on the primary producer resource (density R) (Fig. 1B). As above, I assume that the primary producer is immobile, and that the herbivore, intermediate predator, and top predator can move freely in an environment made up of two patches, a and b, within which resource availability (e.g., plant density) may vary.

To find the joint ESS distribution of consumers across the two patches, I follow Sih (1998) in seeking the distribution in which each individual top predator, intermediate predator, and herbivore has an equal expected fitness in patches a and b. Under this condition, no individual can elevate its fitness by moving from one patch to the other, and thus an equilibrium distribution is achieved. The fitness of the top predator is assumed to be proportional to its feeding rate (f_T), whereas the fitnesses of the intermediate predator and the herbivore are assumed to be proportional to the ratios of their feeding rate and predation rate (f_P/μ_P and f_H/μ_H, respectively).

As in the 3-trophic level model, I incorporate intraspecific competition for the herbivore, intermediate predator, and top predator by letting $f_H = R/H^x$, $f_P = c_P H/P^y$, and $f_T = c_T P/T^z$, where x, y, and z are the competition coefficients for each consumer and c_P and c_T are the predation constants (proportion of prey killed per unit time by one predator).

Assuming again that the two patches do not differ in their inherent riskiness, at the ESS the top predator's feeding rate in patch a ($f_{T,a}$) must equal its feeding rate in patch b ($f_{T,b}$):

$$f_{T,a} = f_{T,b}$$

$$c_T \frac{P_a}{T_a^z} = c_T \frac{P_b}{T_b^z}$$

$$\frac{T_a}{T_b} = \left(\frac{P_a}{P_b}\right)^{\frac{1}{z}} \tag{3}$$

Thus, at the ESS, for all values of $z < 1$, any time the intermediate predator deviates from a uniform density distribution (i.e., any time $P_a \neq P_b$), the top predator will aggregate in the patch type favored by the intermediate predator, and indeed will achieve a higher proportional representation there than does the intermediate predator. This foreshadows the constraining role that top predators will play on the foraging strategies adopted by intermediate predators.

Consider now the intermediate predator. For the intermediate predator to achieve equal (feeding rate)/(predation risk) ratios in the two patches, we must have:

$$f_{P,a}/\mu_{P,a} = f_{P,b}/\mu_{P,b}$$

$$\frac{c_P \dfrac{H_a}{P_a^y}}{\left(c_T T_a^{1-z}\right)} = \frac{c_P \dfrac{H_b}{P_b^y}}{\left(c_T T_b^{1-z}\right)}$$

where the numerator is the intermediate predator's feeding rate and the denominator is the risk that the intermediate predator will be eaten by the top predator. Simplifying and using the result from eq 3, we obtain:

$$\frac{P_a}{P_b} = \left(\frac{H_a}{H_b}\right)^{\frac{z}{1-z(1-y)}} \tag{4}$$

Because $0 \leq z/(1 - z(1 - y)) \leq 1.0$ for any value of y and z, the model predicts that intermediate predators will generally undermatch the distribution of their herbivore prey.

Finally, for the herbivores to maintain equal feeding rate/predation risk ratios in the two patches, we have:

$$f_{H,a}/\mu_{H,a} = f_{H,b}/\mu_{H,b}$$

$$\frac{\dfrac{R_a}{H_a^x}}{\left(c_P P_a^{1-y}\right)} = \frac{\dfrac{R_b}{H_b^x}}{\left(c_P P_b^{1-y}\right)}$$

where the numerator is the herbivore's feeding rate and the denominator is the risk that the herbivore will be eaten by the intermediate predator. Simplifying and using the result from eq 4, we obtain:

$$\frac{H_a}{H_b} = \left(\frac{R_a}{R_b}\right)^{\frac{1-z(1-y)}{z(1-x)(1-y)+x}} \tag{5}$$

We can now use the results (eqs 3, 4, and 5) to express the ESS distributions of the intermediate and top predators in terms of the ratios of primary producer resources in the two patches:

$$\frac{P_a}{P_b} = \left(\frac{R_a}{R_b}\right)^{\frac{z}{z(1-x)(1-y)+x}} \tag{6}$$

$$\frac{T_a}{T_b} = \left(\frac{R_a}{R_b}\right)^{\frac{1}{z(1-x)(1-y)+x}} \tag{7}$$

We can now contrast the predictions of the 4-trophic level model with those of the 3-trophic level model, using the three scenarios described above.

Scenario 1. The herbivores exhibit "ideal" competition ($x = 1$) while predation is strictly prey-dependent ($y = z = 0$). With four trophic levels, the herbivores are predicted to match the distribution of their host plant resources ($H_a/H_b = R_a/R_b$). It is instead the intermediate predators that are now predicted to be uniformly distributed ($P_a/P_b = 1$), under the constraint imposed by the top predators, whose distribution matches that of the herbivore's food ($T_a/T_b = R_a/R_b$). Thus, the paradoxical "leapfrog effect" observed in the 3-trophic level model, wherein the herbivore's distribution is decoupled from that of its host plant, and the herbivore's predator instead tracks the distribution of host plant resources, is eliminated. Adding a top predator to the system reverses the habitat selection predictions for each of the two lower trophic levels. The logic of the model is simple, and suggests that herbivores will track the distribution of their host plants for communities with even numbers of trophic levels, but will be uniformly distributed for communities with odd numbers of trophic levels.

Scenario 2. The herbivores exhibit ideal competition ($x = 1$) while predation is ratio-dependent ($y = z = 1$). Under this scenario, the herbivores, intermediate predators, and top predators are all predicted to match the distribution of host plant resources perfectly ($H_a/H_b = P_a/P_b = T_a/T_b = R_a/R_b$). Model predictions for ideal competition are thus completely insensitive to the number of trophic levels present.

Scenario 3. Herbivores and predators both exhibit intermediate levels of intraspecific competition. As noted above, this is the most general and realistic of the three scenarios. If we let $x = y = z$ and allow these competition coefficients to vary between 0 and 1, we can see that the 4-trophic level model makes very different predictions from those made by the 3-trophic level model (Fig. 2). Herbivores now overmatch the distribution of their host plant resources, rather than undermatching them. Intermediate predators are constrained to undermatch their herbivore prey (and the underlying host plant resources), because the top predators overmatch both the herbivores and the host plant distributions.

Finally, given the focus of this paper on the effect of the top predator, it is important to allow z, the competition coefficient for the top predator, to vary independently of x and y, and see how this affects the model predictions. First, if we let $z = 0$, top predators show no intraspecific competition and we expect them to have their maximum effect on habitat selection decisions made by intermediate predators. This is the case. As is clear from an inspection of eqs 5–7, and letting $x = y$, the distribution of the intermediate predator is always predicted to be uniform, whereas the herbivores and top predators show identical distributions, ranging from total aggregation in the plant-rich patch ($x = y = 0$) to perfect matching of plant resources ($x = y = 1$). Second, if we let $z = 1$, top predators show maximum intraspecific competition, and we expect them to exert their minimum effect on habitat selection decisions made by intermediate predators. This is the case. As is clear from inspection of eqs 6 and 7, the distributions of the intermediate predator and the top predator will be identical to each other. If $x = y = 0$, the

herbivore will be distributed uniformly and both predators will match the host plant distribution perfectly (the "leapfrog effect" appears for both predator trophic levels). If $0 < x = y < 1$, the herbivore aggregates in the richer habitat, but undermatches host plant resources, whereas both predators overmatch host plant resources. And, if $x = y = 1$, we return to Scenario 3, where all three players match host plant resources perfectly. Because z controls the strength of the top predator's impact on the intermediate predator, with smaller values of z the top predator generates stronger constraints on intermediate predator foraging. Indeed, for $0 < x = y < 1$, the leapfrog effect, wherein intermediate predators are aggregated in plant-rich patches more strongly than are herbivores, is completely eliminated for $z < 0.5$ and appears only for some values of x and y when $z > 0.5$ (data not shown).

The most salient prediction of the 4-trophic level model is that the inclusion of top predators in the model largely reverses the counterintuitive leapfrog effect observed in the 3-trophic level model. Predators that consume only herbivores no longer track the spatial distribution of host plants more strongly than do the herbivores that actually eat the plants. Instead, top predators impose a key constraint on the habitat selection decisions made by intermediate predators, opening up new foraging options for herbivores.

DISCUSSION

Models of reciprocal interactions of predators and prey have generally analyzed the interaction as a two-species module, isolated from the rest of the community in which they are imbedded. With such a formulation there is a fundamental asymmetry between the constraints experienced by predators and their prey: predators maximize their fitness simply by maximizing their food intake, whereas prey must balance food intake with their risk of predation. However, real food webs are speciose and highly complex, and virtually all predators forage under the risk of attack by their own predators. Thus, the foraging strategies of predators may evolve under constraints that are quite similar to those experienced by their herbivore prey. In both cases, increased foraging efficiency must be balanced against exposure to increased risk of predation. Here I have analyzed a very simple model incorporating this sort of dynamic, a 4-trophic level model in which an immobile resource (e.g., a plant) is consumed by a prey species (e.g., an herbivore) that is attacked by an intermediate predator, which is finally attacked by a top predator. The model demonstrates that constraints imposed on intermediate predator foraging may provide new opportunities for the herbivore to forage in a resource-rich environment. In particular, the model reverses a dominant and paradoxical result of game theoretic treatments of habitat selection by predators and prey, the leapfrog effect, wherein predators aggregate more strongly in plant-rich habitats than do their prey, even though the predators cannot feed on the plants themselves. With the 4-trophic level model, top predators aggregate strongly in regions of high plant density, constraining intermediate predators from aggregating there, and thus opening up this rich foraging habitat to herbivores.

As noted by Lima (2002), many of the assumptions of habitat selection game models can be questioned, and predictions can be quite sensitive to the exact formulation of the model. A number of factors that are probably important in most predator–prey interactions, such as state-dependent behavior, limited information, and group defensive behavior of prey, are excluded from my model. Another key simplification of my model is the assumption of stacked specialists (e.g., the top predator eats only the intermediate predator, and not the herbivore or any other resources in the environment). Although such species modules do exist (e.g., an herbivore, its specialist primary parasitoid, and a specialist hyperparasitoid; Ayal and Green (1993)), many predators are generalized in their diets to one degree or another. As predator diets increase in breadth, their habitat selection decisions will become increasingly decoupled from the habitat selection decisions of any one species member of their prey species set. As discussed by Heithaus (2001) and Lima (2002), this reduces the "game" context of the interaction, and moves us towards the more familiar situation of a prey organism making habitat selection decisions given a relatively fixed risk of predation in different habitat patches (Mangel and Clark, 1988). Furthermore, whereas my model assigns what is probably a realistic risk of predation to the intermediate predator, it assumes that the top predator is itself free of predation risk. This simply "kicks the can" up one trophic level—not an entirely satisfying arrangement. The qualitative message of the model is, nevertheless, clear: When predators must themselves forage under the constraint of predation risk, their ability to constrain the foraging options of their prey is reduced. When this key asymmetry between predator and prey is eliminated from the model, the most paradoxical model prediction, the leapfrog effect, largely disappears.

Top predators may not only constrain the habitat selection decisions of intermediate predators, but also may act to limit their overall level of foraging activity. For example, many herbivorous insects and mites can feed with little or no movement, because they live right on their host plant resource. In such a system, an intermediate predator must forage actively to encounter prey, but in so doing may enhance its risk of encountering top predators, including sit-and-wait predators (Rosenheim and Corbett, 2003). Under such a scenario, the herbivore may benefit from an indirect mutualism with the top predator, which may suppress populations of the intermediate predator or limit their ability to forage actively for prey (Rosenheim et al., in press). A pervasive risk of predation means that games played by predators and their prey may often be observed and reshaped by other hungry consumers.

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REFERENCES

Agrawal, A.A. 2001. Phenotypic plasticity in the interactions and evolution of species. Science 294: 321–326.

Ayal, Y., Green, R. F. 1993. Optimal egg distribution among host patches for parasitoids subject to attack by hyperparasitoids. Am. Nat. 141: 120–138.

Bouskila, A., Robinson, M.E., Roitberg, B.D., Tenhumberg, B. 1998. Life-history decisions under predation risk: importance of a game perspective. Evol. Ecol. 12: 701–715.

Heithaus, M.R. 2001. Habitat selection by predators and prey in communities with asymmetrical intraguild predation. Oikos 92: 542–554.

Hugie, D.M., Dill, L.M. 1994. Fish and game: a game theoretic approach to habitat selection by predators and prey. J. Fish Biol. 45(A): 151–169.

Iwasa, Y. 1982. Vertical migration of zooplankton: a game between predator and prey. Am. Nat. 120: 171–180.

Kotler, B.P., Brown, J.S., Dall, S.R.X., Gresser, S., Ganey, D., Bouskila, A. 2002. Foraging games between gerbils and their predators: temporal dynamics of resource depletion and apprehension in gerbils. Evol. Ecol. Res. 4: 495–518.

Lima, S.L. 2002. Putting predators back into behavioral predator-prey interactions. Trends Ecol. Evol. 17: 70–75.

Mangel, M., Clark, C.W. 1988. Dynamic modeling in behavioral ecology. Princeton University Press, Princeton, New Jersey.

Polis, G.A. 1991. Complex trophic interactions in deserts: an empirical critique of food web theory. Am. Nat. 138: 123–155.

Polis, G.A., Strong, D.R. 1996. Food web complexity and community dynamics. Am. Nat. 147: 813–846.

Polis, G.A., Myers, C.A., Holt, R.D. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. Ann. Rev. Ecol. Syst. 20: 297–330.

Relyea, R.A. 2003. How prey respond to combined predators: a review and an empirical test. Ecology 84: 1827–1839.

Rosenheim, J.A. 1998. Higher-order predators and the regulation of insect herbivore populations. Annu. Rev. Entomol. 43: 421–447.

Rosenheim, J.A., Corbett, A. 2003. Omnivory and the indeterminacy of predator function: can a knowledge of foraging behavior help? Ecology 84: 2538–2548.

Rosenheim, J.A., Glik, T.E., Goeriz, R.E., Rämert, B. Linking a predator's foraging behavior with its effects on herbivore population suppression. Ecology, in press.

Sih, A. 1998. Game theory and predator-prey response races. In: Dugatkin, L.A., Reeve, H.K., eds. Game theory and animal behavior. Oxford University Press, New York, pp. 221–238.

Sih, A. 2004. Predator prey space use as an emergent outcome of a behavioral response race. In: Barbosa, P., Castellanos, I., eds. Ecology of predator–prey interactions. Oxford University Press, Oxford, UK. in press.

van Baalen, M., Sabelis, M. W. 1993. Coevolution of patch selection strategies of predator and prey and the consequences for ecological stability. Am. Nat. 142: 646–670.

Wardle, D.A. 2002. Communities and ecosystems: linking the aboveground and belowground components. Princeton University Press, Princeton, 392 pp.

Woodward, G., Hildrew, A.G. 2001. Invasion of a stream food web by a new top predator. J. Anim. Ecol. 70: 273–288.

Woodward, G., Hildrew, A.G. 2002. Body-size determinants of niche overlap and intraguild predation within a complex food web. J. Anim. Ecol. 71: 1063–1074.