

OMNIVORY AND THE INDETERMINACY OF PREDATOR FUNCTION: CAN A KNOWLEDGE OF FORAGING BEHAVIOR HELP?

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Abstract. In 1960, N. G. Hairston, F. E. Smith, and L. B. Slobodkin proposed that terrestrial ecosystems are composed of three trophic levels: predators, herbivores, and plants. Under this model, predators act in a predictable manner to suppress herbivore populations, freeing plant populations from the strong effects of herbivory. However, empirical work has recently demonstrated that many predators exhibit trophic-level omnivory, consuming both herbivores and other predators. This creates a problem for terrestrial ecologists: predator function is indeterminate, because predators may operate from either the third trophic level (“intermediate predators”) or the fourth trophic level (“omnivorous top predators”) and have opposite effects on herbivore and plant populations. Here we attempt to use a basic understanding of the foraging behavior of predators and their prey to make predictions about predator function. A simulation model produces four predictions: (1) actively foraging predators may be effective regulators of sedentary herbivore populations; (2) sit-and-wait predators are unlikely to suppress populations of sedentary herbivores, but may act as omnivorous top predators, suppressing populations of widely foraging intermediate predators and thereby increasing herbivore densities; (3) among widely foraging predators attacking a common herbivore prey, predators that are large relative to the body size of their prey will be more mobile, and therefore more vulnerable to predation by sit-and-wait omnivores, compared to predators that are similar in size to their prey; and (4) widely foraging omnivores, unlike sit-and-wait omnivores, are unlikely to disrupt herbivore population suppression generated by intermediate predators, and may instead enhance herbivore suppression. These predictions appear to explain the results of several experimental studies of the function of predatory arthropods in terrestrial ecosystems.

Key words: *biological control; food webs; foraging behavior; generalist predator; herbivore population suppression; higher order predation; indirect effects; individual-based model; intraguild predation; omnivory; trophic cascades.*

INTRODUCTION

In a paper that has proven to be controversial and yet highly influential, Hairston et al. (1960; see also Slobodkin et al. 1967, Hairston and Hairston 1993, 1997) proposed that terrestrial ecosystems are composed of three functionally discrete trophic levels: plants, herbivores, and predators. Under this model, predators suppress populations of herbivores to low levels, freeing plants from the strong effects of herbivory, and producing a world that is predominantly “green.” This model of terrestrial ecosystem function has been criticized on several grounds, with especial attention given to the complementary influences of variable plant quality and plant defenses on herbivore population dynamics (Murdoch 1966, Polis 1999). Less questioned until recently was the thesis that terrestrial predators function in a relatively predictable manner to suppress herbivore populations.

An important shift in our view of terrestrial ecosystems has, however, occurred over the past two decades

as workers have reported the prevalence and importance of predators that consume not only herbivores, but also other predators (reviewed by Polis et al. 1989, Polis 1991, Rosenheim et al. 1995, Rosenheim 1998; this phenomenon has been variously labeled “trophic level omnivory,” “intraguild predation,” “higher-order predation,” or “hyperpredation”). These observations have supported new proposals for the general structure and function of terrestrial ecosystems that incorporate the possibility that predators may function primarily from the third trophic level, suppressing herbivore populations, or primarily from the fourth trophic level, suppressing populations of intermediate predators and thereby potentially releasing herbivore populations from “top down” control (Hurd and Eisenberg 1990, Polis 1991, 1999, Wise 1993, Polis and Strong 1996, Janssen et al. 1998, Rosenheim 1998, Halaj and Wise 2001).

The new models create a problem for ecologists: the indeterminacy of predator function. To address this problem of uncertain predator function, we need to ask: what is it that makes a predator function as a consumer of herbivores vs. a consumer of other predators? This question may not have a simple answer. Predation rates are shaped by many factors, including encounter prob-

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abilities, attack probabilities, capture success, and consumption probabilities, and each of these factors may in turn be influenced by traits of the predator, the prey, and their shared environment (Sih 1993). Researchers exploring predator–predator interactions have indeed demonstrated important roles for habitat structure and physical refuges (MacRae and Croft 1996, Agrawal and Karban 1997, Roda et al. 2000, Norton et al. 2001, Finke and Denno 2002), active prey defenses (Lucas et al. 1998, Snyder and Ives 2001), and predator preferences (Colfer and Rosenheim 2001). Many omnivorous predators are, however, also extreme generalists, consuming any prey that they can capture. For such predators, encounter frequencies with different prey species often become the overriding influence on diet. For this reason, we focus here on determinants of encounter frequency between predators and prey.

Encounter probabilities between predators and prey are heavily influenced by their foraging behaviors. Pianka (1966) introduced one of the most basic descriptors of predator foraging mode when he described the difference between widely foraging predators and sit-and-wait predators. Although these two strategies are probably best viewed as the ends of a continuum of foraging strategies (Perry 1999), both verbal models (Turnbull 1973, Huey and Pianka 1981) and mathematical treatments (Gerritsen and Strickler 1977) predict that predator foraging mode shapes the types of prey that are encountered and potentially consumed. Sedentary prey are consumed by widely foraging “intermediate” predators, which may in turn be captured by sit-and-wait “top” predators; thus “crossovers” in foraging mode occur as one ascends the food chain. Mobile prey, in contrast, may be consumed by either widely foraging or sit-and-wait predators. These ideas have found widespread acceptance among ecologists studying diverse taxa (reviewed by Perry and Pianka 1997), including predatory arthropods (e.g., Turnbull 1973, Polis and McCormick 1987, Johansson 1993).

In this study, we apply the theory of crossovers in foraging mode to understand the ecological roles of omnivorous predators, including their influence on the population dynamics of terrestrial herbivorous arthropods. Using a simulation model, we extend the theory to include the influence of the relative body sizes of predators and prey. Our simulations produce simple, testable predictions for omnivore function that link foraging behavior with population dynamics and community structure.

METHODS

The simulation model

We employed a stochastic individual-based model to explore the link between the foraging behavior of omnivorous predators and their trophic function. An individual-based model is distinguished from a population-state model by explicitly and separately repre-

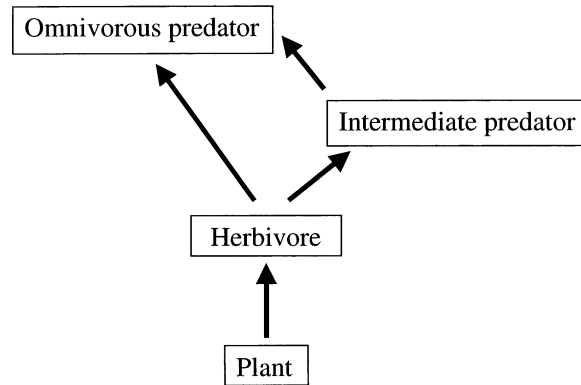


FIG. 1. Trophic web of the arthropod community represented in the simulation model.

sented each individual in the population (DeAngelis and Gross 1992, Judson 1994). The dynamics of the simulated populations and community can then be derived as emergent properties from rules given to individuals governing their movement, feeding, reproduction, and mortality. The individual-based modeling approach is intended to reflect more faithfully the physical reality of the system, and the behavioral rules given to individuals are attempts to simulate actual behavioral traits and variability in those traits.

The model that we developed was designed to represent herbivorous and predatory arthropods foraging on a plant surface. We attempted to ground our model in the real world by choosing parameter values that reflected, at least loosely, the community of predators associated with the herbivorous mite *Tetranychus cinnabarinus* feeding on the foliage of papaya, *Carica papaya* (J. A. Rosenheim, D. D. Limburg, R. G. Colfer, V. Fournier, T. Glik, R. Goeriz, C. L. Hsu, T. E. Leonardo, E. H. Nelson, and B. Rämert, unpublished manuscript). The arthropod community on papaya was useful as a case study because it presented natural contrasts in foraging style (widely foraging vs. sit-and-wait predators) and strong variation in the relative body sizes of predator and prey. The model is general enough, however, that it should allow us to explore predator–prey systems more broadly.

The model community.—We simulated a community (Fig. 1) comprising an herbivore; an intermediate predator, which feeds only on the herbivore; and an omnivorous predator, which can feed on either the herbivore or the intermediate predator. For the papaya case study, the herbivore was *Tetranychus*, a sedentary herbivore that creates small, silk-lined colonies on papaya leaves; two species were present as intermediate predators, both of which are widely foraging specialist consumers of spider mites, *Stethorus siphonulus* (Coleoptera: Coccinellidae) and *Phytoseiulus macropilis* (Acari: Phytoseiidae); and the omnivorous predator was the tangle-web spider *Nesticodes rufipes* (Araneae:

TABLE 1. Baseline set of parameter values used in the simulation model.

Type of individual	Cost of reproduction (resource units)	Walking speed (cm/h)	Move length (cm)				Pause duration (h)	
			Extensive search		Intensive search		Mean	1 SD
			Mean	1 SD	Mean	1 SD		
Herbivore	40	0.5	0.5	0.125	10	2.5
Intermediate predator	1000	10	5	1.25	0.2	0.05	0	0
Omnivorous predator	...	0	0	0

Theridiidae), which detects prey with its web and thus functions as a strict sit-and-wait predator.

The model universe.—The model universe is a simple disk: a two-dimensional, circular surface with a diameter of 30 cm, approximately the size of a papaya leaf. Herbivores experience the disk as a leaf surface, in that they can always obtain food resources at their current location. Predators experience the disk as a neutral, flat surface on which they forage for animal prey. If the edge of the disk is encountered, then the individual simply turns around.

Mortality, reproduction, and resources.—To make the interpretation of our model as simple as possible, we made several simplifying assumptions. First, for the first three sets of simulations, we assumed that the omnivorous predator did not move or reproduce; this choice was appropriate for the papaya case study, because the spider *Nesticodes* is a strict sit-and-wait predator and has a life cycle much longer than the 280 h duration of the simulation (which we chose to match the duration of our manipulative experiments; see J. A. Rosenheim, D. D. Limburg, R. G. Colfer, V. Fournier, T. Glik, R. Goeriz, C. L. Hsu, T. E. Leonardo, E. H. Nelson, and B. Rämert, *unpublished manuscript*). This assumption was relaxed for the last set of simulations, in which we allowed the omnivorous top predator to forage widely and reproduce. Second, for all members of the community, we excluded sources of mortality other than predation. Third, we treated the model universe as a closed community, with no immigration or emigration. Finally, we did not represent age structure in the model; all individuals are considered to be adults from their moment of birth.

All individuals possess a resource pool that is augmented by feeding. When the pool exceeds a given threshold, a birth occurs and the pool is decreased by an amount that represents the cost of reproduction. An individual starts life with the same (x,y) coordinates as its parent at the moment of birth. For herbivores, resources are present in the substrate; whenever they are stationary they can feed. The mean feeding rate is constant unless the size of the population exceeds the carrying capacity for the universe ($N = 1000$ individuals), at which time the feeding rate becomes zero. The actual feeding rate realized by an individual was randomly sampled from a normal distribution having a standard deviation of 10% about the mean. This density-dependent herbivore feeding rate explicitly links our model

with the primary producer trophic level; however, we did not attempt to extend our model to make predictions for plant performance or population dynamics. To ensure that our use of a simple step function for herbivore density dependence did not skew our results, we also evaluated a more complicated form of herbivore density dependence, in which the feeding rate declines by a factor of $(1 - [\text{population size}/\text{carrying capacity}]^2)$. Simulations using this more complicated function produced results very similar to those generated with the simpler step function; results using the step function are reported here.

Predators acquire resources only when they encounter and consume other individuals. When a prey is consumed, the resource pool of the predator is augmented by a constant representing the food value of the prey.

Movement.—With one exception noted below (“Intensive search”), individuals move by executing a random walk punctuated by pauses. The trajectory of an individual during its lifetime consists of a series of “movement sequences,” each consisting of a straight-line displacement followed by a pause; the angle of movement, the distance of the displacement, and the duration of the pause are randomly chosen at the beginning of each movement sequence. The angle of movement is randomly chosen from a uniform distribution ($0-360^\circ$). The distance of the move and the duration of the pause are randomly chosen from a normal distribution of constant mean and standard deviation for the type of individual, e.g., herbivore, intermediate predator, or omnivorous predator (Table 1). The number of time intervals required to traverse the distance chosen is dependent on the individual’s speed, which is determined by its type.

Predator foraging rules and encounters.—All predators possess an “area of discovery” defined as a circle of fixed radius centered on their current location. An intermediate-level predator will detect as potential prey only herbivores that are in its area of discovery; it will consume the closest herbivore within the area. An omnivorous predator detects both intermediate-level predators and herbivores within its area of discovery and will consume the closest individual, regardless of whether it is an herbivore or an intermediate predator.

We implemented three foraging modes for mobile predators:

1) *Extensive search.* The predator is walking at a relatively high speed. The direction of movement for

TABLE 1. Extended.

Feeding rate (resource units/h)	Area of discovery radius (cm)	Value as food (resource units)	Handling time (h)
5	...	10	...
...	0.5	50	0.1
...	2	...	0.25

a new movement sequence is chosen from a 360° range, i.e., the predator executes a pure random walk. A predator shifts from extensive search into handling mode upon encountering a prey.

2) *Handling*. The predator is handling (e.g., ingesting or digesting) a prey item. The predator remains stationary and does not consume other prey within its area of discovery. A predator shifts from handling into intensive search mode upon completion of a fixed handling time.

3) *Intensive search*. The predator is walking at a relatively low speed and engages in a correlated random walk (Kareiva and Shigesada 1983), where the angle of movement is chosen from a normal distribution with mean equal to the current angle of movement and standard deviation of 28.6° (0.5 radians). This foraging mode is designed to represent the local search that widely foraging predators often express once within a patch of prey (Bell 1991). A predator shifts from intensive search mode into extensive search mode once 0.1 h of search time has passed without encountering a prey.

Intermediate predator body size.—To represent predators of varying body sizes attacking a common prey, we varied the prey handling time and the cost of reproduction. Handling time reflects body size because larger predators can consume and digest more individuals of a given prey per unit time than can smaller predators, largely because their larger gut contents mean that many prey can be digested simultaneously. The cost of reproduction reflects body size, because larger predators must consume more prey to produce a copy of themselves than do smaller predators. Handling time and the cost of reproduction were varied in concert so that the reproductive rate of a food-satiated intermediate predator was held constant. Although body size may also be associated with other trait differences (e.g., walking speed, or the area of discovery radius), we held all other parameters constant for predators of different sizes to isolate what we consider to be the most essential features of larger predators, namely that they must eat more prey to reproduce, and they process individual prey more quickly.

Implementing the model.—A simulation update occurs in two phases. First, each individual engages in all activities other than predation; these include, in order, reproduction, feeding by herbivores, and movement. Populations are updated as a group; the omnivorous predator population, the intermediate-level predator population, then the herbivore population. Next, all predatory interactions are resolved, with omnivorous predators feeding before intermediate predators. Since there is only one direction of predation in any one interaction, no unintended advantage is afforded the omnivorous predator by virtue of its “going first.” Time intervals between updates are short relative to the walking speed and area-of-discovery of predators; thus, predators are, in effect, continuously checking their area of discovery for potential prey as they forage.

The simulation is initialized at time 0 with 10 herbivores. After allowing the herbivores 25 h to feed and initiate small “colonies” on the leaf surface, predators ($N = 4$, with a single exception noted in the *Results* section) are added to the system. These predators are initialized by assigning (x,y) coordinates randomly throughout the universe. Predators are initialized with a single unit of resources in their resource pool. Individuals immediately initiate a movement sequence; thus angle of movement, movement distance, and pause duration are randomized at initialization.

The model was compiled with Microsoft Visual C++ (Microsoft, Redmond, Washington, USA). Pseudo-random numbers were generated using the “RAN0” routine and normal deviates were generated using the “GASDEV” routine in Press et al. (1988). A copy of the programming code is available upon request from JAR.

Simulations.—We report here four sets of simulations, which examined (1) the influence of intermediate predator mobility in the presence of a sedentary herbivore population and a sit-and-wait omnivore, (2) the influence of herbivore mobility in the presence of a mobile intermediate predator and a sit-and-wait omnivore, (3) the influence of the body size of a widely foraging intermediate predator in the presence of a sedentary herbivore and a sit-and-wait omnivore, and (4) the influence of the body size of a widely foraging intermediate predator in the presence of a widely foraging omnivore and either a sedentary or a mobile herbivore. For each set of simulations, we applied four “treatments”: (1) herbivores alone, (2) herbivores plus the intermediate predator, (3) herbivores plus the omnivorous predator, and (4) herbivores plus both the intermediate and omnivorous predators. All simulations were run for 280 h, with 75 iterations per hour, and were replicated 10 times for each parameter set (see Table 1). We report the mean herbivore density over the 280-h simulation as our primary index of herbivore population dynamics. Thus, our focus is on short-term population suppression, rather than equilibrium densities or the stability properties of the community. Although it is useful to understand equilibrium dynamics (e.g., Holt and Polis 1997), transient dynamics are also important (Hastings 2001), and are particularly relevant to predator–predator interactions in arthropod com-

munities, which are often highly seasonal or disturbed (e.g., Snyder and Ives 2003).

RESULTS AND DISCUSSION

To apply the notion of crossovers in foraging mode to herbivorous terrestrial arthropods and their associated community of predators, we begin by considering the foraging behavior of the focal herbivore. Many herbivorous arthropods live right on their key food resource: their host plant. Indeed, herbivores often complete their entire immature development on one host plant individual, adopting a parasite-like life style (Price 1980). Our first key observation is that because an individual host plant often represents a large pool of resources relative to the nutritional demands of a developing arthropod, many herbivores can be relatively sedentary. Hawkins (1994) identified seven feeding styles by herbivores, of which five involve high degrees of concealment within the host plant or soil, with minimal opportunities for movement (rollers/webbers, leaf miners, gallers, borers, root feeders), leaving only two groups with any significant opportunity for movement (external feeders and case bearers). Many of the external feeders, like the spider mites in our case study, may still be highly sedentary.

Our first set of simulations therefore focused on a sedentary herbivore population, and explored the consequences of predator foraging mode for the ability of predators to suppress herbivore densities. We used the base set of parameters shown in Table 1, and varied predator foraging mode by adjusting the duration of pauses between movement bouts (widely foraging predators have no pauses; sit-and-wait predators have lengthy pauses). Our simulations supported the most basic predictions of Gerritsen and Strickler's (1977) mathematical model of encounter frequencies and Huey and Pianka's (1981) verbal model of predator-prey interactions: a widely foraging intermediate predator can suppress a sedentary prey population effectively, whereas a sit-and-wait ambush predator cannot (Fig. 2). This is a highly intuitive result; a sit-and-wait predator and a sedentary herbivore are essentially two immobile objects in space. They do not have a high probability of encountering each other, and therefore the predation rate is negligible. Indeed, searching ability has been a universally appreciated trait for predators employed in biological control programs targeting herbivorous arthropods (Van Driesche and Bellows 1996).

What influence does an omnivorous predator employing a sit-and-wait foraging mode have on the dynamics of this system? When we simulate a community with the omnivore present as the only predator of the sedentary herbivore, we obtain minimal population suppression (Fig. 2). This simply reiterates the result that a sit-and-wait predator is unlikely to function as an effective regulator of a sedentary prey population. Furthermore, if we simulate a three-species community, comprising the herbivore, the intermediate pred-

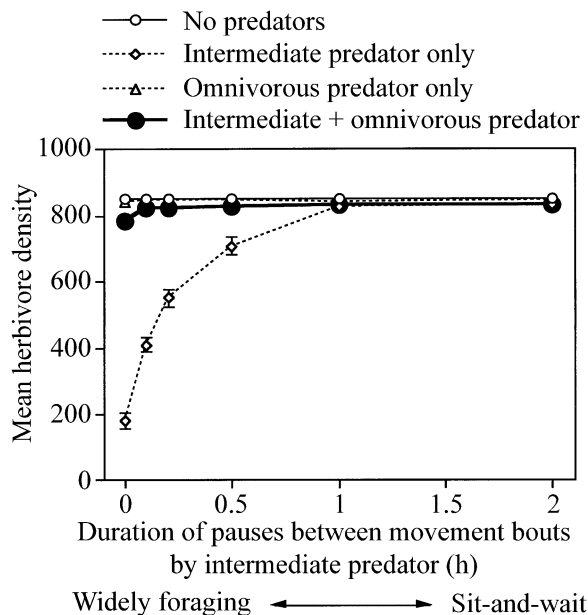


FIG. 2. Influence of intermediate predator mobility on its efficacy as a regulator of a sedentary herbivore population. Mean herbivore densities in the absence of predators ("No predators") and in the presence of only the omnivorous predator ("Omnivorous predator only") are shown as points of reference. The baseline parameters (Table 1) were used except for the pause duration of the intermediate predator, which was varied from 0 (widely foraging) to 2 h (highly sedentary ambush predator). Values are mean \pm 1 SE density of herbivores across 10 replicate simulation runs from time 0 to time 280 h; in some cases, error bars (\pm 1 SE) are too small to be shown.

ator, and the omnivorous predator, we see that the omnivore disrupts the strong suppression of the herbivore population that is generated by the widely foraging intermediate predator (Fig. 2). In this case, the omnivore is acting from the fourth trophic level, releasing the herbivore population from strong top-down control.

Although it may be useful to view herbivorous arthropods as a generally sedentary class of animals, it is certainly true that some herbivores are quite mobile. For instance, some caterpillars and grasshoppers feed as grazers, taking small meals from different plant individuals and even mixing diets of many plant species (Howard et al. 1994, Schmitz and Suttle 2001, Singer and Stireman 2001). Furthermore, even herbivores that are highly sedentary during their immature stages may have a much more mobile, winged adult stage, when females must seek out suitable oviposition sites. We therefore performed simulations to explore the influence of herbivore mobility on the dynamics of our predator-prey system. We modified the base parameter set by assigning the herbivore a 0.5-h feeding period between 1-h movement bouts, and varied the distance moved over the course of the hour from 0.5 cm (sedentary) to 20 cm (highly mobile). A widely foraging intermediate predator produced strong suppression of

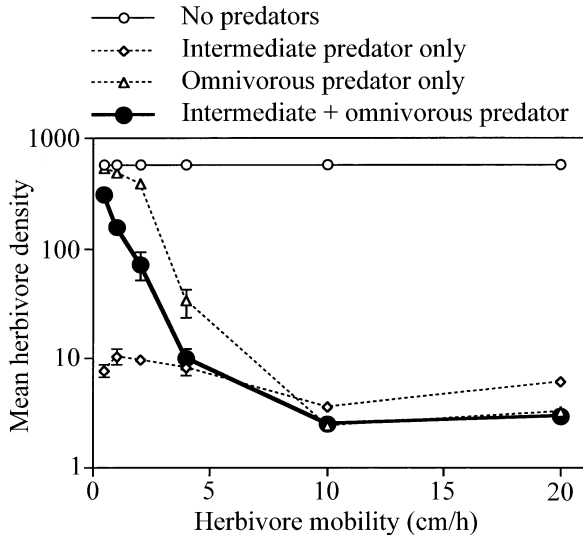


FIG. 3. Influence of herbivore mobility on herbivore population suppression by predators. Curves are shown for the individual and combined abilities of a widely foraging intermediate predator and a sit-and-wait omnivorous top predator to suppress the herbivore's population density. The baseline parameters (Table 1) were used for the predators; herbivore parameters were baseline, with the following modifications: walking speed, 0.5–20 cm/h; move length, 0.5–20 cm (1 SD, 0.125–5 cm); pause duration, 0.5 h (1 SD = 0.125 h). Values are mean \pm 1 SE density of herbivores across 10 replicate simulation runs from time 0 to time 280 h; in some cases, error bars (\pm 1 SE) are too small to be shown.

the herbivore population for all values of herbivore mobility (Fig. 3). The sit-and-wait omnivore, on the other hand, was only effective as a regulator of highly mobile herbivores, a result again consistent with the model of crossovers in foraging mode between predator and prey. Although the combined effects of the intermediate predator and the omnivore produced strong suppression of highly mobile herbivores, relatively sedentary herbivore populations were poorly regulated, reaching densities close to those seen in the absence of any predators (Fig. 3).

Is there, then, no way in which a sedentary herbivore population can be regulated by intermediate predators in the face of a potentially disruptive sit-and-wait omnivore? The papaya case study suggests a possible answer to this question. For widely foraging intermediate predators, and indeed for virtually all foraging animals, a key determinant of exposure to predation risk is the amount of movement (Werner and Anholt 1993, Anholt and Werner 1995, Lima 1998). Movement produces opportunities for encounters with sedentary predators, and also enhances the likelihood of detection by consumers that use visual, vibratory, or auditory cues produced by movement to detect prey (Foelix 1982, Skelly 1994, Meyhöfer and Casas 1999, Eubanks and Denno 2000). A primary determinant of the movement requirements of widely foraging predators is their body size relative to the body size of their prey. Predators

like the beetle *Stethorus*, which are large relative to the size of their prey (spider mites), must consume many prey to develop and reproduce successfully, and thus must move large distances through their foraging environment to harvest many prey. In contrast, a predator like the mite *Phytoseiulus*, which is similar in size to its prey, may be satiated for lengthy periods after consuming just one or a few prey individuals. We may expect, then, that movement requirements will be more modest. This does not mean that a small predator like *Phytoseiulus* cannot be highly mobile; instead, our suggestion is that small predators may not need to use their mobility very often, because their prey needs are smaller.

We used our simulation model to explore the role of body size of the intermediate predator. We represented larger predators by giving them shorter handling times (e.g., *Stethorus* has a handling time of \sim 0.13 h), whereas smaller predators were given longer handling times (e.g., *Phytoseiulus* has a handling time of \sim 4 h; J. A. Rosenheim, D. D. Limburg, R. G. Colfer, V. Fournier, T. Glik, R. Goeriz, C. L. Hsu, T. E. Leonardo, E. H. Nelson, and B. Rämert, *unpublished manuscript*). We varied the cost of reproduction in concert with the prey handling time to hold the reproductive rate of a food-satiated intermediate predator constant (all food-satiated intermediate predators could produce one offspring after 10 h). We emphasize that we did not vary any of the parameters that directly control movement (e.g., walking speed, move lengths, pause durations, etc.); rather, we used the simulation model to explore the possibility that mobility would vary as an emergent property of predator body size through prey handling times.

The simulations showed that predator body size has a major influence on community dynamics. Larger predators, which have shorter prey handling times, did indeed move more than smaller predators (Fig. 4A). This movement translated into an enhanced risk of predation by the sit-and-wait omnivorous predator: the intermediate predators were very strongly over-represented in the diet of the omnivore relative to herbivore prey (Fig. 4B). In the absence of the omnivore, the widely foraging intermediate predator was highly effective as a suppressor of the herbivore population across the full range of handling times (Fig. 4C). Thus, large and small widely foraging predators have similar basic potentials to suppress sedentary herbivore populations. However, herbivore suppression by the larger, more mobile intermediate predators was strongly disrupted by the omnivorous predator, whereas the smaller, less mobile intermediate predator continued to produce substantial levels of herbivore suppression even when the omnivore was present. Thus, the predictions of the crossovers model can be significantly altered by body size effects.

Small-bodied intermediate predators may generate control of herbivore populations that is robust to the

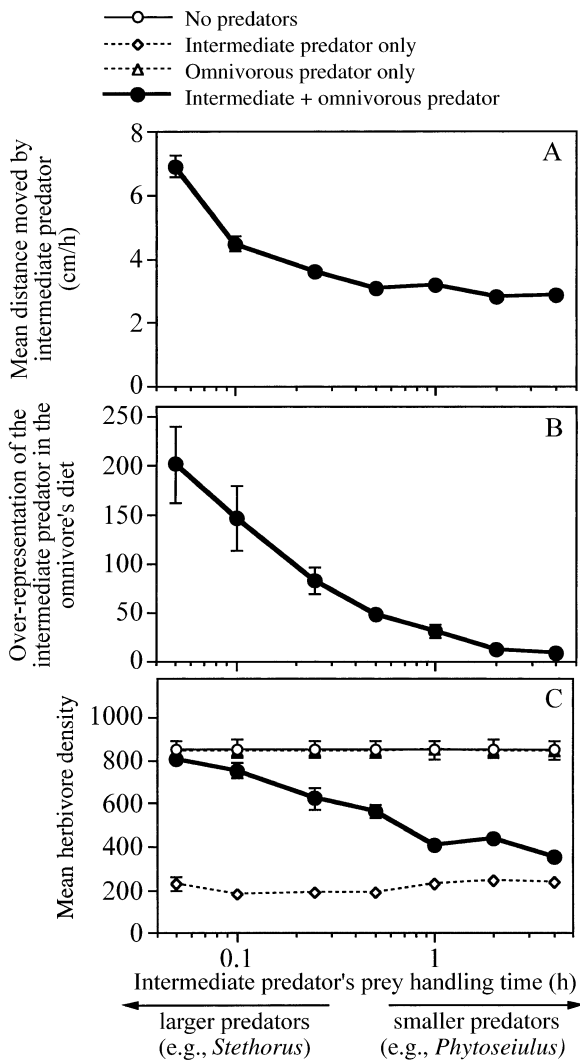


FIG. 4. Influence of prey handling time of the intermediate predator on interactions in a community of an herbivore, an intermediate predator, and a sit-and-wait omnivorous top predator. Predators with body sizes much larger than their prey (e.g., *Stethorus*) have short prey handling times, whereas predators whose body sizes are similar to that of their prey (e.g., *Phytoseiulus*) have long prey handling times. The baseline parameters (Table 1) were used except that the prey handling time was varied from 0.05 to 4 h, and the cost of reproduction was simultaneously varied from 25 to 2000 to maintain a constant maximum possible rate of reproduction. (A) Mobility of the intermediate predator (mean displacement per hour alive for intermediate predators foraging on leaves with prey and omnivorous predators; data shown are means from $t = 0$ until the herbivore population density peaked and began to decline). (B) Over-representation of the intermediate predator in the diet of the omnivorous predator (data shown are means from $t = 0$ until the herbivore population peaked). This was calculated as (proportion of omnivore's diet made up of intermediate predators)/(proportion of all potential prey arthropods present on the leaf that were intermediate predators). (C) Mean herbivore densities in the presence of different combinations of predators. Herbivore densities in the absence of predators ("No predators") and in the presence of only the omnivorous predator ("Omnivorous predator

presence of omnivorous predators by building up large populations, with each member of the population eating only a relatively small number of prey. For example, small predators with a 4-h handling time ate only 4.04 ± 0.03 (mean ± 1 SE) prey per capita on average, but developed large populations (mean population size of 614 ± 11 individuals over the course of the 280-h simulation). An intermediate predator that is larger-bodied may be able to consume many more prey per capita, but the movement that is required to find so many prey may expose them to such intense predation risks at the hands of omnivorous predators that they rarely survive to reproduce. For example, when we simulated a large predator with a prey handling time of 0.05 h, each predator consumed an average of 194 ± 10 prey, but predator populations declined from the starting population of four individuals and averaged only 1.4 ± 0.16 individuals over the course of the simulation. Despite the large per capita prey consumption, the population of these larger-bodied predators was unable to suppress *Tetranychus* populations in the presence of an omnivorous predator.

Finally, what level of herbivore population suppression do we expect if both the intermediate predator and the omnivorous top predator are widely foraging? The papaya system motivates a consideration of this question because one of the "specialist" spider mite predators, *Stethorus*, also eats the eggs and motile stages of the other specialist spider mite predator, *Phytoseiulus*. The simulation model suggests that a widely foraging omnivore functions very differently from the sit-and-wait omnivore explored in the earlier simulations: the omnivore no longer disrupts the herbivore population suppression generated by the intermediate predator, but instead produces a similar or a somewhat greater level of suppression when present in combination with the intermediate predator (Fig. 5). This result holds for both sedentary (Fig. 5A) and mobile herbivores (Fig. 5B), and is observed across a wide range of intermediate predator body sizes. Thus, at least under the simple scenario explored here, in which the intermediate predator and the omnivore have similar abilities to suppress the herbivore population when present singly and the omnivore expresses no preference for either prey type (herbivore vs. intermediate predator), we do not expect herbivore populations to escape from top-down control when a widely foraging omnivore is added to the system.

GENERAL DISCUSSION

Our study is an attempt to grapple with the indeterminacy of omnivorous predator function. Our model

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only") are shown as points of reference. Values are means ± 1 SE density of herbivores across 10 replicate simulation runs from time 0 to time 280 h; in some cases, error bars (± 1 SE) are too small to be shown.

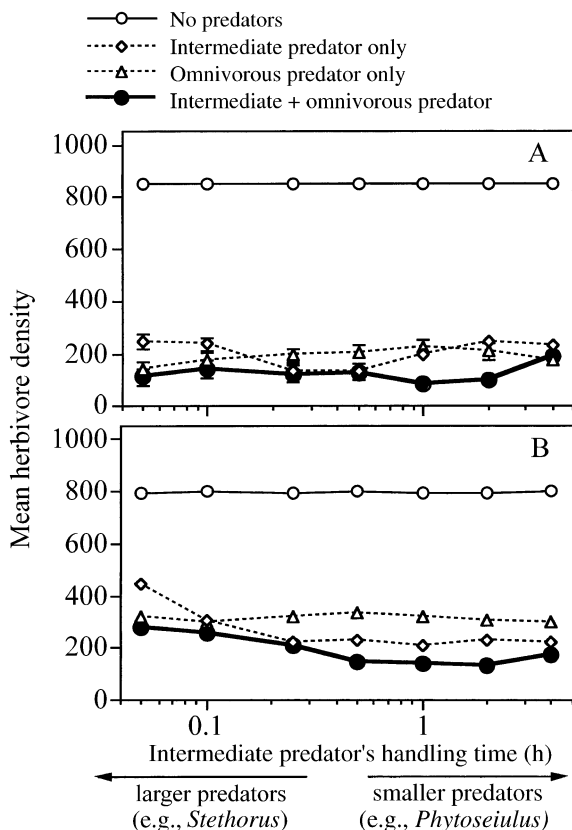


FIG. 5. Influence of prey handling time of the intermediate predator on interactions in a community of a widely foraging intermediate predator, a widely foraging omnivorous top predator, and either (A) a sedentary herbivore or (B) a mobile herbivore. Intermediate predators with body sizes much larger than their prey have short prey handling times, whereas predators whose body sizes are similar to that of their prey have long prey handling times. The baseline parameters (Table 1) were used with the following modifications: for both (A) and (B), the intermediate predator's handling time was varied from 0.05 to 4 h, and the cost of reproduction simultaneously varied from 25 to 2000 to maintain a constant maximum possible rate of reproduction; the widely foraging omnivore was given the same parameters as the baseline widely foraging intermediate predator (Table 1), but it could prey upon either the herbivore or the intermediate predator. For (B) the herbivore had a walking speed of 10 cm/h, a mean move length of 5 cm (1 SD = 1.25 cm), a pause duration of 1 h (1 SD = 0.25 h), and simulations were initiated with only a single intermediate predator and a single omnivorous predator. Mean herbivore densities in the absence of predators ("No predators") and in the presence of only the omnivorous predator ("Omnivorous predator only") are shown as points of reference. Values are means \pm 1 SE density of herbivores across 10 replicate simulation runs from time 0 to time 280 h; in some cases, error bars (\pm 1 SE) are too small to be shown.

suggests that in terrestrial ecosystems dominated by sedentary herbivores, predator foraging mode can provide useful insights into predator function. Widely foraging predators are predicted to have the potential to act as effective regulators of herbivore populations, even when they also act as omnivores, consuming other

predators. Sit-and-wait predators, in contrast, are unlikely to act in this way. Instead, sit-and-wait predators are predicted to consume a diet that includes not only herbivores but also a heavy over-representation of widely foraging intermediate predators. Sit-and-wait predators are therefore predicted to function as omnivorous top predators, acting from the fourth trophic level. All of these results are straightforward applications of the long-established model of crossovers in foraging mode to arthropod predator-prey dynamics; it is perhaps surprising that similar predictions have not, to our knowledge, been discussed previously in the literature.

Our results also suggest that the relative body sizes of predator and prey can modify the predictions of the crossover model. Smaller predators, even if they are widely foraging, have reduced prey consumption capacities, and therefore have less need to travel to harvest prey. Thus, they may incur a smaller risk of encountering a sit-and-wait predator or being detected by a motion-sensitive predator. As a result, our model predicts that the omnivore's impact will be ameliorated, and the system as a whole will be more likely to exhibit three-trophic-level dynamics.

Finally, our model suggests that a consideration of encounter frequencies alone will probably be inadequate for predicting predator function in communities dominated by mobile herbivores (e.g., Moran and Hurd 1998, Schmitz and Suttle 2001). For these communities we will need to understand more about predator preferences and prey defenses to address the question of predator function.

Experimental evidence

The crossovers in foraging mode across four trophic levels predicted by our model have been observed in several terrestrial arthropod communities (Jaffee et al. 1996, Strong et al. 1996, Gastreich 1999, Snyder and Wise 2001, Finke and Denno 2002). Indeed, part of our motivation for building a model linking predator foraging behavior with predator-prey dynamics was to create a tool to help us understand the results of our earlier work on the aphid, *Aphis gossypii* (Rosenheim et al. 1993, 1999, Cisneros and Rosenheim 1997, Rosenheim 2001). Field experimentation showed that this highly sedentary aphid could be suppressed to very low densities by a guild of widely foraging predatory lacewings (family Chrysopidae), but that this control was not observed in nature because lacewings were suppressed by another guild of omnivorous top predators (Order Hemiptera), several of which use visual cues associated with movement to identify prey.

The empirical literature also supports the prediction that widely foraging omnivorous predators are unlikely to disrupt herbivore population suppression generated by a widely foraging intermediate predator, and may instead enhance herbivore suppression. Excluding those widely foraging omnivores that use cues associated with prey movement to detect prey (e.g., praying

mantids and spiders), experimental studies have demonstrated that herbivore population suppression is most often unchanged or enhanced when a widely foraging omnivore is added to an existing predator-prey system (Croft and MacRae 1992, Obrycki et al. 1998, Lucas and Alomar 2002; Colfer et al., *in press*).

We tested our model's predictions with field experimentation in the papaya arthropod community (J. A. Rosenheim, D. D. Limburg, R. G. Colfer, V. Fournier, T. Glik, R. Goeriz, C. L. Hsu, T. E. Leonardo, E. H. Nelson, and B. Rämert, *unpublished manuscript*). Each of the main predictions from the model was supported. First, the widely foraging predators *Stethorus* and *Phytoseiulus* were both capable of generating strong suppression of *Tetranychus* populations. Second, the sit-and-wait predator *Nesticodes* never produced detectable levels of spider mite suppression. *Nesticodes* did, however, consume both of the widely foraging predators. Third, spider mite suppression exerted by the larger-bodied predator, *Stethorus*, was found to be vulnerable to the disruptive effects of *Nesticodes*, producing four-trophic-level dynamics, whereas spider mite suppression exerted by the smaller-bodied predator, *Phytoseiulus*, was relatively insensitive to *Nesticodes*, yielding robust three-trophic-level dynamics. Finally, spider mite suppression produced by *Phytoseiulus* was not disrupted, but rather was slightly enhanced by adding a widely foraging omnivore, *Stethorus*, to the system. Thus, there is some initial support for our model. We wish to emphasize, however, that a model that examines only encounter frequencies and ignores active predator preferences and prey defenses will almost certainly fail to explain the dynamics of many systems. For example, the prediction that predators that are similar in size to their prey will be relatively insensitive to the impacts of omnivorous top predators was decisively rejected in another system that otherwise has many parallels with the papaya community (Colfer et al., *in press*). We hope, however, that our model will be a starting point for additional work on resolving the ecological roles of omnivorous predators.

Proximate and ultimate explanations for omnivory

Tinbergen (1963) suggested that a richer understanding of a behavioral trait can be obtained by considering both the "proximate" or mechanistic basis for the behavior and the "ultimate" or functional consequences of its expression. In this study, we have proposed a proximate explanation for one expression of trophic-level omnivory, namely when a predator consumes another predator. We have suggested that this type of omnivory may be a direct outcome of the foraging modes of the interacting species. Our explanation should complement, rather than compete with, functional explanations for trophic-level omnivory. For instance, Polis et al. (1989) suggested that it may be advantageous for one predator to consume another predator because it may (1) eliminate a potential com-

petitor ("intraguild predation") or (2) eliminate an individual that could subsequently attack them or their progeny ("reciprocal intraguild predation") (see also Singer and Bernays [2003]). Similarly, Denno and Fagan (2003) have argued that because arthropod growth and reproduction are often nitrogen limited, and because nitrogen concentrations in arthropod tissues increase as one moves up the food chain, that a typical predator is a higher-quality meal than is a typical herbivore. These hypotheses are not mutually exclusive. On the contrary, it is possible that sit-and-wait foraging strategies and the use of cues associated with prey movement may have been selectively favored in part because they led to a diet that was enriched in nitrogen, while eliminating potential competitors or predators.

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