

SPECIAL FEATURE

Why Omnivory?¹

Omnivory, broadly defined as feeding on more than one trophic level, is an ecological habit that ought to be widespread. At the most basic level, the omnivorous animal, as a generalist, should have higher performance in variable environments than some more specialized feeder. Yet the problem of which, why, and how organisms are omnivorous was somehow supplanted by the apparent observation that omnivory is rare in nature and destabilizing in food webs. From an historical perspective, Joel E. Cohen and Stuart L. Pimm independently began to advocate the “rare and destabilizing” position in the late 1970s. Unfortunately, naturalists who knew better failed to displace this notion.

Not until the late Gary Polis published his now classic study (G. A. Polis 1991. Complex trophic interactions in deserts: an empirical critique of food web theory. *American Naturalist* 138:123–155) was there a resurgence of interest in understanding the biology and ecological importance of omnivores. The ubiquity of omnivory is now widely recognized, and theory has demonstrated conditions under which omnivores can stabilize food webs. As theoreticians continue to work out the influence of omnivory on the stability and lengths of food chains, empiricists have gotten busy in identifying and studying the causes and consequences of omnivory in nature. The question about why omnivores have such diversified feeding strategies remains a critical question that is ripe for diverse hypotheses. Ironically, although arthropods are probably not omnivory-dominated as a taxon (vertebrates probably are), a large portion of omnivory research is focused on omnivorous arthropods. As such, this Special Feature focuses mostly on the causes of omnivory in arthropods and touches on the consequences across taxa.

The authors of this Special Feature each take a different creative approach to understanding omnivory. There are clear differences in the paradigms (stoichiometry of the essential elements, costs and benefits of diet mixing, behaviorally motivated decisions, and dynamic constraints) and approaches (literature review, models, and phylogenetic analyses) that the authors employ. The result is a stimulating set of papers that should be evaluated, challenged, and tested.

—ANURAG A. AGRAWAL
Special Features Editor

Key words: dynamic constraints models; food selection; host range evolution; intraguild predation; omnivory; optimal diet theory; plant–animal interactions.

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MIGHT NITROGEN LIMITATION PROMOTE OMNIVORY AMONG CARNIVOROUS ARTHROPODS?

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Abstract. Omnivory is a frequent feeding strategy in terrestrial arthropods, occurring across a diversity of taxa occupying a wide array of habitats. Because omnivory has important consequences for broad areas of theoretical and applied ecology, it is essential to understand those factors that favor its occurrence. Here we address the limiting role of nitrogen in promoting omnivory, not so much from the historical perspective of herbivores supplementing their nutrient-poor plant diet, but by extending the argument to higher trophic levels where predators feed on each other as well as herbivores. Drawing on the historically documented mismatch in nitrogen stoichiometry between herbivores and their host plants ($C:N_{\text{plants}} \gg C:N_{\text{herbivores}}$), and a recently documented, though smaller, difference in nitrogen content between predators and their herbivore prey ($C:N_{\text{herbivores}} > C:N_{\text{predators}}$), we discuss the existence of a trade-off between nutrient quality and quantity that occurs across trophic levels. The existence of this trade-off suggests that arthropod predators, which we show to be frequently nitrogen-limited in nature, can enhance their nitrogen intake by broadening their diet to include nitrogen-rich predators. We conclude by outlining the consequences of this trade-off for the relative balance between dietary specialization and supplementation among consumers, emphasizing the divergent roles that large vs. small stoichiometric mismatches may have had for the evolution of omnivory.

Key words: arthropods; carnivores; intraguild predation; nitrogen limitation; nutrient stoichiometry; omnivory.

INTRODUCTION

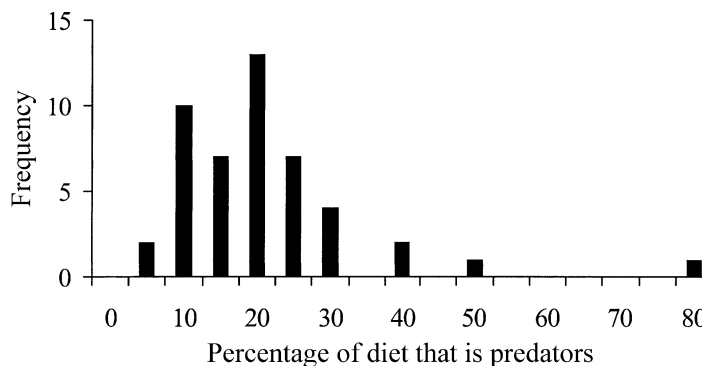
For our consideration of omnivory, we focus on the contribution of nitrogen (N) limitation to feeding strategies in terrestrial arthropods. We adopt a broad view in which omnivory is defined as feeding on two or more trophic levels (Menge and Sutherland 1987, Polis and Strong 1996), a definition that includes “herbivores” that extract nutrients from nonplant sources (e.g., engage in cannibalism), “predators” that feed on both herbivores and selected plant tissues (e.g., seeds, pollen), as well as predators that feed on herbivores and other predators (e.g., intraguild predators, facultative hyperparasitoids) (Coll 1998, Rosenheim 1998, Sullivan and Völkl 1999, Coll and Guershon 2002). Omnivory is widespread in terrestrial arthropods, occurring across a diversity of taxa that occupy a wide variety of habitats (Coll and Guershon 2002). The profound consequences of omnivory for population and food web dynamics (Menge and Sutherland 1987, Fagan 1997, McCann et al. 1998, Rosenheim 1998, Eubanks and Denno 2000a), landscape ecology (Polis et al. 1997), and biological control (Rosenheim et al. 1995, Hodge 1999) are just beginning to be realized. Thus, understanding the factors that promote and maintain omnivory in ecosystems is critical across a broad

spectrum of ecology. In this paper, we explicitly address the limiting role of N in promoting omnivory, not so much in the historical context of herbivores supplementing their nutrient-poor plant diets (Mattson 1980, White 1993), but instead extending the discussion to include species feeding at higher trophic levels.

Recently, important connections between omnivory and nutrient flow in ecosystems have emerged (e.g., Ostrom et al. 1997). One such linkage has been identified using the framework of ecological stoichiometry, the study of the relative balance of nutrients and energy in organisms from different trophic levels (Elser et al. 1996, 2000; Sterner and Elser 2002). This emerging framework provides opportunities for connecting omnivory with larger-scale processes such as food web and ecosystem dynamics through its focus on the functional consequences of nutrient and energy flow between trophic levels. One of the most profound consequences of a stoichiometric perspective is that gross growth efficiencies of consumers are influenced by their demands for limiting resources (Sterner and Elser 2002). A classic example is the mismatch in C:N content between herbivores and their host plants that has led to a diversity of behavioral, physiological, and ecological adaptations in herbivores that help offset this inherent discrepancy (McNeill and Southwood 1978, Mattson 1980, White 1993). Because of stoichiometric mismatches, an herbivore with a specific body composition (e.g., C:N ratio) cannot take full advantage of

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FIG. 1. Predators regularly incorporate other predators in their diets. Plotted data (Hodge 1999) summarize the frequency of intraguild predation (percentage of diet) for spiders. Additional examples show that there are predators specializing at both ends of the diet spectrum such as aphidophagous syrphids feeding exclusively on herbivores (Rotheray and Gilbert 1989) and pompilid wasps and aranaeophagic spiders specializing on predators (Li and Jackson 1997).



resource biomass with insufficiently low nutrient content. In a sense, available C in excess of the consumer's body requirement for N is "wasted" (Sterner and Elser 2002), because it cannot be utilized for growth. However, this excess C may be available for other uses such as foraging or dispersal. Stoichiometric limitations are especially critical to herbivore growth processes (Elser et al. 2000), but dietary mismatches can also limit the processes of reproduction and self-maintenance. Based on accumulating evidence concerning the stoichiometric structure of foodwebs (Fagan et al. 2002, Sterner and Elser 2002), we will argue here that stoichiometric mismatches, similar but less severe than the well-known herbivore-plant mismatch, also exist at higher trophic levels, and that these disparities appear functionally connected to the preponderance of omnivory among terrestrial arthropods.

Here, we explore how stoichiometric imbalances across trophic levels, particularly those involving N, may generate trophic complexity via omnivory in terrestrial arthropod food webs. We first detail the background for our thinking, outlining the regularity of prey limitation for terrestrial arthropod predators and its manifold consequences, including extensive omnivory. We next discuss the evidence for N-limitation in predators, and outline the consequences of such N-limitation for predator fitness and prey selection. To synthesize our views we describe the conditions favoring omnivory and intraguild predation over strict predation on herbivores. We conclude by discussing some of the ecological consequences of omnivory, emphasizing how mismatches in nutrient stoichiometry across trophic levels may influence patterns of diet breadth, lineage diversification, and food web structure.

THE WIDESPREAD OCCURRENCE OF OMNIVORY

An extensive literature documents instances of "herbivorous" arthropods occasionally or frequently feeding at higher trophic levels (McNeil and Southwood 1978, Coll and Guershon, 2002). These include instances of cannibalism and interspecific predation that are often viewed as mechanisms for obtaining supplemental N from sources other than host plants (McNeill and Southwood 1978). In some cases, such as some

conocephaline katydids, extensive plant feeding occurs, but individuals cannot complete development without consuming prey (R. Denno, *unpublished data*). For omnivorous flower thrips, reductions in plant quality cause shifts from herbivory to predation (Agrawal et al. 1999). Similarly, many "predators" either occasionally or frequently feed on N-rich plant parts (e.g., pollen and seeds) in addition to animal prey (Coll 1998, Coll and Guershon 2002), and in so doing, can persist through periods of prey scarcity (Polis and Strong 1996, Eubanks and Denno 1999). Numerous omnivores perform best on mixed diets of plants and prey when compared to restricted feeding on either diet (Coll 1998). Nonetheless, across a diversity of omnivorous arthropods, a spectrum of dietary mixing exists with the fraction of plant material and prey varying greatly, and with both obligate and facultative mixing strategies represented (Coll 1998, Thompson 1999).

Omnivory is also prevalent at higher trophic levels, where predators or parasitoids not only attack herbivores but also prey extensively on other predators (Rosenheim 1998, Sullivan and Völkl 1999). For example, intraguild prey comprised 3% to 75% (mean ~20%) of prey taken for 45 spider species in 12 families (Hodge 1999; Fig. 1). Facultative hyperparasitoids and predators that feed on parasitized herbivores are omnivorous by virtue of intraguild or multitrophic-level predation (Rosenheim 1998, Hodge 1999, Sullivan and Völkl 1999). The behavior underlying these diverse examples of omnivory can be categorized as either coincidental or directed in nature (reviewed in Polis et al. 1989).

PREY LIMITATION AND ITS CONSEQUENCES FOR PREDATORS

Spiders (Riechert and Harp 1987, Tanaka 1991, Wise 1993, Hodge 1999), mites (McRae and Croft 1997), scorpions (Polis and McCormick 1986), mantids (Hurd and Eisenberg 1984), heteropterans (Spence and Carcamo 1991), beetles (Lenski 1984, Bommarco 1999), caddisflies (Wissinger et al. 1996), neuropterans (Rosenheim et al. 1993), and wasps (Mead et al. 1994, Stamp 2001) are among the many predatory arthropod taxa that routinely face prey limitation. Evidence for

this limitation includes a variety of responses to local increases in prey density, such as aggregation in areas of high prey density (Döbel and Denno 1994), increased population growth (Wise 1993, Denno et al. 2002), or enhanced survival or fecundity (Wise 1979, 1993). Similar effects have been shown for parasitoids whose fitness and or population size is affected by host availability (Thompson 1999). However, this extensive documentation of prey limitation generally leaves unresolved the issue of what specifically limits predator success. In some cases, prey scarcity may limit predators (see Wise 1993), but other studies strongly suggest that limitation occurs at a more fundamental biochemical level, such that gross protein or essential amino acids are in fact the limiting constituents of an arthropod predator's diet (e.g., Bonnot 1986, Thompson 1999, Pennacchio et al. 1999, Toft 1999). Thus, N limitation, documented historically at the plant–herbivore interface (Mattson 1980, White 1993), may also constrain predator performance.

C:N RATIOS OF HERBIVORES EXCEED THOSE OF PREDATORS

How does prey limitation of predators fit within a larger food web context? To begin answering this question, consider a trade-off between the quantity and quality of resources that appears to exist across trophic levels in food webs (Fig. 2A). For example, ecologists have long recognized that biomass decreases with increasing trophic level, with transfer efficiencies of 4 to 33% being documented (e.g., Price 1984, Pauly and Christensen 1995). In contrast, resource quality increases with trophic position, starting with the major jump in quality across the plant–herbivore interface. More recently, however, a difference between the N content of arthropod predators and herbivores also has been observed. In particular, terrestrial arthropod predators have consistently higher N content (Fagan et al. 2002) and a lower C:N ratio than do phylogenetically related herbivores (Fig. 2B). Indeed, on an absolute basis, predatory insects were found to have from 0.5 to 3 percentage points more N per unit biomass than their herbivorous relatives, with these percentage-point differences representing a 5% to 27% relative increase in N-content and thus dietary demand. This difference persists after accounting for allometry, gut dilution, and other potentially confounding factors.

Several potential explanations for the elevated N content, and thus lower C:N ratio, of predators over herbivores are detailed in Fagan et al. (2002). We only briefly touch on these here. First, predators may have higher N content than herbivores simply as a consequence of eating food with higher N content. Second, differential body composition may be selected for directly (in herbivores, predators, or both) in response to the differential scarcity of dietary N. For example, herbivores might be able to adapt to low-N food by substituting low-N materials for high-N materials in con-

structing some body parts, such as cuticle. Third, differential N content may be an indirect consequence of adaptation to different trophic habits. For example, herbivory and predation might select for different allocations to muscle vs. other lower-N structures. Fourth, higher N in predators may reflect sequestration or other adaptive (or maladaptive) responses to problems created by a dietary N supply that exceeds their needs. Carefully planned experiments where omnivores are fed diets of N-rich (predators) or N-poor prey (herbivores), coupled with tissue dissection and analysis would help distinguish among these potential explanations. To our knowledge, experiments to identify the relative importance of these mechanisms or clarify the circumstances under which they would operate have yet to be conducted. Regardless of the underlying explanations, however, a clear difference in N content exists between herbivorous and predaceous arthropods.

EVIDENCE FOR NITROGEN LIMITATION IN PREDATORS

Is the elemental mismatch in body content (C:N) sufficient to impose stoichiometric constraints on predator growth, reproduction, and other contributors to fitness? Urabe and Watanabe (1992) explored the issue of prey quality-limitation from a quantitative perspective. They developed the concept of the “threshold elemental ratio” (hereafter TER), which identifies the level at which consumers are limited by the nutritional quality of their prey vs. “energy-” or C-limited. Mathematically, a simple version of the TER can be expressed as

$$(C:N_{\text{prey}}/C:N_{\text{predator}}) > \alpha_N/\alpha_C \quad (1)$$

where α_N is the maximum gross growth efficiency for N (i.e., the fraction of ingested N that the predator converts into new biomass), α_C is the maximum gross growth efficiency for C, and $C:N_{\text{prey}}$ and $C:N_{\text{predator}}$ are the C:N ratios of prey and predator biomass, which are assumed to be species specific and under strong homeostatic regulation. Analysis of our arthropod data set showed consistent evidence for N-limitation, and also suggested that specific herbivore–predator pairs (e.g., aphid–ladybug) could face strong N limitation (Fagan et al. 2002).

Consideration of potential distributions of $C:N_{\text{resource}}/C:N_{\text{consumer}}$ for all possible plant–herbivore, herbivore–predator, and predator–predator pairs from compiled databases (Elser et al. 2000; Fagan et al. 2002) provides additional insight into the TER issue (Fig. 2C). Admittedly, some of these combinations would not occur in nature by virtue of differences in regional distribution, body size, host specificity, and behavior among the species in the database. Nevertheless, they provide a rough estimate of the kinds of consumer-resource combinations that can occur. Several observations can be gleaned from these distributions. For example, even if one excludes the 2.5% of the plant–herbivore com-

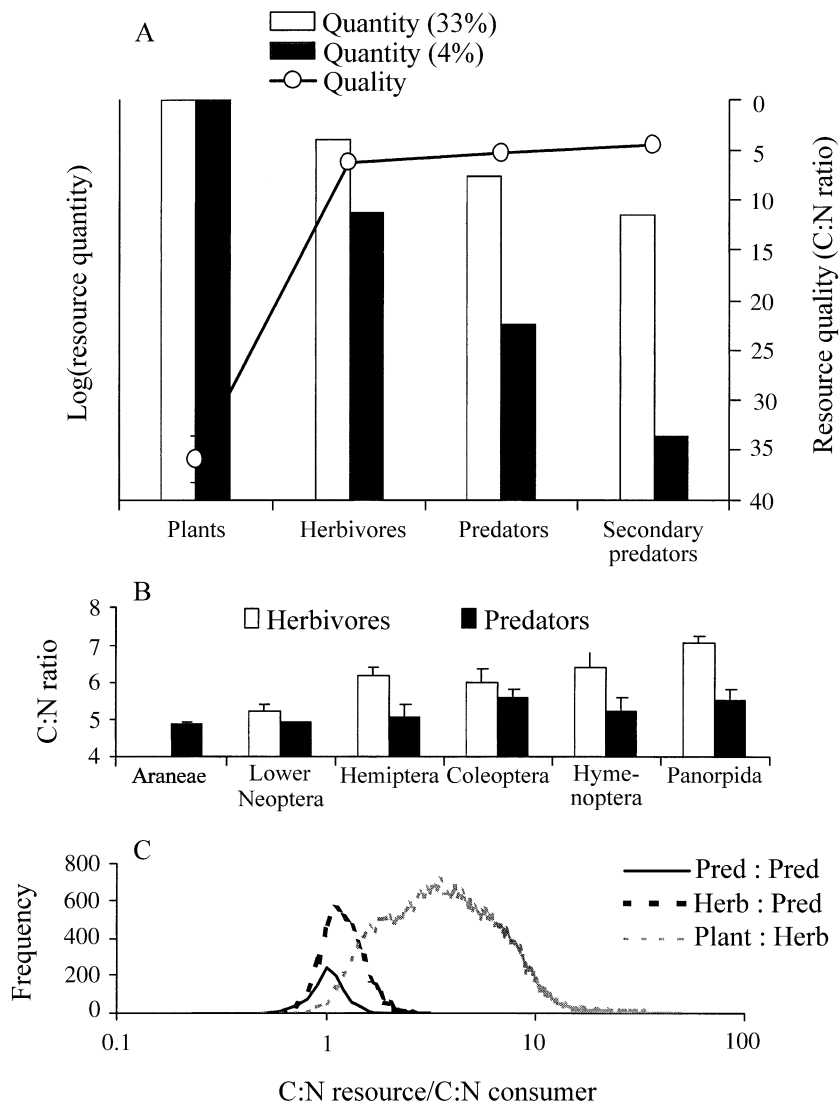


FIG. 2. Ratio of carbon to nitrogen (C:N) content across trophic levels, among taxa, and between potential resource-consumer pairs. Panel (A) outlines a trade-off between decreasing resource availability (standing crop biomass, on a logarithmic axis) and increasing resource quality (i.e., decreasing C:N ratio) across four trophic levels. Resource quantity curves represent hypothetical scenarios assuming trophic transfer efficiencies of 4% and 33% between adjacent trophic levels and are scaled relative to plant biomass. Resource quality data are averaged across phylogenetic, allometric, and other sources of intratrophic-level variation. Panel (B) gives the mean (+1 SE) C:N ratio for herbivorous and predaceous arthropods, grouped phylogenetically according to lineage. The groupings lower Neoptera and Panorpida facilitate comparisons of herbivorous Orthoptera with predaceous Mantodea, and herbivorous Lepidoptera with predaceous Diptera, respectively. Panel (C) gives frequencies of relative C:N ratios of resources and consumers in terrestrial arthropod food webs determined by calculating all pairwise combinations of resource versus consumer C:N ratios. Resource quality data are from Elser et al. (2000) and Fagan et al. (2002), the latter of which provides statistical analyses documenting consistent and significant differences in N content between predaceous and herbivorous arthropods.

binations that are most nutrient rich, 22% of the herbivore-predator combinations are as N limited as are better matched plant-herbivore combinations (C:N ratios ranging from 1.4 to 3.1). In comparison, 48% of predator-predator combinations have ratios ≤ 1 , suggesting substantial opportunities for predators to obtain relatively N-rich diets via intraguild predation.

These findings also have interesting implications for understanding predator foraging strategies. For ex-

ample, one way for a growing predator to avoid nutrient limitation is to increase its expenditure or excretion of C, thus lowering α_c (Stern and Elser 2002). This leads to the expectation that predators with high N requirements will more likely be active hunters rather than sit-and-wait predators.

Stern (1997) extended the TER concept to explore explicitly the interaction between the quality and quantity of prey. He suggested that the TER is a decreasing

function of prey quantity, such that the threshold for nutrient limitation becomes higher as food becomes scarcer. This result makes intuitive sense in that prey quality will not be a major consideration if a consumer is starving for energy. Thus, predators that routinely face severe shortages of prey and/or lack efficient search mechanisms to increase prey availability are more likely to be limited by energy (C) than by mineral nutrients such as N.

CONSEQUENCES OF NITROGEN LIMITATION FOR PREDATOR FITNESS AND PREY SELECTION

On the empirical front, impacts of N limitation and dietary balance on components of fitness occur for spiders (Uetz et al. 1992, Toft 1999) and other invertebrate predators such as predaceous stink bugs (Strohmeyer et al. 1998). For example, the experimental addition of amino acids to the diet of wolf spiders enhanced their growth and survivorship (Mayntz and Toft 2001), and jumping spiders exhibited enhanced survivorship when provisioned with intraguild spider prey than with a mix of N-poor herbivorous insects (Li and Jackson 1997). Web reclamation, in which spiders recycle their protein-rich silk (Opell 1998), may also indicate N limitation. These results are particularly interesting in light of recent data suggesting that on average the N content of spiders (11.7%) not only statistically exceeds that for herbivorous insects (9.5%), but also is higher than that for predatory insects in general (10.8%) (Fagan et al. 2002). Thus, the N demand for spiders may be more difficult to meet than that for most predatory insects, and that may make N limitation especially widespread among spiders.

Parasitoids also typically achieve optimal growth and survival on high-protein diets (Thompson 1999). For example, host feeding (including intraguild predation) in hymenopterous parasitoids improved survival and fecundity (Jervis and Kidd 1986, Thompson 1999) and the protein content of eggs (LeRalec 1995). Likewise, for a tachinid parasitoid, development time was negatively correlated with dietary protein and amino-acid levels (Bonnot 1986). Collectively, these studies suggest that N can limit many predators and parasitoids. Counterexamples occur, suggesting that N limitation of predators is not universal, or can be diminished by other factors, such as temporal variation in resource quality (e.g., Duval and Williams 2000).

Predators and omnivores often eat their exuviae upon molting, a behavior that has been attributed to nitrogen limitation (Mira 2000). Other evidence that N is limiting for arthropod predators comes from species that benefit from cannibalism. Although potentially maladaptive, cannibalism does present an opportunity for a near-perfect stoichiometric match between predator and diet, and thus may represent one way to meet specific nutrient requirements under certain circumstances. Heteropterans (Spence and Carcamo 1991), coccinellid beetles (Snyder et al. 2000), and some mites (Schaus-

berger and Croft 2000) show increased performance or survival when fed conspecifics, but the reverse is true for some spiders (Toft and Wise 1999a) and some mites (Schausberger and Croft 2000).

Further evidence that N is limiting for predators comes from their dietary choice of plant tissues (Eubanks and Denno 1999). Many predatory heteropterans and coccinellid beetles select seeds, flowers, fruits, or pollen on which to feed (Coll 1998, Eubanks and Denno 1999), all plant parts with high N contents (McNeill and Southwood 1980, Mattson 1980). On average, however, the N content of herbivorous prey is higher (6–10%) than that of even these N-rich plant tissues (4–6% N) (Mattson 1980, Elser et al. 2000).

Given the substantial volume of evidence supporting N limitation in arthropod predators, one can ask if predators generally prefer to feed on N-rich prey (other predators) over less nutritious options (herbivores), as suggested by Polis (1981) and as predicted by optimal-foraging models and dynamic optimization (Waldbauer and Friedman 1991, Strand and Obrycki 1996). Indeed, some predators selectively feed on the most nutritious prey available (Greenstone 1979, Rosenheim et al. 1993, Finke and Denno 2002). In other studies, predators or parasitoids preferred larger prey (Endo and Endo 1994), “higher quality prey” (Strand and Obrycki 1996, Toft 1999, Toft and Wise 1999b), “less toxic prey” (Toft 1999, Toft and Wise 1999b, Stamp 2001), or “more palatable prey” (Stamp 2001), but such preferences were not explicitly linked to the N content of the prey. Not all arthropod predators, however, select the most nutritious prey item from the available spectrum (Toft 1999). In some cases, predators do not discriminate among prey of differing N contents (Duval and Williams 2000), and in other instances they choose less nutritious prey (Eubanks and Denno 2000b). In almost all studies of prey selection by predators, however, potential differences in prey nutrition are confounded by differences in prey behavior, size, toxicity, or abundance (Rosenheim et al. 1993, Endo and Endo 1994, Strohmeyer et al. 1998, Toft and Wise 1999a, Eubanks and Denno 2000b, Stamp 2001, Finke and Denno 2002). Overall, only limited data are available to verify that, all else being equal, arthropod predators selectively attack the most nutritious prey.

It could also be argued that predators sequestering N in their exoskeleton (Oxford 1998), and engaging in excessive killing and partial prey consumption (Sih 1987, Riechert and Maupin 1998) stand as evidence against N limitation. However, each of these potential counterexamples has alternative interpretations. For instance, spiders’ guanine-rich exoskeletal pigments are not just waste products but may also serve adaptive functions including crypsis, aposematism, and thermoregulation (Oxford 1998). Also, the partial consumption of prey has multiple explanations (Sih 1987, Cohen 1995, Riechert and Maupin 1998), not the least

of which might be the rapid and selective extraction of N before leaving the remainder behind (Cohen 1995).

Because predatory arthropods contain more N per unit biomass on average than do herbivores (Fagan et al. 2002; Fig. 2B), predators could reduce this inherent stoichiometric mismatch by concentrating their feeding on other predators. Several arthropod predators, including numerous araneophagic spiders (e.g., Li and Jackson 1997), some fireflies (Eisner et al. 1997), and many obligate hyperparasitoids (Sullivan and Völkl 1999) in fact specialize on other predators or primary parasitoids. More commonly, however, predators with specialized diets feed exclusively on herbivorous prey (Rotheray and Gilbert 1989, Strand and Obrycki 1996, Thompson 1999). In the case of many coccinellid and syrphid predators that specialize on aphids and scale insects (Rotheray and Gilbert 1989), their prey are N deficient compared to many other insect herbivores (Fagan et al. 2002). In these instances, the apparent nutritional disadvantage of feeding on such N-deficient prey is offset in part by specializing on prey that are often extremely abundant, aggregated, sessile, and easy to catch (e.g., Dixon 1998; Fig. 2A).

PREDATORS COPING WITH THE STOICHIOMETRIC CONSTRAINTS OF LOW-NITROGEN PREY

Faced with prey of lower than optimal nutritive value, predators employ a diversity of mechanisms to makeup shortfalls in key nutrients. One of the most obvious methods available to a consumer faced with poor-quality resources is feeding compensation, the process of increasing feeding rate (Simpson and Simpson 1990, Slansky 1993). Though extensively employed by herbivores, the extent to which predators employ feeding compensation is not clear. Furthermore, even when used, feeding compensation is not a universally successful solution to problems of nutrient acquisition because physiological constraints such as maximal gut capacity and throughput time limit the degree to which eating more can compensate for eating nutrient-poor food (Johnson et al. 1975, Sih 1987). In addition, compensatory feeding on low-quality food can lead to increased levels of dietary toxins, and these toxins can negatively affect growth, survival, and other contributors to herbivore fitness (Slansky and Wheeler 1992). Predators also accumulate prey-derived toxins with adverse effects (Toft and Wise 1999a, Francis et al. 2001), but the two-way relationship between feeding rate and toxin accumulation has not been investigated extensively in predators. In a stoichiometric context, a possible disadvantage to feeding compensation is that in the process of satisfying an absolute need for nutrients, such feeding increases the absolute amount of extra C that must be used or eliminated.

Predators can also cope with low-quality prey by efficiently extracting nutrients and by increasing extraction rates (Cohen 1995, Furrer and Ward 1995). These processes are enhanced by extra-oral digestion

(hereafter EOD), a mechanism by which an estimated 79% of predatory insects and arachnids feed (Cohen 1995). For example, both heteropterans and carabid beetles are highly efficient at extracting nutrients from prey, reaching efficiencies of 94% and 84%, respectively (Cohen 1995). Some parasitoid larvae selectively ingest particulate materials within their host and employ EOD, a behavior that concentrates nutrients and promotes rapid growth (Wu et al. 2000). The advantages of EOD are reduced handling time, increased extraction rate of nutrients, and an increase in the efficiency of nutrient extraction and concentration, allowing small predators to obtain nutrients from relatively large prey (Cohen 1995).

EOD also allows for the differential extraction of nutrients from prey, whereby proteins are ingested earlier in the feeding process than are lipids (Cohen 1995). In a stoichiometric context, such differential extraction would be advantageous by reducing the intake of C relative to more limiting nutrients. For example, by consuming internal tissues of their prey, the predators avoid consumption of the high C:N exoskeleton and thus avoid dilution of prey tissue N with excess carbohydrate. The rapid and selective ingestion of N from prey may also explain why predators occasionally consume only part of the utilizable portion of their catch (see Johnson et al. 1975, Sih 1987, Riechert and Mau-pin 1998). Thus, when faced with low-quality prey, an alternative to feeding compensation is selective feeding via enhanced discrimination among prey (Greenstone 1979) and differential extraction of high-value nutrients from prey (Cohen 1995, Furrer and Ward 1995, Wu et al. 2000).

THE NUTRITIONAL ADVANTAGE OF AN OMNIVOROUS DIET

Having established a difference between the N content of predators and prey, a key issue that emerges is whether the difference is large enough to promote omnivory? In other words, under what conditions does a predator that feeds on other predators enhance its rate of N uptake over one that feeds only on herbivores? Specifically, might a predator face increases in handling time or difficulties in assimilating N from predator tissues that outweigh the potential gain from feeding on prey with lower C:N content? As a preliminary exploration of this issue, we examined the relative gain in N uptake that a predator would enjoy as a function of three factors: (1) the proportion of diet made up of other predators, (2) the average nutritional advantage from feeding on predators with low C:N tissues, and (3) the cumulative (dis)advantages resulting from differences in handling times or assimilation efficiencies. To calculate a dimensionless measure of nutritional advantage, we used the following equation:

$$z = (1 - \text{pdiet}_p) + \text{pdiet}_p * \Delta N_{p/h} * \Delta e_{p/h} \quad (2)$$

where p_{diet_p} is the proportion of a predator's diet made up of predators (see Fig. 1), $\Delta N_{p/h}$ is the relative nutrient (e.g., N) content of predator tissue vs. herbivore tissues (see Fig. 2C), and $\Delta e_{p/h}$ is the relative rate with which the predator can uptake nutrients from predator vs. herbivore tissues (accounting for the cumulative effects of potential differences in assimilation efficiency, handling time, and related factors). Fig. 3 shows how the conditions favoring omnivory over strict predation on herbivores vary depending on the three factors and nutrient uptake efficiencies. Provided that nutrients are not substantially more difficult to extract from predators than herbivores, predators can increase their nutrient uptake relative to an all-herbivore diet by eating either more predators or more nutrient-rich predators. We don't include search time here because we do not think the pertinent question is whether predators should seek out other predators as prey, but rather if a predator encounters another predator, is it advantageous to include that individual?

SYNTHESIS AND PROSPECTUS

Omnivory occurs ubiquitously among terrestrial arthropods and has important consequences for the theory, practice, and application of ecology. Here, we have argued that ecological stoichiometry should be included in the mix of factors that bear on the prevalence of omnivory. Specifically, we suggest that the mismatch in N content of organisms across trophic levels is one factor promoting extensive omnivory in terrestrial arthropod assemblages, and may help explain the prevalence of predator–predator interactions. That predators should base their foraging decisions on prey nutrition is not a new view (Toft 1999, Thompson 1999). What is novel here is the recognition that predators can more effectively meet their N demands by feeding on other predators rather than on herbivores, because of the recently discovered higher average N content of predators (Fagan et al. 2002; Fig. 2B).

Although stoichiometric mismatches in nutrient content between “herbivores” and “predators” may be an important factor promoting omnivory, such a feeding strategy may require an evolutionary break from specializations associated with feeding either on low quality, abundant resources or higher quality but scarcer resources. Preadaptations may facilitate such transitions from specialist consumer to omnivore. For example, herbivores that use sucking mouthparts and EOD to feed on tough, but nutrient-rich seeds could, with relatively few changes, employ the same physiological adaptations to penetrate arthropod exoskeletons. Likewise, predators that mechanically or chemically subdue mobile herbivore prey would be well equipped to employ the same techniques against mobile predators.

Mismatches in nutrient stoichiometry across trophic levels may also contribute to patterns of diet breadth and diversification. For example, overcoming the se-

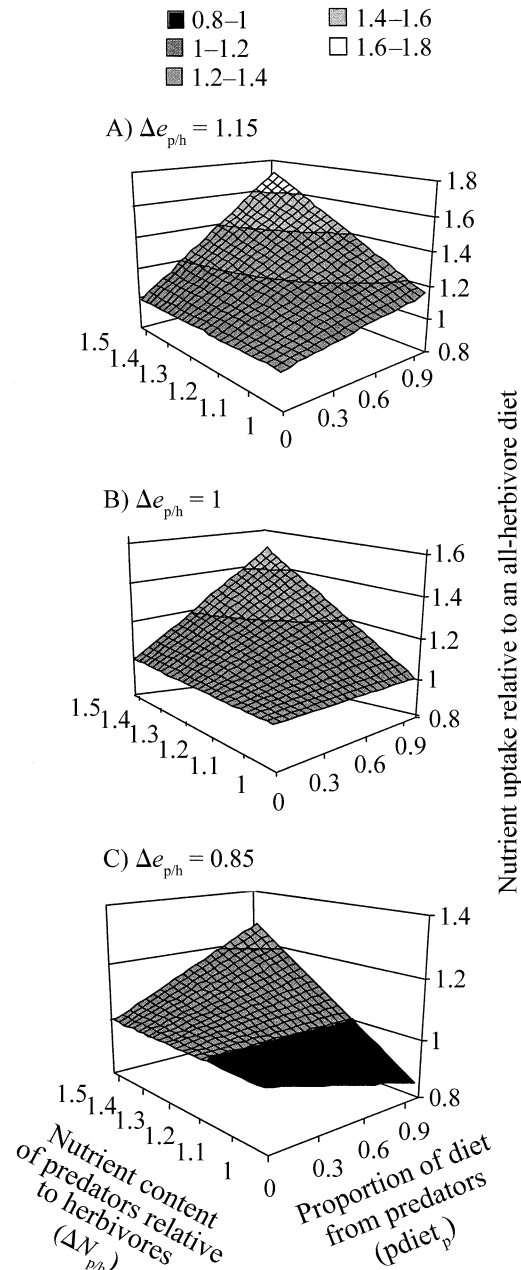


FIG. 3. Nutrient uptake for omnivores with mixed diets of herbivores and predators. Panel (A) depicts the case in which predators more quickly or efficiently take up nutrients from other predators. In (B), nutrient uptake rates from predators and herbivores are equal, whereas in (C), uptake rates from predators are slower or less efficient than from herbivores (see Eq. 2). Provided that nutrients are not more difficult to extract from predators than herbivores, predators can increase their nutrient uptake relative to an all-herbivore diet by eating either more predators or more nutrient-rich predators.

vere plant–herbivore mismatch in N availability likely presents greater ecological/evolutionary challenges than does compensating for the smaller discrepancies among consumer species (Fig. 2A). Evolved solutions

to the plant–herbivore N mismatch (e.g., McNeill and Southwood 1978) may involve physiological, morphological, or behavioral modifications that constrain herbivores from employing alternative strategies for acquiring N such as feeding on a diversity of plant parts or taxa. Such constraints have promoted monophagy, dietary specialization, and diversification in such taxa (Bernays and Graham 1988). In contrast, stoichiometric differences between predators and herbivores are not as extreme, and overcoming these smaller disparities may not constrain predators in the same way that N limitation affects herbivores. In other words, “predators” can make up the difference by dietary supplementation and opportunistic, generalized feeding habits rather than by specialization, thus providing the motivation and prospect for feeding across trophic levels. Thus, as the disparity in C:N stoichiometry between consumers and their resources decreases from lower to higher trophic levels, we expect there to be a general dietary trend from specialization to supplementation and omnivory. We suspect one reason why lineages of herbivorous insects are far more diverse than their predatory sister groups (Mitter et al. 1988) is because dietary specialization and dietary supplementation have very different consequences for speciation processes.

Although some arthropods indeed specialize on plants (strict herbivores) or on predators (araneophagic spiders and obligate hyperparasitoids), many others deviate from this pattern and exhibit broadly diversified diets. Given constraints associated with obtaining N via strict feeding strategies, a trophic compromise may provide an alternative solution. Recognizing that for many organisms such a compromise may not be possible by virtue of phylogenetic constraints, we nonetheless argue that the widespread occurrence of omnivory stands as evidence that a large number of arthropod taxa have satisfied the “trade-off” between resource quality and quantity by adopting a feeding compromise whereby abundant but less nutritious resources are supplemented with N derived from higher trophic levels.

Here we highlight the mismatch in nutrient content between “herbivores” and “predators” as a potentially important factor underlying the evolution of omnivory. Additional investigations along this line are essential for clarifying how nutrient limitation contributes to intraguild predation and trophic complexity in terrestrial food webs, and building a linkage between nutrient dynamics, the preponderance of omnivory, and the stability and complexity of terrestrial arthropod foodwebs. To verify the specific contribution of stoichiometric imbalances to the feeding strategies of consumers, specific controlled experiments are needed to isolate the direct effects of prey nutrition on predator and omnivore performance, independent of prey abundance, behavior, the risk of death or damage, and other species-specific features. Continued research into the functional

consequences of stoichiometric disparities across trophic levels will help link population and community ecology on the one hand, with ecosystem science on the other.

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LITERATURE CITED

- Agrawal, A. A., C. Kobayashi, and J. S. Thaler. 1999. Influence of prey availability and host plant resistance on omnivory by western flower thrips. *Ecology* **80**:518–523.
- Bernays, E. A., and M. Graham. 1988. On the evolution of host specificity in phytophagous arthropods. *Ecology* **69**:886–892.
- Bommarco, R. 1999. Feeding reproduction and community impact of a predatory carabid in two agricultural habitats. *Oikos* **87**:89–96.
- Bonnot, G. 1986. Les particularités de la nutrition des insectes parasites. Pages 227–240 in C. L. Legner, editor. *La nutrition de crustacés et des insectes*. CR Coll, Centre National d'Etudes et de Recommandations sur la Nutrition et L'Alimentation (CNERNA), Paris, France.
- Cohen, A. C. 1995. Extraoral digestion in predaceous terrestrial Arthropoda. *Annual Review of Entomology* **40**:85–103.
- Coll, M. 1998. Living and feeding on plants and predatory Heteroptera. Pages 89–129 in M. Coll and J. R. Ruberson, editors. *Predatory Heteroptera: their ecology and use in biological control*. Entomological Society of America, Lanham, Maryland, USA.
- Coll, M., and M. Guershon. 2002. Omnivory in terrestrial arthropods: mixing plant and prey diets. *Annual Review of Entomology* **47**:267–297.
- Denno, R. F., C. Gratton, M. A. Peterson, G. A. Langellotto, D. L. Finke, and A. F. Huberty. 2002. Bottom-up forces mediate natural-enemy impact in a phytophagous insect community. *Ecology* **83**:1443–1458.
- Dixon, A. F. G. 1998. *Aphid ecology*. Chapman and Hall, London, UK.
- Döbel, H. G., and R. F. Denno. 1994. Predator–planthopper interactions. Pages 325–399 in R. F. Denno and T. J. Perfect, editors. *Planthoppers, their ecology and management*. Chapman and Hall, New York, New York, USA.
- Duval, C. J., and D. D. Williams. 2000. Ontogenetic changes in prey consumption by the stonefly *Paragnetina media* in relation to temporal variation in prey nutrient content. *Canadian Journal of Zoology* **78**:748–763.
- Eisner, T., M. A. Goetz, D. E. Hill, S. R. Smedley, and J. Meinwald. 1997. Firefly “femmes fatales” acquire defensive steroids (lucibufagins) from their firefly prey. *Proceedings of the National Academy of Sciences (USA)* **94**:9723–9728.
- Elser, J. J., D. Dobberfuhl, N. A. MacKay, and J. H. Schampel. 1996. Organism size, life history, and N:P stoichi-

- ometry: towards a unified view of cellular and ecosystem processes. *BioScience* **46**:674–684.
- Elser, J. J., W. F. Fagan, R. F. Denno, D. R. Dobberfuhl, A. Folarin, A. Huberty, S. Interlandi, S. S. Kilham, E. McCauley, K. L. Schulz, E. H. Siemann, and R. W. Sterner. 2000. Nutritional constraints in terrestrial and freshwater food webs. *Nature* **408**:578–580.
- Endo, T., and A. Endo. 1994. Prey selection by a spider wasp, *Batozonellus lacerticida* (Hymenoptera: Pompilidae): effects of seasonal variation in prey species, size and density. *Ecological Research* **9**:225–235.
- Eubanks, M. D., and R. F. Denno. 1999. The ecological consequences of variation in plants and prey for an omnivorous insect. *Ecology* **80**:1253–1266.
- Eubanks, M. D., and R. F. Denno. 2000a. Host plants mediate omnivore–herbivore interactions and influence prey suppression. *Ecology* **81**:936–947.
- Eubanks, M. D., and R. F. Denno. 2000b. Health food versus fast food: the effects of prey quality and mobility on prey selection by a generalist predator and indirect interactions among prey species. *Ecological Entomology* **25**:140–146.
- Fagan, W. F. 1997. Omnivory as a stabilizing feature of natural communities. *American Naturalist* **150**:554–568.
- Fagan, W. F., Siemann, E. C. Mitter, R. F. Denno, A. F. Huberty, H. A. Woods, and J. J. Elser. 2002. Nitrogen in insects: Implications for trophic complexity and species diversification. *American Naturalist* **160**:784–802.
- Finke, D. L., and R. F. Denno. 2002. Intraguild predation diminished in complex-structured vegetation: implications for prey suppression. *Ecology* **83**:643–652.
- Francis, F., G. Lognay, J. P. Wathelet, and E. Haubruge. 2001. Effects of allelochemicals from first (*Brassicaceae*) and second (*Myzus persicae* and *Brevicoryne brassicae*) trophic levels on *Adalia bipunctata*. *Journal of Chemical Ecology* **27**:243–256.
- Furrer, S., and P. I. Ward. 1995. Differential nutrient extraction in the funnel web spider *Agalena labyrinthica*. *Physiological Entomology* **20**:18–22.
- Greenstone, M. H. 1979. Spider feeding behavior optimizes dietary amino acid composition. *Nature* **282**:501–503.
- Hodge, M. A. 1999. The implications of intraguild predation for the role of spiders in biological control. *The Journal of Arachnology* **27**:351–362.
- Hurd, L. E., and R. M. Eisenberg. 1984. Experimental density manipulation of the predator *Tenodora sinensis* (Orthoptera: Mantidae) in an old-field community. II. The influence of mantids on arthropod community structure. *Journal of Animal Ecology* **53**:955–967.
- Jervis, M. A., and N. A. C. Kidd. 1986. Host-feeding strategies in hymenopteran parasitoids. *Biological Review* **61**:395–434.
- Johnson, D. M., B. G. Akre, and P. H. Crowley. 1975. Modeling arthropod predation: wasteful killing by damselfly naiads. *Ecology* **56**:1081–1093.
- Lenski, R. E. 1984. Food limitation and competition: a field experiment with two *Carabus* species. *Journal of Animal Ecology* **53**:203–216.
- LeRalec, A. 1995. Egg contents in relation to host-feeding in some parasitic Hymenoptera. *Entomophaga* **40**:87–93.
- Li, D., and R. R. Jackson. 1997. Influence of diet on survivorship and growth in *Portia fimbriata*, and araneophagic jumping spider (Araneae: Salticidae). *Canadian Journal of Zoology* **75**:1652–1658.
- MacRae, I. V., and B. A. Croft. 1997. Intra- and inter-specific predation by adult female *Metaseiulus occidentalis* and *Typhlodromus pyri* (Acari: Phytoseiidae) when provisioned with varying densities and ratios of *Tetranychus urticae* (Acari: Tetranychidae) and phytoseiid larvae. *Experimental and Applied Acarology* **21**:235–245.
- Mattson, W. J. 1980. Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics* **11**:119–161.
- Mayntz, D., and S. Toft. 2001. Nutrient composition of the preys diet affects growth and survivorship of a generalist predator. *Oecologia* **127**:207–213.
- McCann, K. S., A. Hastings, and D. R. Strong. 1998. Trophic cascades and trophic trickles in pelagic food webs. *Proceedings of the Royal Society of London B* **265**:205–209.
- McNeill, S., and T. R. E. Southwood. 1978. The role of nitrogen in the development of insect/plant relationships. Pages 77–98 in J. B. Harborne, editor. *Biochemical aspects of plant and animal coevolution*. Academic Press, London, UK.
- Mead, F., C. Habersetzer, D. Gabouriau, and J. Gervet. 1994. Dynamics of colony development in the paper wasp *Polistes dominulus* Christ (Hymenoptera: Vespidae): the influence of prey availability. *Journal of Ethology* **12**:43–51.
- Menge, B., and J. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *American Naturalist* **130**:563–576.
- Mira, A. 2000. Exuviae eating, a nitrogen meal? *Journal of Insect Physiology* **46**:605–610.
- Mitter, C., B. Farrell, and B. Wiegmann. 1988. The phylogenetic study of adaptive zones: has phytophagy promoted insect diversification. *American Naturalist* **132**:107–128.
- Opell, B. D. 1998. Economics of spider orb-webs: the benefits of producing adhesive capture thread and of recycling silk. *Functional Ecology* **12**:613–624.
- Ostrom, P. H., M. Colunga-Garcia, and S. H. Gage. 1997. Establishing pathways of energy flow for insect predators using stable isotope ratios: field and laboratory evidence. *Oecologia* **109**:108–113.
- Oxford, G. S. 1998. Guanine as a colorant in spiders: development, genetics, phylogenetics and ecology. Pages 121–131 in P. A. Selden, editor. *Proceedings of the 17th European Colloquium of Arachnology*, Edinburgh 1997. British Arachnological Society, Burnham Beeches, Bucks, UK.
- Pauly, D., and V. Christensen. 1995. Primary production required to sustain global fisheries. *Nature* **374**:255–257.
- Pennacchio, F., P. Fanti, P. Falabella, M. C. Digilio, F. Bisaccia, and E. Tremblay. 1999. Development and nutrition of the braconid wasp, *Aphidius ervi* in aposymbiotic host aphids. *Archives of Insect Biochemistry and Physiology* **40**:53–63.
- Polis, G. A. 1981. The evolution and dynamics of intraspecific predation. *Annual Review of Ecology and Systematics* **12**:225–251.
- Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* **28**:289–316.
- Polis, G., and S. McCormick. 1986. Scorpions, spiders, and solpugids: predation and competition among distantly related taxa. *Oecologia* **71**:111–116.
- Polis, G. A., C. A. Myers, and R. D. Holt. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics* **20**:297–330.
- Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. *American Naturalist* **147**:813–846.
- Price, P. W. 1984. *Insect ecology*. Second edition. Wiley Interscience, New York, New York, USA.
- Riechert, S. E., and J. M. Harp. 1987. Nutritional ecology of spiders. Pages 645–672 in F. Slansky and J. G. Rodriguez, editors. *Nutritional ecology of insects, mites, spiders,*

- and related invertebrates. John Wiley and Sons, New York, New York, USA.
- Riechert, S. E., and J. Maupin. 1998. Spider effects on prey: tests for superfluous killing in five web builders. Pages 203–210 in P. A. Selden, editor. Proceedings of the 17th European Colloquium on Arachnology. British Arachnological Society, Burnham Breeches, Bucks, UK.
- Rosenheim, J. A. 1998. Higher-order predators and the regulation of insect populations. *Annual Review of Entomology* **43**:421–447.
- Rosenheim, J. A., L. R. Wilhoit, and C. A. Armer. 1993. Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population. *Oecologia* **96**:439–449.
- Rotheray, G. E., and F. S. Gilbert. 1989. Systematics and phylogeny of European predaceous Syrphidae (Diptera) based upon larval and pupal stages. *Zoological Journal of the Linnaean Society* **95**:29–70.
- Schausberger, P., and B. A. Croft. 2000. Nutritional benefits of intraguild predation and cannibalism among generalist and specialist phytoseiid mites. *Ecological Entomology* **25**:473–480.
- Sih, A. 1987. Nutritional ecology of aquatic insect predators. Pages 579–607 in F. Slansky and J. G. Rodriguez, editors. *Nutritional ecology of insects, mites, spiders, and related invertebrates*. John Wiley and Sons, New York, New York, USA.
- Simpson, S. J., and C. L. Simpson. 1990. The mechanisms of nutritional compensation by phytophagous insects. Pages 111–160 in E. A. Bernays, editor. *Insect–plant interactions*. Volume II. CRC Press, Boca Raton, Florida, USA.
- Slansky, F., Jr. 1993. Nutritional ecology: the fundamental quest for nutrients. Pages 29–91 in N. E. Stamp and T. M. Casey, editors. *Caterpillars. Ecological and evolutionary constraints on foraging*. Chapman and Hall, New York, New York, USA.
- Slansky, F., and G. S. Wheeler. 1992. Caterpillars' compensatory feeding response to diluted nutrients leads to toxic allelochemical dose. *Entomologica Experimentalis et Applicata* **65**:171–186.
- Snyder, W. E., S. B. Joseph, R. F. Preziosi, and A. J. Moore. 2000. Nutritional benefits of cannibalism for the lady beetle *Harmonia axyridis* (Coleoptera: Coccinellidae) when prey quality is poor. *Environmental Entomology* **29**:1173–1179.
- Spence, J. R., and H. A. Carcamo. 1991. Effects of cannibalism and intraguild predation in pondskaters (Gerridae). *Oikos* **62**:333–341.
- Stamp, N. E. 2001. Effects of prey quantity and quality on predatory wasps. *Ecological Entomology* **26**:292–301.
- Sterner, R. W. 1997. Modelling the interactions between food quantity and food quality in homeostatic consumers. *Freshwater Biology* **38**:473–482.
- Sterner, R. W., and J. J. Elser. 2002. *Ecological stoichiometry*. Princeton University Press, Princeton, New Jersey, USA.
- Strand, M. R., and J. J. Obrycki. 1996. Host specificity of insect parasitoids and predators. *BioScience* **46**:422–429.
- Strohmeyer, H. H., N. E. Stamp, C. M. Jaromski, and M. D. Bowers. 1998. Prey species and prey diet affect growth of invertebrate predators. *Ecological Entomology* **23**:68–79.
- Sullivan, D. J., and W. Völkl. 1999. Hyperparasitism: multitrophic ecology and behavior. *Annual Review of Entomology* **44**:291–315.
- Tanaka, K. 1991. Food consumption and diet composition of the web-building spider *Agelena limbata* in 2 habitats. *Oecologia* **86**:8–15.
- Thompson, S. N. 1999. Nutrition and culture of entomophilous insects. *Annual Review of Entomology* **44**:561–592.
- Toft, S. 1999. Prey choice and spider fitness. *The Journal of Arachnology* **27**:301–307.
- Toft, S., and D. H. Wise. 1999a. Growth, development, and survival of a generalist predator fed single- and mixed-species diets of different quality. *Oecologia* **119**:191–197.
- Toft, S., and D. H. Wise. 1999b. Behavioral and ecophysiological responses of a generalist predator to single- and mixed-species diets of different quality. *Oecologia* **119**:198–207.
- Uetz, G. W., J. Bishoff, and J. Raven. 1992. Survivorship of wolf spiders (Lycosidae) reared on different diets. *The Journal of Arachnology* **20**:207–211.
- Urabe, J., and Y. Watanabe. 1992. Possibility of N or P limitation for planktonic cladocerans: an experimental test. *Limnology and Oceanography* **37**:244–251.
- Waldbauer, G. P., and S. Friedman. 1991. Self-selection of optimal diets by insects. *Annual Review of Entomology* **36**:43–63.
- White, T. C. R. 1993. *The inadequate environment: nitrogen and the abundance of animals*. Springer-Verlag, New York, New York, USA.
- Wise, D. H. 1979. Effects of an experimental increase in prey abundance on the reproductive rates of two orb-weaving spider species (Araneae: Araneidae). *Oecologia* **41**:289–300.
- Wise, D. H. 1993. *Spiders in ecological webs*. Cambridge University Press, Cambridge, UK.
- Wissinger, S. A., G. B. Sparks, G. L. Rouse, W. S. Brown, and H. Steltzer. 1996. Intraguild predation and cannibalism among larvae of detritivorous caddisflies in subalpine wetlands. *Ecology* **77**:2421–2430.
- Wu, Z. X., A. C. Cohen, and D. A. Nordlund. 2000. The feeding behavior of *Trichogramma brassicae*: new evidence for selective ingestion of solid food. *Entomologica Experimentalis et Applicata* **96**:1–8.

UNDERSTANDING OMNIVORY NEEDS A BEHAVIORAL PERSPECTIVE

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Abstract. While the importance of omnivory in community and food web ecology has received recent recognition, the behavioral basis of omnivory has not been thoroughly explored. Here we argue that understanding the basis of food mixing (i.e., eating different food types) and food selection behavior is central to understanding the causes and consequences of omnivory. Despite the existence of several alternative hypotheses, constraints imposed by nutrients are often assumed to explain the function of food mixing by omnivores and herbivores. However, few studies have actually addressed this issue through rigorous tests of multiple hypotheses. To illustrate the importance of non-nutritive factors, we marshal evidence for the roles of toxin dilution, parasite avoidance and resistance, and predation risk in food mixing and food selection by omnivores and polyphagous herbivores. Whether food mixing stabilizes population, community, and food web dynamics is likely to depend on the details of food selection and the spatial and temporal scales of food mixing.

Key words: *deterrents; diet; food selection; foraging; grazing; omnivory; polyphagy; predation risk; toxins; tritrophic interactions.*

INTRODUCTION

In the last few decades, omnivory has assumed an important position in the study of population, community, and food web ecology (e.g., Pimm and Lawton 1978, Polis and Strong 1996). Here we argue that studying the causes and consequences of omnivory could also benefit from the perspective of behavioral ecology. Namely, we need to understand how and why omnivores make particular foraging decisions. Central among these is the habit of eating different food types, i.e., food mixing. We define food mixing as the ingestion of multiple food types over an animal's lifetime or stage of a complex life cycle; we consider food types as different species that differ qualitatively to the consumer. Food mixing is a fundamental type of foraging strategy that includes omnivory, as well as polyphagy by individual herbivores and carnivores. Because our focus is on food mixing and our expertise is herbivores, we will draw examples from both omnivores and food mixing herbivores from terrestrial and marine ecosystems.

We think that understanding the behavioral causes of omnivory will inform its ecological consequences. It is too often assumed, for example, that nutritional constraints (including food availability) uniquely determine the function of food mixing behavior underlying omnivory. Here we consider some alternative, functional explanations for food mixing. One of our main points is that food mixing per se and selecting particular foods are actually different issues and may need separate consideration, conceptually and empir-

ically. We then discuss why the function of food mixing and food selection might determine the ecological consequences of omnivory. Finally, we suggest that the spatial and temporal scale of food mixing might determine its ecological consequences.

WHY EAT A MIXED DIET?

Here we consider several hypotheses (summarized in Hailey et al. 1998) proposed to explain "varied diets," "diet mixing," or "food mixing" in our terminology. As applied to omnivores (e.g., mixing plant and animal foods), these hypotheses are: (1) a qualitatively superior food type exists but is limited in supply (e.g., prey), necessitating the inclusion of suboptimal (e.g., plant) food in the diet; (2) no single food type is qualitatively superior, so food mixing allows the intake of nutritionally complementary foods (e.g., animal and plant material), enhancing digestion or the postdigestive utilization of nutrients; (3) foods contain toxins (e.g., plants and noxious prey), so food mixing limits the ingestion of particular compounds from particular food types; (4) the relative quality of food types changes over time, so food mixing allows the animal to periodically sample different food types and switch to a currently superior food type; (5) food mixing may minimize exposure to other environmental risks (e.g., natural enemies, abiotic factors).

A potentially separate but related issue is the functional basis for selecting particular food types in the mixture. Indeed, there may be functional differences between the basis for mixing and the basis for selecting particular foods. While both contribute to an individual's pattern of foraging and diet, they are separate issues and addressing them may require separate experiments. For example, a food mixing animal that encounters hypothetical food types A, B, and C may select

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all three, or only two of them. Food selection patterns may differ for a given mixture of food types: this animal may eat a large amount of A relative to B and C, or feed in some other pattern. Although food mixing per se and specific food selection go hand in hand, they may have different functional explanations. To continue the above example, the function of mixing foods A, B, and C may be to obtain a balanced intake of nutrients, or to minimize the intake of particular toxins associated with each food. However, food A may be eaten in the largest amount because it is the most abundant food type or it provides a physical or chemical defense against natural enemies. It is also possible that a food of seemingly less importance, like food B or C, provides a critical micronutrient or chemical used in reproduction, making it essential for survival and reproduction. The numerous possible reasons for selecting particular foods have been reviewed elsewhere (e.g., Stephens and Krebs 1986), and we will not attempt this here as it is not an issue unique to food mixers.

Despite the abundance of nonexclusive hypotheses for both mixing and selecting foods, studies of food mixing by omnivores have often focused on how nutritional constraints may drive food mixing (hypotheses 1, 2, and 4 above) and food selection, with scant empirical attention given to the rest. We do not think any of the above hypotheses (for food mixing or food selection) is generally tested at present because few studies have employed critical experiments to distinguish among them. Nevertheless, several current notions in community, food web, and ecosystem ecology assume that constraints imposed by nutrients primarily, if not exclusively, determine patterns of mixing and selecting food by omnivores and herbivores. This assumption, for example, apparently underlies the recent approach of reducing such trophic interactions to the ratios of essential atomic elements across trophic levels ("ecological stoichiometry") to understand food web dynamics and nutrient cycling (e.g., Elser et al. 2000, Sterner and Elser 2002, Denno and Fagan 2003). Extrapolating trophic interactions to food web dynamics strictly on the basis of nutritive elements ignores much empirically documented, meaningful complexity in terrestrial (e.g., Stamp and Casey 1993, Abrahamson and Weis 1997, Dicke 2000, Schmitz and Suttle 2001) and marine (reviewed in Paul et al. 2001) trophic interactions. For example, it is often assumed that animal food is more nutritious than plant food. Several recent studies show that this is not necessarily the case (e.g., Eubanks and Denno 1999, Cruz-Rivera and Hay 2000). While it may be true that nutrient ratios of prey tissues are usually more similar to an animal consumer than those of plant tissues, a consumer's growth, survival, and reproductive responses depend on its particular feeding behavior (i.e., tissue selection) and physiology as well as other aspects of food quality (e.g., toxins).

There is no doubt that nutritive needs are important determinants of foraging choices by omnivores and

other animals. However, the critical decisions to eat a particular food in the first place, and to continue eating it rather than the available alternatives are likely to depend proximately and ultimately on other aspects of food quality (e.g., secondary metabolites, physical barriers to feeding), ecological risks (e.g., natural enemies) and competing needs (e.g., thermoregulation) that may modify or take precedence over responses to food's nutritive value. Further, foraging decisions of this sort that accumulate into patterns of mixing and selecting foods (i.e., diet) may vary according to the consumer's experience and the prevailing environmental conditions (e.g., availability and quality of alternative foods). We expect the relative importance of these factors, and precisely how they interact, to vary depending on the natural history of the omnivore. However, we will emphasize the complex roles of noxious chemicals and natural enemies because their importance has been relatively neglected.

EVIDENCE FOR ALTERNATIVE DETERMINANTS OF FOOD MIXING AND FOOD SELECTION

We believe the importance of mixing and selecting foods to avoid overingestion of particular secondary metabolites (toxin dilution: Freeland and Janzen 1974) is vastly underappreciated. Freeland et al. (1985) showed that food mixing by mice can counteract negative effects of individually harmful secondary metabolites. This laboratory study demonstrated reduced growth rates for mice given foods with tannins or saponins, and for those given a food containing set concentrations of both toxins (no-choice trials). However, when mice were allowed to choose between foods containing either tannins or saponins, growth rates were no different from those of control mice given food without toxins. Similar studies with other species and their natural foods are needed. Agrawal et al. (1999) showed that the induction of elevated secondary metabolites in cotton plants promoted switching from herbivory to predation of mite eggs by the omnivorous thrips, *Frankliniella occidentalis*. Thrips performance was reduced on induced plants without mite eggs, suggesting that the deterrence or toxicity of secondary metabolites in cotton was driving switching behavior. Various studies have shown that secondary metabolites deter food-mixing insects. For example, secondary metabolites produced by plants (Dyer et al. 2001) and various compounds sequestered by caterpillars from their host plants (Dyer 1995, Dyer and Bowers 1996) deter omnivorous ants, suggesting that toxin avoidance influences food selection by this ecologically important group of omnivores (Tobin 1994). To our knowledge, no studies have yet tested the influence of secondary metabolites on food mixing per se by omnivorous ants.

Many secondary metabolites evoke a "bitter" taste response in mammals, yet behavioral responses by food mixing mammals to ecologically relevant mixtures of food types containing them are rarely measured. In a

test of 30 mammal species with differing foraging strategies (carnivores, omnivores, grazers, browsers), Glendinning (1994) found the bitter rejection response threshold to be related to the expected likelihood of encountering toxins in food: carnivores were most sensitive, followed by omnivores, grazers, then browsers. This pattern implies that deterrents and toxins may negatively influence food selection by omnivores to an even greater extent than by generalist herbivores, which are well known to reject food on the basis of secondary metabolites. For example, we have found food mixing by the forb-feeding woolly bear caterpillar *Grammia geneura* (Arctiidae) to be predominantly a negative, behavioral response to plant secondary metabolites consistent with toxin dilution (Singer et al. 2002). Yet food selection (i.e., preference) is likely based on both the nutritive and defensive value of particular host-plant species (Singer and Stireman 2003). In this case, feeding on certain "toxic" plant species may increase a caterpillar's resistance to parasitoids at a nutritional cost; we suspect this tritrophic effect is mediated by secondary metabolites acquired from preferred host-plant species.

Accumulating evidence suggests that a wide range of food-mixing animals select food partly on the basis of parasite avoidance and resistance, and the use of secondary metabolites for the latter may be quite general. Parasite avoidance, for example, explains patterns of food selection by vertebrate grazers (Hutchings et al. 1999, 2002) and omnivorous tadpoles (Pfennig 2000). In both of these cases, there is evidence for a trade-off between a food's nutritive value and its likelihood of transmitting parasites. Various studies (e.g., Hart 1997) suggest that food-mixers select foods with secondary metabolites for parasite resistance. In one interesting laboratory study, mice routinely ingested small amounts of chloroquine, thereby increasing their resistance to malaria (Vitazkova et al. 2001). Field studies addressing this issue with omnivorous rodents are needed.

Some food-mixing animals change their food preference in response to parasite attack. The food mixing woolly bear caterpillar, *Platyprepia virginalis* (Arctiidae) changes its host-plant preference in response to parasitoid infection, thereby increasing its survival (Karbon and English-Loeb 1997). In this particular case, both the parasitoid and the host frequently survive. Sick primates commonly exhibit pharmacophagy (specifically termed zoopharmacognosy) in nature by selectively ingesting parts of particular plant species that reduce parasite infections (Huffman 2001). This type of behavior has only been revealed through careful observation, and may be far more widespread than is currently known or suspected (Clayton and Wolfe 1993).

Many studies argue that predation risk places important evolutionary and ecological constraints on foraging (e.g., Lima and Dill 1990, Houtman and Dill

1998, Lima and Bednekoff 1999, Sih and McCarthy 2002). Food-mixing animals have figured prominently in such work. For example, the omnivorous ant *Lasius pallitarsis* selected food patches in a laboratory environment by balancing food quality with predation risk from another ant species (Nonacs and Dill 1990). Field studies show that the omnivorous fire ant *Solenopsis richteri* reduced foraging activity in the presence of phorid parasitoids (effectively predators to the ants) in the same manner regardless of food quantity (Folgarait and Gilbert 1999). These studies suggest that ant colonies in nature would vary the range and quantity of particular foods taken in response to different levels of predation risk in a way that may or may not depend on a food's nutritional reward. In another example, different types of predation risk from species of hunting spiders within a guild cause different feeding responses by polyphagous grasshoppers, in turn causing different patterns of herbivory in old fields (Schmitz and Suttle 2001).

Temporal variation in the threat of predation may influence foraging (Lima and Bednekoff 1999, Sih and McCarthy 2002), and limit feeding to particular times and places, thus changing the range of available food species. Highly polyphagous rodents may feed exclusively in habitat patches with vegetative cover (e.g., Abramsky et al. 1996) and lower food abundance (Abramsky et al. 2002) and ants may forage only at certain times of day (Orr and Seike 1998) in response to risks imposed by key predators and parasitoids, respectively.

ECOLOGICAL CONSEQUENCES OF FOOD MIXING

How much does variation in the bases of food mixing and of food selection matter at larger ecological scales? There are limited data to address this question at present. Yet, it is clear that food mixing by one omnivore cannot be assumed to be ecologically equivalent to food mixing by another. The range and relative quantities of food types consumed by omnivores in nature varies among related species (birds, O'Donnell and Dilks 1994; rodents, Ellis et al. 1998), populations or environments (Wilson and Bradtke 1999), and conspecific individuals within a population (e.g., sexual differences, Hailey et al. 2001; immigrants vs. residents, Tardiff and Gray 1978). Furthermore, we think the precise factors that govern variation in food mixing and food selection may determine their ecological consequences. To illustrate this, we point to the example of zoopharmacognosy in primates (Huffman 2001). Although the amount of medicinal foods ingested may be small relative to other food types, their consumption may have a relatively great impact on both resource and consumer populations. In the case of resources, for example, the removal of some critical medicinal tissue (e.g., extracting pith from young shoots) may greatly increase the likelihood of killing individual plants in a population. For consumers, a relatively small dose of a medicinal

plant may determine the life or death of infected individuals, with important consequences for the population's demography.

The flexibility of food selection exhibited by individual omnivores has pivotal but complex consequences for population, community, and food web dynamics. Several authors have recently made this general point (Agrawal et al. 1999, Agrawal and Klein 2000, Coll and Guershon 2002). Here we elaborate a bit further. While it is currently argued that omnivory stabilizes population dynamics of both consumers and their resources (e.g., prey and plants), this putative stabilizing effect depends on food-mixing behavior. The stabilization of omnivore populations follows from the ability to switch from one food type to another (i.e., food mixing) when the first food is depleted or absent (e.g., Naranjo and Gibson 1996, Fagan 1997, Eubanks and Denno 1999). Populations of prey or plants may be stabilized by the refuge created when their omnivorous consumers switch to alternative food rather than continuing to reduce populations at low levels (e.g., Cottrell and Yeagan 1998, Lalonde et al. 1999) or when the trophic interaction between omnivores and their food is dampened by intraguild predation (Rosenheim 2001). However, the existence of this refuge over the long term is not clear. High quality alternative food may maintain large omnivore populations that continue to suppress populations of prey (Eubanks and Denno 2000) and perhaps those of competing carnivores (M. E. Hay, *personal communication*).

How do these population level effects extrapolate into food web dynamics and community structure? There is presently no clear answer. The stabilizing effect of food mixing by omnivores is associated with weak trophic links in the web. Recent theory (e.g., Polis and Strong 1996, McCann et al. 1998) and empirical evidence from simple food webs (Fagan 1997, Holyoak and Sachdev 1998) support the idea that omnivory stabilizes food webs via weak trophic interactions. In "weak" interactions, however, indirect effects of alternative foods can magnify the variance in interaction strength between consumers and prey, with seemingly important, unstudied consequences for community structure (Berlow 1999). Furthermore, evidence from complex ecosystems shows that it is the pattern of weak trophic interactions that accounts for food web stability rather than interaction strength per se (de Ruiter et al. 1995).

SPATIAL AND TEMPORAL SCALE OF FOOD MIXING

We think the ecological impact of food mixing results from its spatial and temporal scale, in addition to the functional bases of food mixing and food selection. Murdoch (1969) made a similar point, but few studies have followed this line of work. Large-scale food mixing may typically involve dietary specificity at particular times and places with consequences similar to the impact of feeding by dietary specialists. At large spatial

scales, for example, omnivorous birds may forage by migrating between patches with different food types. Some species may feed primarily on plant or fungal material or arthropod prey in each one (O'Donnell and Dilks 1994). At large temporal scales, a related strategy is switching between food types over the season. O'Donnell and Dilks (1994) show that omnivorous birds in a temperate New Zealand forest switched between specific foods during the year. Seasonal food switching by omnivores typically involves relatively increased carnivory during the breeding season and relatively increased herbivory (including granivory) during the rest of the year (Polis and Strong 1996). A third related food-mixing strategy at relatively large temporal scales involves ontogenetic shifts in food selection. Such omnivores may typically feed primarily on prey during periods of rapid growth (e.g., early development; McCauley and Bjorndal 1999, Choat and Clements 1998) and during reproductive periods, while feeding primarily on plant material during other parts of the life cycle.

Small-scale food mixing may result in weak and dispersed trophic interactions in food webs, however its impact is relatively unstudied. This type of food mixing occurs within small-scale patches of variable food types and a temporal scale of days, hours, or minutes. Highly omnivorous rodents (Ellis et al. 1998) and arthropods (e.g., ants; Stradling 1987) exemplify such extreme food mixers, and undoubtedly have important roles in food webs. In most cases studied to date, the community and food web consequences of mixing and food selection have yet to be tested. A few recent studies have been done with food mixing grasshoppers (e.g., Beckerman et al. 1997, Schmitz et al. 1997, Schmitz and Suttle 2001), showing that predator-induced changes in small-scale food mixing by grasshoppers can have a large impact on the plant community.

CONCLUSION

The causes and consequences of omnivory depend on foraging behavior. We have focused on some functional reasons for mixing foods and selecting particular foods that have received less attention than constraints imposed by nutrients. Nutritive factors alone cannot be assumed to explain the ecologically important variation in food mixing and food selection in terrestrial and marine ecosystems. We think an understanding of omnivory will be advanced by the use of critical experiments that consider multiple, ecologically relevant, functional hypotheses for mixing and selecting food. Some key questions include: What factors influence decisions to leave one food and accept others? What choices are made when food-mixing species face multiple food types with different benefits and costs? Direct observations in nature will be valuable in designing appropriate experiments because the central issue is how factors such as nutrient balancing, toxin dilu-

tion, pharmacophagy, and avoidance of risk play out in nature. Under what circumstances does one such factor or several drive food-mixing behavior? And what are the ecological consequences of food mixing that is driven by one cause versus another or several? Only by answering such questions can investigators firmly connect variation in food mixing (e.g., different causes, different spatial and temporal scales) to consequences for population, community, food web, and ecosystem dynamics.

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LITERATURE CITED

- Abrahamson, W. G., and A. E. Weis. 1997. Evolutionary ecology across three trophic levels: goldenrods, gallmakers, and natural enemies. Princeton University Press, Princeton, New Jersey, USA.
- Abramsky, Z., M. L. Rosenzweig, and A. Subach. 2002. The costs of apprehensive foraging. *Ecology* **83**:1330–1340.
- Abramsky, Z., E. Strauss, A. Subach, and B. P. Kotler. 1996. The effect of barn owls (*Tyto alba*) on the activity and microhabitat selection of *Gerbillus allenbyi* and *G. pyramidum*. *Oecologia* **105**:313–319.
- Agrawal, A. A., and C. N. Klein. 2000. What omnivores eat: direct effects of induced plant resistance on herbivores and indirect consequences for diet selection by omnivores. *Journal of Animal Ecology* **69**:525–535.
- Agrawal, A. A., C. Kobayashi, and J. S. Thaler. 1999. Influence of prey availability and induced host plant resistance on omnivory by western flower thrips. *Ecology* **80**:518–523.
- Beckerman, A. P., M. Uriarte, and O. J. Schmitz. 1997. Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. *Proceedings of the National Academy of Sciences (USA)* **94**:10735–10738.
- Berlow, E. L. 1999. Strong effects of weak interactions in ecological communities. *Nature* **398**:330–334.
- Choat, J. H., and K. D. Clements. 1998. Vertebrate herbivores in marine and terrestrial environments: a nutritional ecology perspective. *Annual Review of Ecology and Systematics* **29**:375–403.
- Clayton, D. H., and N. D. Wolfe. 1993. The adaptive significance of self-medication. *Trends in Ecology and Evolution* **8**:60–63.
- Coll, M., and M. Guershon. 2002. Omnivory in terrestrial arthropods: mixing plant and prey diets. *Annual Review of Entomology* **47**:267–297.
- Cottrell, T. E., and K. V. Yeorgan. 1998. Effect of pollen on *Coleomegilla maculata* (Coleoptera: Coccinellidae) population density, predation, and cannibalism in sweet corn. *Environmental Entomology* **27**:1402–1410.
- Cruz-Rivera, E., and M. E. Hay. 2000. The effects of diet mixing on consumer fitness: macroalgae, epiphytes, and animal matter as food for marine amphipods. *Oecologia* **123**:252–264.
- Denno, R. F., and W. F. Fagan. 2003. Might nitrogen limitation promote omnivory among carnivorous arthropods? *Ecology* **84**:2522–2531.
- De Ruiter, P. C., A. Neutel, and J. C. Moore. 1995. Energetics, patterns of interactions strengths, and stability in real ecosystems. *Science* **269**:1257–1260.
- Dicke, M. 2000. Chemical ecology of host-plant selection by herbivorous arthropods: a multitrophic perspective. *Biochemical Systematics and Ecology* **28**:601–617.
- Dyer, L. A. 1995. Tasty generalists and nasty specialists? A comparative study of antipredator mechanisms in tropical lepidopteran larvae. *Ecology* **76**:1483–1496.
- Dyer, L. A., and M. D. Bowers. 1996. The importance of sequestered iridoid glycosides as a defense against an ant predator. *Journal of Chemical Ecology* **22**:1527–1539.
- Dyer, L. A., C. D. Dodson, J. Beihoffer, and D. K. Letourneau. 2001. Trade-offs in antiherbivore defense in *Piper cenocladum*: ant mutualists versus plant secondary metabolites. *Journal of Chemical Ecology* **27**:581–592.
- Ellis, B. A., J. N. Mills, G. E. Glass, K. T. McKee, Jr., D. A. Enria, and J. E. Childs. 1998. Dietary habits of the common rodents in an agroecosystem in Argentina. *Journal of Mammalogy* **79**:1203–1220.
- Elser, J. J., W. F. Fagan, R. F. Denno, D. R. Dobberfuhl, A. Folarin, A. Huberty, S. Interlandi, S. S. Kilham, E. McCauley, K. L. Schulz, E. H. Siemann, and R. W. Sterner. 2000. Nutritional constraints in terrestrial and freshwater food webs. *Nature* **408**:578–580.
- Eubanks, M. D., and R. F. Denno. 1999. The ecological consequences of variation in plants and prey for an omnivorous insect. *Ecology* **80**:1253–1266.
- Eubanks, M. D., and R. F. Denno. 2000. Host plants mediate omnivore–herbivore interactions and influence prey suppression. *Ecology* **81**:936–947.
- Fagan, W. F. 1997. Omnivory as a stabilizing feature of natural communities. *American Naturalist* **150**:554–567.
- Folgarait, P. J., and L. E. Gilbert. 1999. Phorid parasitoids affect foraging activity of *Solenopsis richteri* under different availability of food in Argentina. *Ecological Entomology* **24**:163–173.
- Freeland, W. J., P. H. Calcott, and L. R. Anderson. 1985. Tannins and saponin: interaction in herbivore diets. *Biochemical Systematics and Ecology* **13**:189–193.
- Freeland, W. J., and D. H. Janzen. 1974. Strategies in herbivory by mammals: the role of plant secondary compounds. *American Naturalist* **108**:889–894.
- Glendinning, J. I. 1994. Is the bitter rejection response always adaptive? *Physiology and Behavior* **56**:1217–1227.
- Hailey, A., R. L. Chidavaenzi, and J. P. Loveridge. 1998. Diet mixing in the omnivorous tortoise *Kinixys spekii*. *Functional Ecology* **12**:373–385.
- Hailey, A., I. M. Coulson, and T. Mwabvu. 2001. Invertebrate prey and predatory behaviour of the omnivorous African tortoise *Kinixys spekii*. *African Journal of Ecology* **39**:10–17.
- Hart, B. L. 1997. Behavioural defence. Pages 59–77 in D. H. Clayton and J. Moore, editors. *Host–parasite evolution: general principles and avian models*. Oxford University Press, Oxford, UK.
- Holyoak, M., and S. Sachdev. 1998. Omnivory and the stability of simple food webs. *Oecologia* **117**:413–419.
- Houtman, R., and L. M. Dill. 1998. The influence of predation risk on diet selectivity: a theoretical analysis. *Evolutionary Ecology* **12**:251–262.
- Huffman, M. A. 2001. Self-meditative behavior in the African great apes: an evolutionary perspective into the origins of human traditional medicine. *BioScience* **51**:651–661.
- Hutchings, M. R., I. Kyriazakis, I. J. Gordon, and F. Jackson. 1999. Trade-offs between nutrient intake and faecal avoidance in herbivore foraging decisions: the effect of animal parasitic status, level of feeding motivation and sward nitrogen content. *Journal of Animal Ecology* **68**:310–323.
- Hutchings, M. R., J. M. Milner, I. J. Gordon, I. Kyriazakis, and F. Jackson. 2002. Grazing decisions of Soay sheep, *Ovis aries*, on St. Kilda: a consequence of parasite distribution? *Oikos* **96**:235–244.
- Karban, R., and G. English-Loeb. 1997. Tachinid parasitoids affect host plant choice by caterpillars to increase caterpillar survival. *Ecology* **78**:603–611.

- Lalonde, R. G., R. R. McGregor, D. R. Gillespie, and B. D. Roitberg. 1999. Plant-feeding by arthropod predators contributes to the stability of predator-prey dynamics. *Oikos* **87**:603–608.
- Lima, S. L., and Bednekoff. 1999. Temporal variation in danger drives antipredator behavior: the predation allocation hypothesis. *American Naturalist* **153**:649–659.
- Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation—a review and prospectus. *Canadian Journal of Zoology* **68**:619–640.
- McCann, K., A. Hastings, and G. R. Huxel. 1998. Weak trophic interactions and the balance of nature. *Nature* **395**:794–798.
- McCauley, S. J., and K. A. Bjørndal. 1999. Response to dietary dilution in an omnivorous freshwater turtle: implications for ontogenetic dietary shifts. *Physiological and Biochemical Zoology* **72**:101–108.
- Murdoch, W. W. 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecological Monographs* **39**:335–354.
- Naranjo, S. E., and R. L. Gibson. 1996. Phytophagy in predaceous Heteroptera: effects on life history and population dynamics. Pages 57–93 in O. Alomar and R. N. Wiedenmann, editors. *Zoophytophagous Heteroptera: implications for life history and integrated pest management*. Thomas Say Publication in Entomology, Entomological Society of America, Lanham, Maryland, USA.
- Nonacs, P., and L. M. Dill. 1990. Mortality risk vs. food quality trade-off in a common currency: ant patch preferences. *Ecology* **71**:1886–1892.
- O'Donnell, C. F. J., and P. J. Dilks. 1994. Foods and foraging of forest birds in temperate rainforest, South Westland, New Zealand. *New Zealand Journal of Ecology* **18**:87–107.
- Orr, M. R., and S. H. Seike. 1998. Parasitoids deter foraging by Argentine ants (*Linepithema humile*) in their native habitat in Brazil. *Oecologia* **117**:420–425.
- Paul, V. J., E. Cruz-Rivera, and R. W. Thacker. 2001. Chemical mediation of macroalgal-herbivore interactions: ecological and evolutionary perspectives. Pages 227–265 in J. B. McClintock and B. J. Baker, editors. *Marine chemical ecology*. CRC Press, Boca Raton, Florida, USA.
- Pfennig, D. W. 2000. Effect of predator-prey phylogenetic similarity on the fitness consequences of predation: a trade-off between nutrition and disease? *American Naturalist* **155**:335–345.
- Pimm, S. L., and J. H. Lawton. 1978. On feeding on more than one trophic level. *Nature* **275**:542–544.
- Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. *American Naturalist* **147**:813–846.
- Rosenheim, J. A. 2001. Source-sink dynamics for a generalist insect predator in habitats with strong higher-order predation. *Ecological Monographs* **71**:93–116.
- Schmitz, O. J., A. P. Beckerman, and K. M. O'Brien. 1997. Behaviorally mediated trophic cascades: the effects of predation risk on food web interactions. *Ecology* **78**:1388–1399.
- Schmitz, O. J., and K. B. Suttle. 2001. Effects of top predator species on direct and indirect interactions in a food web. *Ecology* **82**:2072–2081.
- Sih, A., and T. M. McCarthy. 2002. Prey responses to pulses of risk and safety: testing the risk allocation hypothesis. *Animal Behaviour* **63**:437–443.
- Singer, M. S., E. A. Bernays, and Y. Carriere. 2002. The interplay between nutrient balancing and toxin dilution in foraging by a generalist insect herbivore. *Animal Behaviour* **64**:629–643.
- Singer, M. S., and J. O. Stireman III. 2003. Does anti-parasitoid defense explain host-plant selection by a polyphagous caterpillar? *Oikos* **100**:554–562.
- Stamp, N. E., and T. M. Casey. 1993. *Caterpillars: ecological and evolutionary constraints on foraging*. Chapman and Hall, New York, New York, USA.
- Stephens, D. W., and J. R. Krebs. 1986. *Foraging theory*. Princeton University Press, Princeton, New Jersey, USA.
- Sterner, R. W., and J. J. Elser. 2002. *Ecological stoichiometry*. Princeton University Press, Princeton, New Jersey, USA.
- Stradling, D. J. 1987. Nutritional ecology of ants. Pages 927–969 in F. Slansky, Jr. and J. G. Rodriguez, editors. *Nutritional ecology of insects, mites, spiders, and related invertebrates*. Wiley, New York, New York, USA.
- Tardiff, R. R., and L. Gray. 1978. Feeding diversity in resident and immigrant *Peromyscus leucopus*. *Journal of Mammalogy* **59**:559–562.
- Tobin, J. E. 1994. Ants as primary consumers: diet and abundance in the Formicidae. Pages 279–307 in J. H. Hunt and C. A. Nalepa, editors. *Nourishment and evolution in insect societies*. Westview Press, Boulder, Colorado, USA.
- Vitazkova, S. K., E. Long, A. Paul, and J. I. Glendinning. 2001. Mice suppress malaria infection by sampling a “bitter” chemotherapy agent. *Animal Behaviour* **61**:887–894.
- Wilson, B. A., and E. Bradtke. 1999. The diet of the New Holland mouse, *Pseudomys novaehollandiae* (Waterhouse) in Victoria. *Wildlife Research* **26**:439–451.

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-

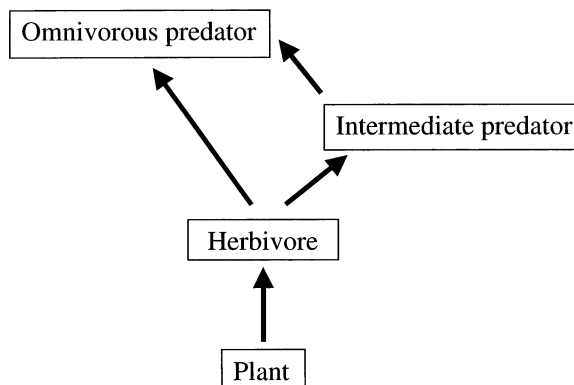


FIG. 1. Trophic web of the arthropod community represented in the simulation model.

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-

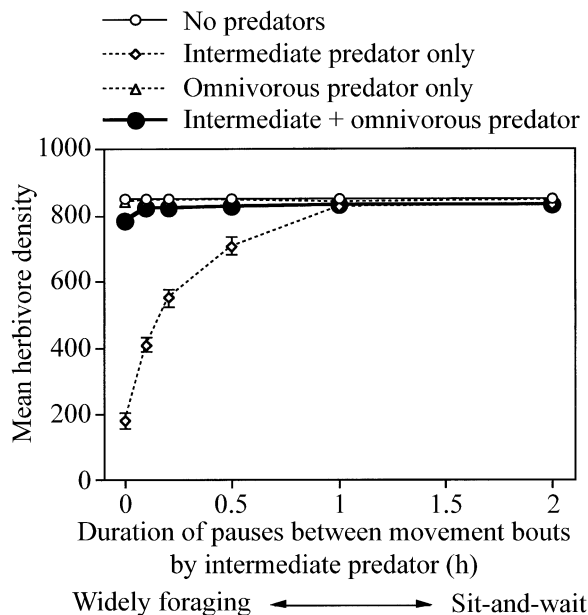


FIG. 2. Influence of intermediate predator mobility on its efficacy as a regulator of a sedentary herbivore population. Mean herbivore densities in the absence of predators ("No predators") and in the presence of only the omnivorous predator ("Omnivorous predator only") are shown as points of reference. 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

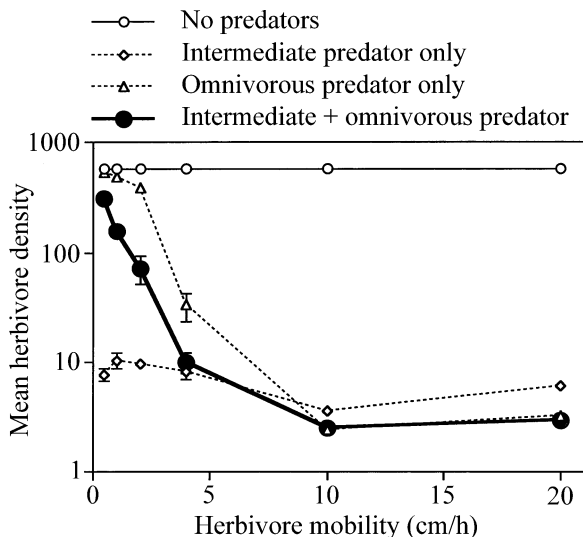


FIG. 3. Influence of herbivore mobility on herbivore population suppression by predators. Curves are shown for the individual and combined abilities of a widely foraging intermediate predator and a sit-and-wait omnivorous top predator to suppress the herbivore's population density. The baseline parameters (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

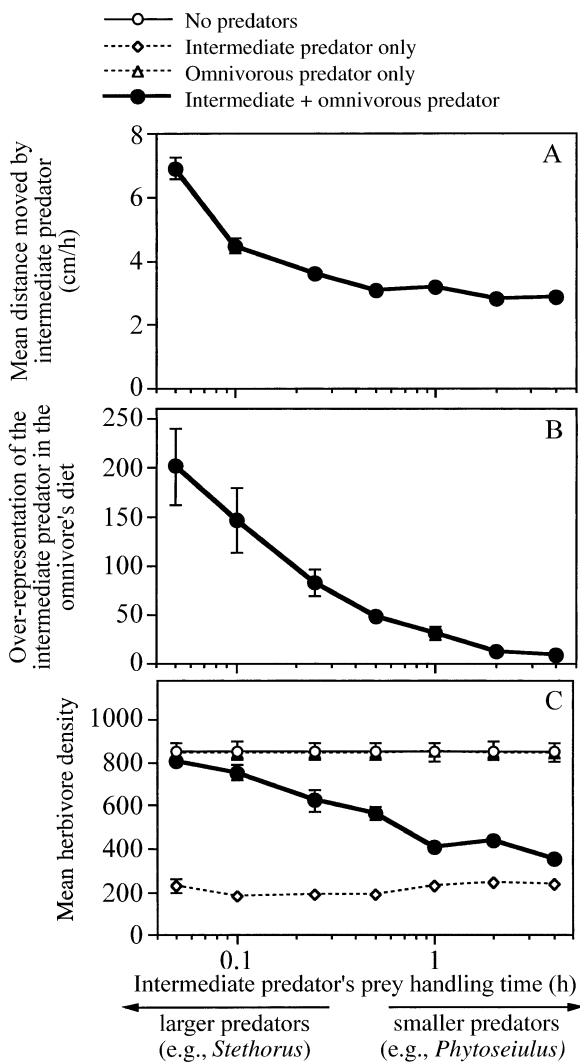


FIG. 4. Influence of prey handling time of the intermediate predator on interactions in a community of an herbivore, an intermediate predator, and a sit-and-wait omnivorous top predator. Predators with body sizes much larger than their prey (e.g., *Stethorus*) have short prey handling times, whereas 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.

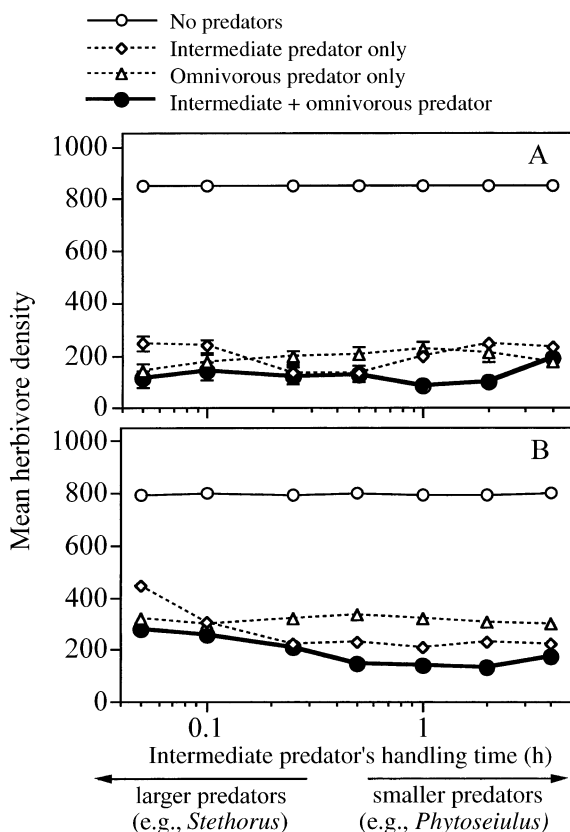


FIG. 5. Influence of prey handling time of the intermediate predator on interactions in a community of a widely foraging intermediate predator, a widely foraging omnivorous top predator, and either (A) a sedentary herbivore or (B) a mobile herbivore. Intermediate predators with body sizes much larger 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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LITERATURE CITED

- Agrawal, A. A., and R. Karban. 1997. Domatia mediate plant-arthropod mutualism. *Nature* **387**:562-563.
- Anholt, B. R., and E. E. Werner. 1995. Interaction between food availability and predation mortality mediated by adaptive behavior. *Ecology* **76**:2230-2234.
- Bell, W. J. 1991. *Searching behaviour*. Chapman and Hall, London, UK.
- Cisneros, J. J., and J. A. Rosenheim. 1997. Ontogenetic change of prey preference in a generalist predator, *Zelus renardii*, and its influence on the intensity of predator-predator interactions. *Ecological Entomology* **22**:399-407.
- Colfer, R. G., and J. A. Rosenheim. 2001. Predation on immature parasitoids and its influence of aphid population suppression. *Oecologia* **126**:292-304.
- Colfer, R. G., J. A. Rosenheim, L. D. Godfrey, and C. L. Hsu. *In press*. Interactions between augmentatively released predaceous mites and naturally-occurring generalist predators. *Environmental Entomology*.
- Croft, B. A., and I. V. MacRae. 1992. Persistence of *Typhlodromus pyri* and *Metaseiulus occidentalis* (Acari: Phytoseiidae) on apple after inoculative release and competition with *Zetzellia mali* (Acari: Stigmaeidae). *Environmental Entomology* **21**:1168-1177.
- DeAngelis, D. L., and L. J. Gross, editors. 1992. *Individual-based models and approaches in ecology: populations, communities, and ecosystems*. Chapman and Hall, New York, New York, USA.
- Denno, R. F., and W. F. Fagan. 2003. Might nitrogen limitation promote omnivory among carnivorous arthropods? *Ecology* **84**:2522-2531.
- Eubanks, M. D., and R. F. Denno. 2000. Health food vs. fast food: the effects of prey quality and mobility on prey selection by a generalist predator and indirect interactions among prey species. *Ecological Entomology* **25**:140-146.
- Finke, D. L., and R. F. Denno. 2002. Intraguild predation diminished in complex-structured vegetation: implications for prey suppression. *Ecology* **83**:643-652.
- Foelix, R. F. 1982. *Biology of spiders*. Harvard University Press, Cambridge, Massachusetts, USA.
- Gastreich, K. R. 1999. Trait-mediated indirect effects of a theridiid spider on an ant-plant mutualism. *Ecology* **80**:1066-1070.

- Gerritsen, J., and J. R. Strickler. 1977. Encounter probabilities and community structure in zooplankton: a mathematical model. *Journal of the Fisheries Research Board of Canada* **34**:73–82.
- Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. *American Naturalist* **94**:421–425.
- Hairston, N. G., Jr., and N. G. Hairston, Sr. 1993. Cause-effect relationships in energy flow, trophic structure and interspecific interactions. *American Naturalist* **142**:379–411.
- Hairston, N. G., Jr., and N. G. Hairston, Sr. 1997. Does food web complexity eliminate trophic-level dynamics? *American Naturalist* **149**:1001–1007.
- Halaj, J., and D. H. Wise. 2001. Terrestrial trophic cascades: how much do they trickle? *American Naturalist* **157**:262–281.
- Hastings, A. 2001. Transient dynamics and persistence of ecological systems. *Ecology Letters* **4**:215–220.
- Hawkins, B. A. 1994. Pattern and process in host-parasitoid interactions. Cambridge University Press, Cambridge, UK.
- Holt, R. D., and G. A. Polis. 1997. A theoretical framework for intraguild predation. *American Naturalist* **149**:745–764.
- Howard, J. J., D. Raubenheimer, and E. A. Bernays. 1994. Population and individual polyphagy in the grasshopper *Taeniopoda eques* during natural foraging. *Entomologia Experimentalis et Applicata* **71**:167–176.
- Huey, R. B., and E. R. Pianka. 1981. Ecological consequences of foraging mode. *Ecology* **62**:991–999.
- Hurd, L. E., and R. M. Eisenberg. 1990. Arthropod community responses to manipulation of a bitrophic predator guild. *Ecology* **71**:2107–2114.
- Jaffee, B. A., D. R. Strong, and A. E. Muldoon. 1996. Nematode-trapping fungi of a natural shrubland: tests for food chain involvement. *Mycologia* **88**:554–64.
- Janssen, A., A. Pallini, M. Venzon, and M. W. Sabelis. 1998. Behaviour and indirect interactions in food webs of plant-inhabiting arthropods. *Experimental and Applied Acarology* **22**:497–521.
- Johansson, F. 1993. Intraguild predation and cannibalism in odonate larvae: effects of foraging behaviour and zooplankton availability. *Oikos* **66**:80–87.
- Judson, O. P. 1994. The rise of the individual-based model in ecology. *Trends in Ecology and Evolution* **9**:9–14.
- Kareiva, P. M., and N. Shigesada. 1983. Analyzing insect movement as a correlated random walk. *Oecologia* **56**:234–238.
- Lima, S. L. 1998. Nonlethal effects in the ecology of predator-prey interactions. *BioScience* **48**:25–34.
- Lucas, É., and O. Alomar. 2002. Impact of the presence of *Dicyphus tamaninii* Wagner (Heteroptera: Miridae) on whitefly (Homoptera: Aleyrodidae) predation by *Macrolophus caliginosus* (Wagner) (Heteroptera: Miridae). *Biological Control* **25**:123–128.
- Lucas, É., D. Coderre, and J. Brodeur. 1998. Intraguild predation among aphid predators: characterization and influence of extraguild prey density. *Ecology* **79**:1084–1092.
- MacRae, I. V., and B. A. Croft. 1996. Differential impact of egg predation by *Zetzellia mali* (Acari: Stigmaeidae) on *Metaseiulus occidentalis* and *Typhlodromus pyri* (Acari: Phytoseiidae). *Experimental & Applied Acarology* **20**:143–154.
- Meyhöfer, R., and J. Casas. 1999. Vibratory stimuli in host location by parasitic wasps. *Journal of Insect Physiology* **45**:967–971.
- Moran, M. D., and L. E. Hurd. 1998. A trophic cascade in a diverse arthropod community caused by a generalist arthropod predator. *Oecologia* **113**:126–132.
- Murdoch, W. W. 1966. "Community structure, population control, and competition"—a critique. *American Naturalist* **100**:219–226.
- Norton, A. P., G. English-Loeb, and E. Belden. 2001. Host plant manipulation of natural enemies: leaf domatia protect beneficial mites from insect predators. *Oecologia* **126**:535–542.
- Obrycki, J. J., K. L. Giles, and A. M. Ormrod. 1998. Experimental assessment of interactions between larval *Coleomegilla maculata* and *Coccinella septempunctata* (Coleoptera: Coccinellidae) in field cages. *Environmental Entomology* **27**:1280–1288.
- Perry, G. 1999. The evolution of search modes: ecological vs. phylogenetic perspectives. *American Naturalist* **153**:98–109.
- Perry, G., and E. R. Pianka. 1997. Animal foraging: past, present and future. *Trends in Ecology and Evolution* **12**:360–364.
- Pianka, E. R. 1966. Convexity, desert lizards, and spatial heterogeneity. *Ecology* **47**:1055–1059.
- Polis, G. A. 1991. Complex trophic interactions in deserts: an empirical critique of food-web theory. *American Naturalist* **138**:123–155.
- Polis, G. A. 1999. Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. *Oikos* **86**:3–15.
- Polis, G. A., and S. J. McCormick. 1987. Intraguild predation and competition among desert scorpions. *Ecology* **68**:332–343.
- Polis, G. A., C. A. Myers, and R. D. Holt. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics* **20**:297–330.
- Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. *American Naturalist* **147**:813–846.
- Press, W. H., B. P. Flannery, S. A. Teukolsky, and W. T. Vetterling. 1988. Numerical recipes in C. Cambridge University Press, Cambridge, UK.
- Price, P. W. 1980. Evolutionary biology of parasites. Princeton University Press, Princeton, New Jersey, USA.
- Roda, A., J. Nyrop, M. Dicke, and G. English-Loeb. 2000. Trichomes and spider-mite webbing protect predatory mite eggs from intraguild predation. *Oecologia* **125**:428–435.
- Rosenheim, J. A. 1998. Higher-order predators and the regulation of insect herbivore populations. *Annual Review of Entomology* **43**:421–447.
- Rosenheim, J. A. 2001. Source-sink dynamics for a generalist insect predator in a habitat with strong higher-order predation. *Ecological Monographs* **71**:93–116.
- Rosenheim, J. A., H. K. Kaya, L. E. Ehler, J. J. Marois, and B. A. Jaffee. 1995. Intraguild predation among biological control agents: theory and evidence. *Biological Control* **5**:303–335.
- Rosenheim, J. A., D. D. Limburg, and R. G. Colfer. 1999. Impact of generalist predators on a biological control agent, *Chrysoperla carnea*: direct observations. *Ecological Applications* **9**:409–417.
- Rosenheim, J. A., L. R. Wilhoit, and C. A. Armer. 1993. Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population. *Oecologia* **96**:439–449.
- Schmitz, O. J., and K. B. Suttle. 2001. Effects of top predator species on direct and indirect interactions in a food web. *Ecology* **82**:2072–2081.
- Sih, A. 1993. Effects of ecological interactions on forager diets: competition, predation risk, parasitism and prey behaviour. Pages 182–211 in R. N. Hughes, editor. Diet selection: an interdisciplinary approach to foraging behaviour. Blackwell, Oxford, UK.
- Singer, M. S., and E. A. Bernays. 2003. Understanding omnivory needs a behavioral perspective. *Ecology* **84**:2532–2537.

- Singer, M. S., and J. O. Stireman III. 2001. How foraging tactics determine host-plant use by a polyphagous caterpillar. *Oecologia* **129**:98–105.
- Skelly, D. K. 1994. Activity level and the susceptibility of anuran larvae to predation. *Animal Behaviour* **47**:465–468.
- Slobodkin, L., F. Smith, and N. Hairston. 1967. Regulation in terrestrial ecosystems, and the implied balance of nature. *American Naturalist* **101**:109–124.
- Snyder, W. E., and A. R. Ives. 2001. Generalist predators disrupt biological control by a specialist parasitoid. *Ecology* **82**:705–716.
- Snyder, W. E., and A. R. Ives. 2003. Interactions between specialist and generalist natural enemies: parasitoids, predators, and pea aphid biocontrol. *Ecology* **84**:91–107.
- Snyder, W. E., and D. H. Wise. 2001. Contrasting trophic cascades generated by a community of generalist predators. *Ecology* **82**:1571–1583.
- Strong, D. R., H. K. Kaya, A. V. Whipple, A. L. Child, S. Kraig, M. Bondonno, K. Dyer, and J. L. Maron. 1996. Entomopathogenic nematodes: natural enemies of root-feeding caterpillars on bush lupine. *Oecologia* **108**:167–173.
- Tinbergen, N. 1963. On aims and methods of ethology. *Zeitschrift für Tierpsychologie* **20**:410–433.
- Turnbull, A. L. 1973. Ecology of the true spiders (Araneomorphae). *Annual Review of Entomology* **18**:305–348.
- Van Driesche, R. G., and T. S. Bellows, Jr. 1996. *Biological control*. Chapman & Hall, New York, New York, USA.
- Werner, E. E., and B. R. Anholt. 1993. Ecological consequences of the trade-off between growth and mortality-rates mediated by foraging activity. *American Naturalist* **142**:242–272.
- Wise, D. H. 1993. *Spiders in ecological webs*. Cambridge University Press, Cambridge, UK.

THE EVOLUTION OF OMNIVORY IN HETEROPTERAN INSECTS

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Abstract. Although omnivory is common and widespread across many animal taxa, the evolutionary origin of omnivory, the selective forces that promote or constrain omnivory, and the morphological, physiological, and behavioral hurdles that animals have to overcome to become omnivores have not been studied. The goal of this paper is to stimulate the development of ideas concerning the evolution of omnivory. We focus on the terrestrial lineages of the insect order Heteroptera and use published life history data and recent phylogenies to test two hypotheses concerning the evolutionary origin of feeding on both plants and prey: (1) that the propensity to feed on seeds and pollen is correlated with the evolution of omnivory, and (2) that broad host range (polyphagy) is correlated with the evolution of omnivory. In order to test these hypotheses, we mapped the plant part consumed and host plant range of insect species in two heteropteran suborders onto their respective phylogenies and used phylogenetically independent contrasts to test for correlations of these traits with omnivory. We found evidence that seed and pollen feeding and broad host ranges are correlated with the evolution of omnivory within both ancestrally herbivorous and ancestrally predaceous lineages of terrestrial heteropterans.

Key words: feeding habits; herbivory; Heteroptera; omnivory; predation; seed and pollen feeding; sister-group comparisons.

INTRODUCTION

Feeding on both prey and plant food is a widespread feeding habit in insects (Whitman et al. 1994, Alomar and Wiedenmann 1996, Coll and Guershon 2002). Thousands of omnivorous insect species occur throughout a broad range of insect taxa, including grasshoppers, earwigs, thrips, true bugs, beetles, and ants. These insects represent a unique blend of morphological, physiological, and behavioral adaptations found in their predaceous and herbivorous relatives. Omnivorous insects in the order Heteroptera (true bugs), for example, possess digestive tracts and accessory salivary glands that are intermediate in length, size, and placement of those found in their herbivorous and predaceous relatives (Slater and Carayon 1963, Goodchild 1966). In addition, many species of omnivorous heteropterans produce protein-digesting enzymes (proteinases and phospholipases) and plant-digesting enzymes (amylases and pectinases) whereas their strictly herbivorous and predaceous cousins produce only a subset (Baptist 1941, Goodchild 1966, Kahn and Ford 1967, Miles 1972, Varis et al. 1983, Cohen 1990, 1996, Schaefer and Panizzi 2000, Wheeler 2001). Omnivorous heteropterans also have piercing-sucking mouthparts (stylets) with characteristics of both herbivorous heteropterans (smooth stylets to penetrate plants) and predaceous heteropterans (toothed or curved stylets for

holding prey) (Faucheux 1975, Cobben 1979, Cohen 1996).

The ecological significance of omnivory has historically received little attention. Recent studies, however, suggest that omnivory can deny prey density-related refugia from predation, dictate the strength of top-down control and resulting trophic cascades, alter the stability of food webs, and profoundly influence the movement of energy and nutrients through ecosystems (Polis et al. 1989, Polis 1991, Polis and Strong 1996, Fagan 1997, Holt and Polis 1997, Ostrum et al. 1997, Holyoak and Sachdev 1998, McCann et al. 1998, Rosenheim 1998, Eubanks and Denno 1999, 2000).

Studies of the evolution of omnivory, in contrast, are almost nonexistent in the literature (but see Cooper 2002, Denno and Fagan 2003, Diehl 2003). We know relatively little about the adaptive advantages of omnivory and the selective forces that favor or constrain the evolution of omnivory. The evolution of the morphological, physiological, and behavioral traits associated with omnivory have not been studied and we do not know if these traits evolve as a suite of correlated characters. Further, we know very little about the evolutionary consequences of evolving the ability to feed on both plants and prey. For example, the evolution of omnivory might influence the diversification rate of omnivorous taxa, but questions such as this have not been raised in the literature.

The goal of this paper is to stimulate the development of ideas concerning the evolution of omnivory. Insight into the evolutionary origin of omnivory will help us understand the adaptive significance of

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omnivory and elucidate the morphological, physiological, and behavioral hurdles that animals must overcome to consume both prey and plant food. We focus on the terrestrial lineages of the insect order Heteroptera and use published life history data and recent phylogenies to test two hypotheses concerning the evolutionary origin of feeding on both plants and prey: (1) that the tendency to feed on seeds and pollen is correlated with the evolution of omnivory, and (2) that broad host range (polyphagy) is associated with the evolution of omnivory.

In the evolution of omnivory from an ancestral state of herbivory, the propensity of an herbivorous species to evolve the ability to capture and consume prey may be related to the plant part consumed by the species (Sweet 1979, Cobben 1979). Different parts of the same host plant can vary tremendously in concentrations of nitrogen and nitrogen is an important limiting nutrient for most insects (Strong et al. 1984). Seeds and pollen frequently contain up to 10% nitrogen whereas leaves often contain as little as 0.7% nitrogen. Phloem and xylem tissues contain even less nitrogen than leaves (0.005% and 0.0002%, respectively) (Andrews 1935, Evans 1982, Murray and Cordova-Edwards 1984, Strong et al. 1984, Douglas and Weaver 1989). Plant parts also vary in the concentrations of other nutrients, carbohydrates, defensive allelochemicals, and the type and degree of antiherbivore mechanical defenses (Tamas et al. 1979, Strong et al. 1984, Thomison et al. 1988). As a result, herbivorous insects are usually adapted to feed on a particular part of their host plant or plants (Janzen 1979, Kirk 1985). For example, foliage-feeding species do not produce the digestive enzymes that would allow them to digest the proteins found in seeds and pollen, but these enzymes are produced by their seed and pollen-feeding relatives (Houseman et al. 1984, Kirk 1985, Cohen 1996, Schaefer and Panizzi 2000, Wheeler 2001). Some authors have hypothesized that seed and pollen-feeding herbivores may be preadapted to consume nitrogen-rich prey and, consequently, that lineages of seed or pollen-feeding herbivores will give rise to omnivores more frequently than lineages of foliage-feeding herbivores (Sweet 1979, Cobben 1979). This is predicted on the basis of a nutritional match between nitrogen-rich plant parts and nitrogen-rich prey. Conversely, predaceous lineages of insects are hypothesized to be more likely to give rise to omnivores that feed on seeds and pollen than omnivores that feed on plant foliage because high nitrogen plant parts (seeds and pollen) are nutritionally more similar to prey (Sweet 1979, Cobben 1979). Feeding on seeds and pollen is, therefore, hypothesized to be a transitional state in the evolution of omnivory from both herbivory and predation.

The host range of herbivorous insect species may also affect their propensity to evolve the adaptations necessary for prey feeding (Sweet 1979, Cobben 1979).

Host range is defined by the diversity of plant taxa consumed by an herbivorous or omnivorous insect species. The morphological, physiological, and behavioral adaptations associated with polyphagy (feeding on diverse plants representing two or more plant families) may lend themselves to an omnivorous lifestyle. For example, polyphagous insects produce the enzymes necessary to digest a variety of plant species and have the ability to detoxify a variety of allelochemical-based plant defenses (Bernays and Minkenberg 1997). Some authors have suggested that adaptations such as detoxifying enzymes make polyphagous species more likely to consume prey than monophagous species (Sweet 1979, Cobben 1979). Polyphagous herbivores may also have behavioral traits that make it more likely that they will be omnivorous than their monophagous or oligophagous relatives. Polyphagous herbivores move among plants far more often than their monophagous relatives and this may affect their nutrient requirements as well as their predisposition to attack and consume prey (Wheeler 2001). Lineages of polyphagous herbivores, therefore, may be more likely to evolve omnivorous species than are their monophagous relatives. Conversely, omnivorous species that have recently evolved within predaceous lineages are also likely to be polyphagous. Until they undergo selection for specialization on specific plant taxa, these omnivores are unlikely to be very specific about the host plants they consume.

We evaluated these hypotheses by focusing on the life histories and evolutionary history of several terrestrial lineages of the insect order Heteroptera. Terrestrial heteropterans are an ideal group for studying the evolution of feeding habits because they have diverse feeding habits, contain many omnivorous species, have well-known biologies, and have relatively well-established taxonomic and evolutionary relationships. In addition, the three feeding habits have evolved multiple times within this order, with herbivorous lineages giving rise to predators and predaceous lineages giving rise to herbivores (Cobben 1979, Sweet 1979, Schuh 1986, Schuh and Slater 1995, Coll 1998). Heteropterans, therefore, provide a rich biological and historical framework to test ideas regarding the evolution of omnivory.

In order to test our two hypotheses concerning the evolutionary origin of omnivory, we mapped the plant parts consumed and host plant range of insects in two heteropteran suborders onto their respective phylogenies and used phylogenetically independent contrasts to test for correlations between these traits and omnivory.

METHODS

We extracted life history information for 398 species of terrestrial heteropterans distributed in 232 genera, 22 families, and two suborders from 146 published sources (see Appendices). We focused on the terrestrial

heteropterans in the suborders Cimicomomorpha and Pentatomomorpha because they include large numbers of herbivores, omnivores, and predators, and because strict herbivory, omnivory, and strict predation have evolved independently multiple times within these groups (Cobben 1979, Sweet 1979, Schuh 1986, Schuh and Slater 1995, Alomar and Wiedenmann 1996). We used the most recent phylogenies for each suborder, Schuh and Stys (1991) for the Cimicomomorpha (Appendix A) and Henry (1997) for the Pentatomomorpha (Appendix B), for our analyses. Both of these phylogenies are based on morphological characters. These two lineages are particularly useful for this study because the Cimicomomorpha is ancestrally predaceous and the Pentatomomorpha is ancestrally herbivorous (Sweet 1979, Cobben 1979, Schuh 1986, Schuh and Stys 1991, Henry 1997). The correlation of seed and pollen feeding and broad host range with the evolution of omnivory in both lineages would suggest that these traits play a pivotal role in the evolutionary transition from herbivory to omnivory and from predation to omnivory.

For each heteropteran species surveyed, we scored the family and subfamily classification, the plant part consumed by the species, and whether or not the species consumed prey. From this information, we characterized the species' feeding habit as strictly herbivorous (consumes only plants), omnivorous (consumes plants and prey), or strictly predaceous (consumes only prey). We also characterized the species host range as monophagous (consumes plants belonging to one genus), oligophagous (consumes plants in two or more genera within the same plant family), or polyphagous (consumes plants in two or more families).

We used two analyses to control for possible phylogenetic nonindependence among heteropteran species. Our approach follows that of Fagan et al. (2002) and all methods are based on the principal of phylogenetically independent contrasts (Felsenstein 1985). The two tests represent each end of the continuum between strictness of correction for similarity due to common ancestry and potential statistical power (Mazer 1998, Ackerly and Reich 1999). We used both liberal and conservative techniques to control for phylogenetic constraints because omnivory has evolved multiple times within multiple heteropteran lineages and is unlikely to be highly conserved (i.e., is phylogenetically labile).

The first analysis partitioned species into a set of family-level groups each containing at least one phylogenetically independent contrast between herbivores and omnivores (sensu Fagan et al. 2002). These groupings corresponded to single, monophyletic taxa in the case of the superfamily Pentatomoidea, the families Berytidae, Miridae, Pyrrhocoridae, and Rhopalidae, and the subfamily Lygaeinae. In other cases, these family-level groups consisted of pairs of sister taxa with different feeding life histories (omnivorous vs. herbiv-

TABLE 1. Numbers of omnivores and herbivores used in eight independent contrasts to test for correlations of feeding habit with plant part consumed (foliage vs. reproductive parts) and with host range (monophagy or oligophagy vs. polyphagy).

Taxa	No. omnivores in contrast	No. herbivores in contrast
Miridae	54	66
Pentatomoidea†	28	64
Alydidae + Coreidae	1	14
Rhopalidae	1	3
Pyrrhocoridae	2	7
Berytidae	7	4
Ishnorhynchinae + Orsillinae	1	8
Lygaeinae	3	7

† Includes families Acanthosomatidae, Cydnidae, Pentatomidae, Scutelleridae, and Thyrocoridae.

orous; Table 1). This procedure reduced our data to eight family-level groups (Table 1). We then conducted a logistic regression analysis with family group, plant part consumed (foliage or reproductive), and host range (restricted or polyphagous) as predictor variables and feeding habit (herbivory or omnivory) as the dependent variable (SAS version 8.2, Proc Logistic with class statement; Stokes et al. 2000).

This analysis corrects for phylogenetic nonindependence among family-level groups, but treats species within these groups as independent and does not control for phylogenetic non-independence at levels above family. The second analysis controls for phylogenetic nonindependence at all levels and is considered a conservative test of correction for similarity due to common ancestry. In this analysis, we reduced the data set further to include only phylogenetically independent contrasts among sister taxa (Ridley 1983, Felsenstein 1985, Harvey and Pagel 1991). This required that we assign a feeding habit to each family-level group. If all species within a group were herbivorous, then we scored that group as herbivorous. If some or all species within the group were omnivorous, then we scored that group as omnivorous. We identified four meaningful phylogenetically independent contrasts using the phylogenies of Schuh and Stys (1991) and Henry (1997): Miridae (omnivorous) vs. Tingidae (herbivorous), Coreidae (herbivorous) vs. Alydidae (omnivorous), Berytidae (omnivorous) vs. Colobathristidae (herbivorous), and Ishnorhynchinae (omnivorous) vs. Orsillinae (herbivorous). We used two 2×2 contingency table analyses to test the hypotheses that evolutionary changes in feeding habit were independent of plant part consumed and host range. A significant G is evidence that pairs of character states are not independent, but that some combinations of characters are more or less common than expected by chance (Ridley 1983, Harvey and Pagel 1991).

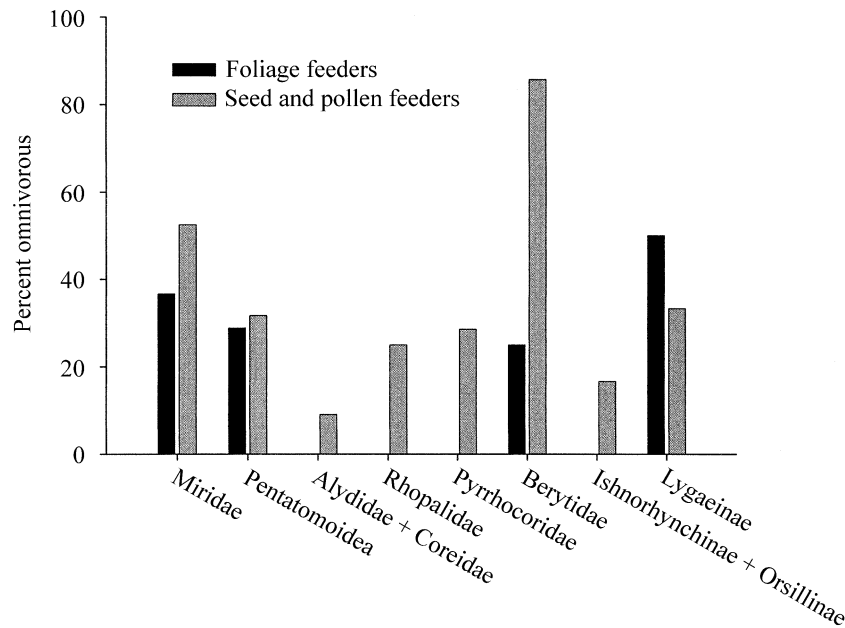


FIG. 1. Percentages of species that are omnivorous among species that feed on foliage or on seeds and pollen, in each of the eight family-level groups used in our logistic regression analysis. Missing bars indicate “zero” values.

RESULTS

Feeding on seeds and pollen is correlated with omnivory.—We found strong support for the hypothesis that the evolution of omnivory is correlated with the consumption of seeds and pollen. There was a significant effect of plant part on feeding habit in the analysis that controlled for phylogenetic nonindependence at the level of family group (Wald $\chi^2 = 4.01$, $df = 1$, $P = 0.045$). Overall, heteropteran species that consumed seeds and pollen were more likely to be omnivorous than foliage-feeding species (Fig. 1). In the Miridae, for example, 53% of the species that fed on reproductive plant parts were omnivorous whereas only 37% of the species that fed on foliage were omnivorous (Fig. 1). This pattern was even more striking in the Berytidae: 85% of the species that fed on seeds and pollen were omnivorous and only 25% of the species that fed on foliage were omnivorous (Fig. 1). The effect of family group in this analysis was not significant (Wald $\chi^2 = 11.10$, $df = 7$, $P = 0.134$).

We found the same pattern in the analysis that controlled for phylogenetic nonindependence at all levels. In this analysis, taxa that fed on seeds and pollen were significantly more likely to be omnivorous than their foliage-feeding sister taxa ($G = 6.1$, $df = 1$, $P < 0.025$). In addition, feeding on seeds and pollen appeared to be correlated with omnivory in both the ancestrally predaceous lineage (Cimicomorpha) (e.g., Miridae in Fig. 1) and the ancestrally herbivorous lineage (Pentatomomorpha) (e.g., Berytidae in Fig. 1).

Polyphagy is correlated with omnivory.—We also found evidence that the host range of a heteropteran species affects its propensity to be omnivorous. There

was a statistically significant affect of host range on feeding habit in the analysis that controlled for phylogeny at the family-group level (Wald $\chi^2 = 26.52$, $df = 1$, $P < 0.001$). This was evident in the Miridae, the Pentatomoidea, the Alydidae + Coreidae, the Berytidae, the Ischnorhynchinae + Orsillinae, and the Lygaeinae (Fig. 2). The opposite pattern was evident in the Rhopalidae and the Pyrrhocoridae (Fig. 2). These results suggest that there may be an interactive effect of family group and host range such that in some groups polyphagous species are more likely to be omnivorous and in other groups monophagous species are more likely to be omnivorous, but our data set was neither large enough nor balanced enough to test this hypothesis statistically. There was a statistically significant effect of family group (Wald $\chi^2 = 14.83$, $df = 7$, $P = 0.038$), indicating that there was an effect of phylogeny on the distribution of omnivores.

We saw the same pattern in the analysis that controlled for phylogenetic nonindependence at all levels: polyphagous taxa were significantly more likely to contain omnivorous species than their monophagous or oligophagous sister taxa ($G = 6.0$, $df = 1$, $P < 0.025$). Host range and omnivory appeared to be correlated in both the ancestrally predaceous lineage (Cimicomorpha) (e.g., Miridae in Fig. 2) and the ancestrally herbivorous lineage (Pentatomomorpha) (e.g., Berytidae in Fig. 2).

DISCUSSION

Our results support the hypotheses that seed and pollen feeding and broad host plant range are correlated with the evolution of omnivory in terrestrial heterop-

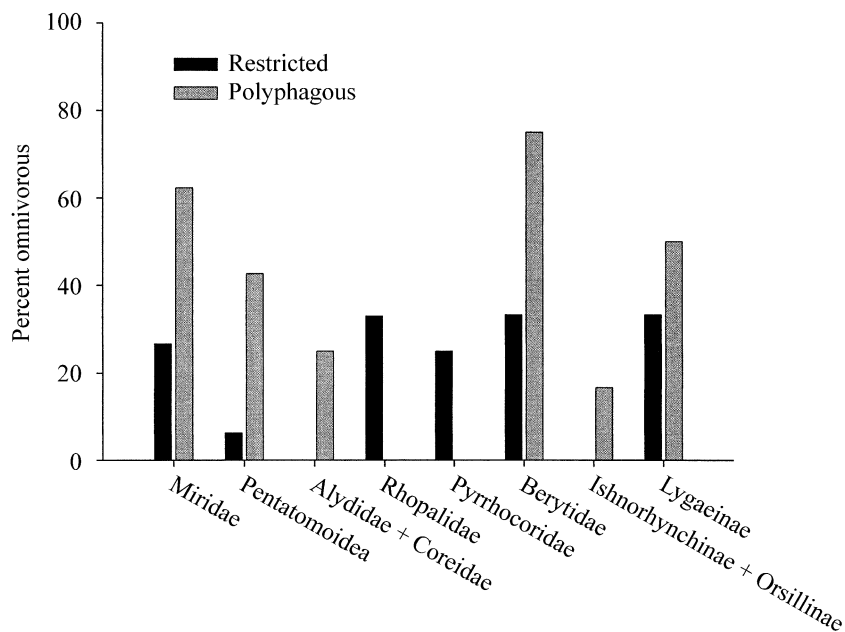


FIG. 2. Percentage of species that are omnivorous among species with restricted host ranges (monophagous + oligophagous) or broad host ranges (polyphagous) in each of the eight family-level groups used in our logistic regression analysis. Missing bars indicate “zero” values.

terans. Heteropteran species that fed on seeds and pollen were significantly more likely to be omnivorous than their foliage-feeding relatives (Fig. 1). Likewise, polyphagous species were significantly more likely to be omnivorous than their relatives with restricted host ranges (monophagous or oligophagous), although this effect may vary to some extent among family-level groups (Fig. 2). These patterns were apparent when we used both liberal and conservative methods to control for the effects of phylogeny on the evolution of omnivory and were apparent in both ancestrally predaceous (Cimicomomorpha) and ancestrally herbivorous (Pentatomomorpha) lineages.

We suggest that seed and pollen-feeding insects are preadapted to consume prey and that predaceous insects are similarly predisposed to consume nitrogen-rich plant parts. Preadaptation may be associated with physiological traits. For example, the digestive enzymes produced by seed and pollen-feeding herbivores may be able to digest prey. Similarly, the digestive enzymes produced by predators may be able to digest seeds and pollen. Further, some morphologies or behaviors of seed and pollen-feeding herbivores and predators may be functionally interchangeable. For example, how similar do the mouthparts of omnivores have to be to their herbivorous and predaceous relatives to function adequately in both prey and plant consumption? Do host-plant identification behaviors and mobility associated with polyphagous heteropterans allow them to track prey? To our knowledge, these hypotheses have never been tested; however, questions like these could

be addressed by comparative studies of closely related herbivores, omnivores, and predators.

Ecological consequences

The consumption of seeds and pollen as well as polyphagy could dramatically affect the spatial and temporal abundance of omnivorous insects. Omnivores that consume seeds and pollen may be forced to track changes in the abundance of these plant resources in space and time (Eubanks and Denno 1999, 2000). Omnivorous insects are noted for their attraction to pollen and seeds (Kiman and Yeargan 1985, Read and Lampman 1989, Coll and Bottrell 1991, 1992) and some studies even suggest that omnivorous “predators” actually track variation in the production of seeds and pollen more than they track variation in the population size of prey (Cottrell and Yeargan 1998, Eubanks and Denno 2000). The impact of these omnivores on prey is largely dictated by variation in the abundance of seeds and pollen because the presence of high quality plant food not only affects omnivore abundance, but also alters the per capita consumption of prey by omnivores (Cottrell and Yeargan 1998, Eubanks and Denno 2000). Likewise, the abundance of polyphagous plant feeders is affected by spatial and temporal variation in host plants, and polyphagous herbivores are frequently more widespread and abundant than monophagous relatives, especially if the monophagous insects specialize on relatively rare plants (Ehrlich and Raven 1964).

Evolutionary consequences

Omnivory may be a key innovation that leads to taxonomic diversification if the ecological flexibility provided by the ability to consume both prey and plant food allows omnivorous species to be more “successful” than their strictly herbivorous or predaceous relatives. We did not have enough data to test this hypothesis statistically, but our preliminary results are intriguing. We found three independent contrasts of omnivorous and herbivorous sister taxa for which we could readily find the number of described species and/or estimates of the number of extant species: Miridae (omnivorous) vs. Tingidae (herbivorous), Coreidae (herbivorous) vs. Alydidae (omnivorous), and Berytidae (omnivorous) vs. Colobathristidae (herbivorous). In two out of the three contrasts, the omnivorous taxa were dramatically more diverse than their herbivorous sister taxa (Miridae vs. Tingidae and Berytidae vs. Colobathristidae). This interesting result suggests that the evolution of omnivory may have profound consequences for the generation of biodiversity.

In conclusion, we found evidence that the evolution of omnivory is correlated with the consumption of seeds and pollen and broad host range within heteropteran insects. Our results suggest that herbivorous species that consume these nitrogen-rich, reproductive plant parts are far more likely to evolve the adaptations necessary to include prey in their diet than their foliage-feeding relatives. Likewise, polyphagous species are more likely to evolve the ability to include prey in their diet than their relatives that specialize on a single or few plant species. Conversely, predators may be preadapted to feed on seeds and pollen and may be preadapted to have a broad host range. We hope our assessment of the evolution of omnivory in heteropteran insects stimulates the development of ideas concerning the evolutionary origin and consequences of this important feeding habit.

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LITERATURE CITED

- Ackerly, D. D., and P. B. Reich. 1999. Convergence and correlations among leaf size and function in seed plants: a comparative test using independent contrasts. *American Journal of Botany* **86**:1272–1281.
- Alomar, O., and R. N. Wiedenmann, editors. 1996. *Zoophytophagous Heteroptera: implications for life history and integrated pest management*. Thomas Say Publications in Entomology, Entomological Society of America, Landham, Maryland, USA.
- Andrews, F. S. 1935. Physiological factors associated with the fruiting of the bush lima bean. *Proceedings of the American Society of Horticultural Science* **33**:473–476.
- Baptist, B. A. 1941. The morphology and physiology of the salivary glands of Hemiptera–Heteroptera. *Quarterly Journal of Microscopic Science* **83**:91–139.
- Bernays, E. A., and O. P. J. Minkenbergh. 1997. Insect herbivores: different reasons for being a generalist. *Ecology* **78**:1157–1169.
- Cobben, R. H. 1979. On the original feeding habits of the Hemiptera (Insecta): a reply to Merrill Sweet. *Annals of the Entomological Society of America* **72**:711–715.
- Cohen, A. C. 1990. Feeding adaptations of some predaceous Hemiptera. *Annals of the Entomological Society of America* **83**:1215–1223.
- Cohen, A. C. 1996. Plant feeding by predatory Heteroptera: evolutionary and adaptational aspects of trophic switching. Pages 1–17 in O. Alomar and R. N. Wiedenmann, editors. *Zoophytophagous Heteroptera: implications for life history and integrated pest management*. Thomas Say Publications in Entomology, Entomological Society of America, Lanham, Maryland, USA.
- Coll, M. 1998. Living and feeding on plants in predatory Heteroptera. Pages 89–130 in M. Coll and J. R. Ruberson, editors. *Predatory Heteroptera: their ecology and use in biological control*. Thomas Say Publications in Entomology, Entomological Society of America, Lanham, Maryland, USA.
- Coll, M., and D. G. Bottrell. 1991. Microhabitat and resource selection of the European corn borer (Lepidoptera: Pyralidae) and its natural enemies in Maryland field corn. *Environmental Entomology* **20**:526–533.
- Coll, M., and D. G. Bottrell. 1992. Mortality of European corn borer larvae by enemies in different corn microhabitats. *Biological Control* **2**:95–103.
- Coll, M., and M. Guershon. 2002. Omnivory in terrestrial arthropods: mixing plant and prey diets. *Annual Review of Entomology* **47**:267–297.
- Cooper, W. 2002. Convergent evolution of plant chemical discrimination by omnivorous and herbivorous sceroglossan lizards. *Journal of Zoology* **257**:53–66.
- Cottrell, T. E., and K. V. Yeargan. 1998. Effect of pollen on *Coleomegilla maculata* (Coleoptera: Coccinellidae) population density, predation, and cannibalism in sweet corn. *Environmental Entomology* **27**:1402–1410.
- Denno, R. F., and W. F. Fagan. 2003. Might nitrogen limitation promote omnivory among carnivorous arthropods? *Ecology* **84**:2522–2531.
- Diehl, S. 2003. The evolution and maintenance of omnivory: dynamic constraints and the role of food quality. *Ecology* **84**:2557–2567.
- Douglas, L. A., and R. W. Weaver. 1989. Partitioning of biologically fixed nitrogen in cowpea during pod development. *Plant Soil* **116**:129–131.
- Ehrlich, P. R., and P. H. Raven. 1964. Butterflies and plants: a study in coevolution. *Evolution* **18**:586–608.
- Eubanks, M. D., and R. F. Denno. 1999. The ecological consequences of variation in plants and prey for an omnivorous insect. *Ecology* **80**:1253–1266.
- Eubanks, M. D., and R. F. Denno. 2000. Host plants mediate omnivore–herbivore interactions and influence prey suppression. *Ecology* **81**:936–947.
- Evans, J. 1982. Symbiosis, nitrogen and dry matter distribution in chickpea (*Cicer arietinum*). *Experimental Agriculture* **18**:339–351.
- Fagan, W. F. 1997. Omnivory as a stabilizing feature of natural communities. *American Naturalist* **150**:554–568.
- Fagan, W. F., E. Siemann, C. Mitter, R. F. Denno, A. F. Huberty, H. A. Woods, and J. J. Elser. 2002. Nitrogen in insects:

- implications for trophic complexity and species diversification. *American Naturalist* **160**:784–802.
- Faucheux, M. J. 1975. Relations entre l'ultrastructure des stylets mandibulaires et maxillaires et la prise de nourriture chez les insectes Hemipteres. *C. R. Hebd. Seances Academic Science (Series D)* **281**:41–44.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist* **125**:1–15.
- Goodchild, A. J. P. 1966. Evolution of the alimentary canal in the Hemiptera. *Biological Review of the Cambridge Philosophical Society* **41**:97–140.
- Harvey, P. H., and M. D. Pagel. 1991. *The comparative method in evolutionary biology*. Oxford University Press, New York, New York, USA.
- Henry, T. J. 1997. Phylogenetic analysis of family groups within the infraorder Pentatomomorpha (Hemiptera: Heteroptera), with emphasis on the Lygaeoidea. *Annals of the Entomological Society of America* **90**:275–301.
- Holt, R. D., and G. A. Polis. 1997. A theoretical framework for intraguild predation. *American Naturalist* **149**:745–764.
- Holyoak, M., and S. Sachdev. 1998. Omnivory and the stability of simple food webs. *Oecologia* **117**:413–419.
- Houseman, J. G., W. K. MacNaughton, and A. E. R. Down. 1984. Cathepsin B and aminopeptidase activity in the posterior midgut of *Euschistus euschistoides* (Hemiptera: Pentatomidae). *Canadian Entomologist* **116**:1393–1396.
- Janzen, D. H. 1979. New horizons in the biology of plant defenses. Pages 331–350 in G. A. Rosenthal and D. H. Janzen, editors. *Herbivores: their interaction with secondary plant metabolites*. Academic Press, New York, New York, USA.
- Kahn, M. R., and J. B. Ford. 1967. The distribution and localization of digestive enzymes in the alimentary canal and salivary glands of the cotton stainer, *Dysdercus fasciatus*. *Journal of Insect Physiology* **13**:1619–1627.
- Kiman, Z. B., and K. V. Yeorgan. 1985. Development and reproduction of the predator *Orius insidiosus* (Hemiptera: Anthocoridae) reared on diets of selected plant material and arthropod prey. *Annals of the Entomological Society of America* **78**:464–467.
- Kirk, W. D. J. 1985. Pollen-feeding and the host specificity and fecundity of flower thrips (Thysanoptera). *Ecological Entomology* **10**:281–289.
- Mazer, S. J. 1998. Alternative approaches to the analysis of comparative data: compare and contrast. *American Journal of Botany* **85**:1194–1199.
- McCann, K. S., A. Hastings, and D. R. Strong. 1998. Trophic cascades and trophic trickles in pelagic food webs. *Proceedings of the Royal Society of London B* **265**:205–209.
- Miles, P. W. 1972. The saliva of Hemiptera. *Advances in Insect Physiology* **9**:183–255.
- Murray, D. R., and M. Cordova-Edwards. 1984. Amino acid and amide metabolism in the hulls and seeds of developing fruits of garden pea, *Pisum sativum*. II. Asparagine. *New Phytologist* **97**:253–260.
- Ostrum, P. H., M. Colunga-Garcia, and S. H. Gage. 1997. Establishing pathways of energy flow for insect predators using stable isotope ratios: field and laboratory evidence. *Oecologia* **109**:108–113.
- Polis, G. A. 1991. Complex trophic interactions in deserts: an empirical critique of food web theory. *American Naturalist* **138**:123–155.
- Polis, G. A., C. A. Myers, and R. D. Holt. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics* **20**:297–330.
- Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. *American Naturalist* **147**:813–846.
- Read, C. D., and R. L. Lampman. 1989. Olfactory responses of *Orius insidiosus* (Hemiptera: Anthocoridae) to volatiles of corn silks. *Journal of Chemical Ecology* **15**:1109–1115.
- Ridley, M. 1983. *The explanation of organic diversity: the comparative method and adaptations for mating*. Oxford University Press, New York, New York, USA.
- Rosenheim, J. A. 1998. Higher-order predators and the regulation of insect populations. *Annual Review of Entomology* **43**:421–447.
- Schaefer, C. W., and A. R. Panizzi. 2000. Economic importance of Heteroptera: a general view. Pages 3–8 in C. W. Schaefer and A. R. Panizzi, editors. *Heteroptera of economic importance*. CRC Press, New York, New York, USA.
- Schuh, R. T. 1986. The influence of cladistics on heteropteran classification. *Annual Review of Entomology* **31**:67–93.
- Schuh, R. T., and J. A. Slater. 1995. *True bugs of the world (Hemiptera: Heteroptera)*. Cornell University Press, Ithaca, New York, USA.
- Schuh, R. T., and P. Stys. 1991. Phylogenetic analysis of cimiciforman family relationships (Heteroptera). *Journal of the New York Entomological Society* **99**:298–350.
- Slater, J. A., and J. Carayon. 1963. Ethiopian Lygaeidae IV: a new predatory lygaeid with a discussion of its biology and morphology (Hemiptera: Heteroptera). *Proceedings of the Royal Entomological Society of London A* **38**:1–11.
- Stokes, M. E., C. S. Davis, and G. G. Koch. 2000. *Categorical data analysis using the SAS system*. Second edition. SAS Institute, Cary, North Carolina, USA.
- Strong, D. R., J. H. Lawton, and T. R. E. Southwood. 1984. *Insects on plants: community patterns and mechanisms*. Blackwell Scientific, Oxford, UK.
- Sweet, M. H. 1979. On the original feeding habits of Hemiptera (Insecta). *Annals of the Entomological Society of America* **72**:575–579.
- Tamas, I. A., D. H. Wallace, P. M. Ludford, and J. Ozbun. 1979. Effect of older fruits on abortion and abscisic acid concentration of younger fruits in *Phaseolus vulgaris* L. *Plant Physiology* **64**:620–622.
- Thomison, P. R., D. L. Jeffers, and A. F. Schmitthenner. 1988. Phomopsis seed infection and nutrient accumulation in pods of soybean with reduced fruit loads. *Agronomy Journal* **80**:55–59.
- Varis, A. L., S. Laurema, and H. Miettinen. 1983. Variation of enzyme activities in the salivary glands of *Lygus rufipennis* (Hemiptera, Miridae). *Annales Zoologici Fennici* **49**:1–10.
- Wheeler, A. G. 2001. *Biology of the plant bugs (Heteroptera: Miridae)*. Cornell University Press, Ithaca, New York, USA.
- Whitman, D. W., M. S. Blum, and F. Slansky, Jr. 1994. Carnivory in phytophagous insects. Pages 161–205 in T. N. Ananthakrishnan, editor. *Functional dynamics of phytophagous insects*. Science Publishers, Lebanon, New Hampshire, USA.

APPENDIX A

The phylogeny of family relationships in the heteropteran suborder Cimicimomorpha is available in ESA's Electronic Data Archive: *Ecological Archives* E084-063-A1.

APPENDIX B

The phylogeny of family relationships in the heteropteran suborder Pentatomomorpha is available in ESA's Electronic Data Archive: *Ecological Archives* E084-063-A2.

APPENDIX C

Taxonomic placement, host range, plant part feeding preference, and feeding habit of 398 terrestrial heteropteran insects in suborders Cimicimomorpha and Pentatomomorpha is available in ESA's Electronic Data Archive: *Ecological Archives* E084-063-A3.

THE EVOLUTION AND MAINTENANCE OF OMNIVORY: DYNAMIC CONSTRAINTS AND THE ROLE OF FOOD QUALITY

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Abstract. In several taxa, the ability to feed omnivorously from more than one trophic level has evolved from more specialized feeding habits. A prerequisite for this evolutionary scenario is initial coexistence (on the same or different trophic levels) of the consumers subsequently involved in omnivory. Evolution of omnivory should also be favored by prior asymmetries in consumer interactions. I use a dynamic model to explore conditions for coexistence of two consumers depending on a single biotic resource in simple food webs of increasing asymmetry between consumers: (1) pure resource competition, (2) resource competition with unidirectional interference, (3) omnivory, and (4) pure predation. If consumers are energy limited, omnivory is unlikely to evolve from a competitive system, because stable coexistence of two consumers on a single resource is impossible, even if there is a trade-off between resource exploitation and interference abilities. Initial coexistence of two consumers is easier to achieve, if the species are arranged in a food chain. If costs of diet generalization are low, selection should then favor the inclusion of the resource in the top consumer's diet. In systems with high resource carrying capacity, the intermediate consumer will then, however, be frequently driven to extinction—in which case omnivory is not maintained. Low nutritional quality of the resource can stabilize the omnivory system and allow three-species coexistence at high resource carrying capacities. Low nutritional quality of the resource may also create conditions for the evolution of omnivory from a competitive system. If the content of an essential nutrient in resource biomass is dynamic, stable coexistence of two competitors becomes possible if both are limited by the nutrient content of the resource. In this case, selection may favor the evolution of omnivory, because competitor biomass is usually of higher nutritional quality than resource biomass. An explicit treatment of flexible resource stoichiometry thus broadens the possibilities for the evolution of omnivory.

Key words: coexistence; conversion efficiency; food web; interference competition; intraguild predation; invasibility; nutritional quality; omnivory; population model; predation; resource competition; stoichiometry.

INTRODUCTION

It is now widely accepted that omnivory, the consumption of resources from more than one trophic level, is very common in natural communities (Polis et al. 1989, Diehl 1993, Coll and Guershon 2002). From the perspective of an individual consumer, being an omnivore seems advantageous, because food abundance is usually highest at lower trophic levels, whereas food quality (e.g., content in proteins) normally increases with position in the food chain (Hastings and Conrad 1979, Hairston and Hairston 1993, Whitman et al. 1994, Elser et al. 2000, Denno and Fagan 2003). An omnivorous feeding mode may thus enable the harvesting of both more abundant but less nutritious and of less abundant but more nutritious food sources in variable proportions (Coll and Guershon 2002).

Omnivory should, however, also involve trade-offs. Omnivores are, by definition, generalists that must be

able to find, catch, ingest, and digest food types spanning a potentially vast range of behaviors, morphologies, and biochemical compositions. Coping with a wide variety of food types may have to involve specific adaptations. For example, omnivores that feed on both animals and plants must possess a morphology allowing them to physically harm and subdue animal prey while at the same time carrying a digestive tract capable of processing both plant and animal material (Coll and Guershon 2002, Eubanks et al. 2003). Morphological and phylogenetic evidence suggests that, for many omnivorous taxa, the ability to feed on resources from more than one trophic level is a derived trait that has evolved from more specialized, ancestral states (Whitman et al. 1994, Cohen 1996, Eubanks et al. 2003). This begs the question: which ecological circumstances would favor the evolution of omnivory from more specialized feeding habits?

A related question is: under which ecological circumstances is omnivory maintained in a community? From a population dynamical perspective, the commonness of omnivory poses a puzzle, because omnivory frequently causes extinctions in simple model

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communities (Pimm and Lawton 1978, Holt and Polis 1997, Diehl and Feiel 2000, Mylius et al. 2001). In particular, intermediate prey species are prone to go extinct in the presence of an omnivore, the omnivore being both a direct consumer and a resource competitor of the intermediate prey. Under such circumstances, omnivory is de facto lost from the community and the former omnivore should evolve into a specialist consumer of the formerly shared resources.

The factors involved in the evolution and maintenance of traits enabling consumers to feed on more than one trophic level are likely to be complex. Still, three simple, plausible assumptions can be made. First, evolution of omnivory requires prior coexistence of the species subsequently involved in it. Second, the evolution of omnivory should be facilitated, if the subsequent omnivore is already physically superior to the subsequent intermediate consumer. Third, the maintenance of traits enabling omnivorous feeding requires continuous coexistence of the omnivore with both intermediate consumers and shared resources. Based on these assumptions, I use a dynamical model to explore conditions for coexistence of two consumers depending on a single biotic resource in simple food webs of increasing asymmetry in consumer interactions: (1) pure resource competition, (2) resource competition combined with unidirectional interference, (3) intraguild predation, and (4) pure predation. Food webs 1, 2, and 4 can be viewed as potential precursors to food web 3, which represents the simplest possible case of omnivory.

Because the potential advantages of an omnivorous diet are related to differences in the relative abundance and quality of food types at various trophic levels, I emphasize the influences of carrying capacity and nutritional quality of the basal resource on coexistence of the two consumers. Nutritional quality is frequently related to the stoichiometric elemental composition of tissues and can be a dynamic trait itself (Droop 1974, Eubanks and Denno 1999, Elser et al. 2000). I therefore consider systems in which the nutritional quality of the basal resource is either fixed or flexible. In the latter case, I relate nutritional quality to nutrient stoichiometry of the resource and the consumers. I will show that low nutritional quality of the basal resource (be it a fixed trait or the result of feedback processes) may facilitate both the expression and the maintenance of omnivory in simple three-species food webs.

THE GENERAL APPROACH AND THE BASIC MODEL

I consider three potential scenarios for the evolution of omnivory in one-resource–two-consumer systems: (1) the precursor is a competitive system with fixed resource quality; (2) the precursor is a food chain with fixed resource quality; (3) the precursor is a competitive system with flexible resource quality. To investigate dynamical constraints on the evolution and maintenance of omnivory, I use the following general model

of a three-species system with omnivory, of which the potential precursor systems are special cases:

$$\frac{dR}{dt} = r\rho(R, K, B, N, P)R - a_{RN}(R, P)N - a_{RP}(R, N)P \quad (1a)$$

$$\frac{dN}{dt} = e_{RN}(B, R, N, P)a_{RN}(R, P)N - a_{NP}(R, N)P - m_N N \quad (1b)$$

$$\frac{dP}{dt} = e_{RP}(B, R, N, P)a_{RP}(R, N)P + e_{NP}(q_N, q_P)a_{NP}(R, N)P - m_P P. \quad (1c)$$

This system consists of a biotic resource R that is consumed by consumers N and P , whose densities are all measured in units of biomass. The resource has a maximum specific growth rate r , of which only a fraction ρ is realized at any given time. Consumer j feeds on resource/consumer i with rate a_{ij} , converts its food into own biomass with efficiency e_{ij} , and loses biomass (through metabolism and mortality) at a rate m_j . The specific forms of the functions ρ , a_{ij} , and e_{ij} for the three different evolutionary scenarios are listed in Table 1 and will be explained in detail in later sections (see also Table 2).

I do not investigate the three scenarios with a truly evolutionary approach, in which the capacity to feed on more than one trophic level would be a dynamically evolving trait. Rather, I ask two much more basic questions. First, do the scenarios fulfill the fundamental requirement that the three species must coexist prior to evolution of omnivory? Second, once omnivory has evolved, how is the persistence of a three-species system with omnivory affected by the productive capacity and quality of the basal resource?

Because the focus of this paper is on the second question, I limit the analysis for simplicity to cases where potential precursor systems must have locally stable equilibria. I thus apply the following approach to all three evolutionary scenarios. I first investigate the invasibility of boundary sets of the full system (i.e., of systems with only one consumer) by the missing consumer and whether stable three-species coexistence is possible prior to the evolution of omnivory. I then ask whether mutual invasibility of locally stable boundary equilibria remains possible after the evolution of omnivory [which are sufficient conditions for the persistence of the omnivory system (Hutson and Law 1985)]. Effects of resource abundance and quality on these issues are addressed by varying the resource carrying capacity K and the conversion efficiency e_{RP} of resources into omnivore biomass. Persistence of both the precursor and the omnivory systems does, however, not require the existence of locally stable equilibria (Armstrong and McGehee 1980, McCann and Hastings 1997, Kooi et al. 2002). The applicability of the results

TABLE 1. Specific forms of the functions describing resource renewal, functional responses, and conversion efficiencies used in the examples to illustrate the cases of (1) a competitive system with ($c > 0$) or without ($c = 0$) unidirectional interference and with fixed resource quality (Model I), (2) a food chain with ($a_{RP} > 0$) or without ($a_{RP} = 0$) omnivory and with fixed resource quality (Model II), and (3) a competitive system with ($a_{NP} > 0$) or without ($a_{NP} = 0$) omnivory and with flexible resource quality (Model III).

Description	General function	Specific function		
		Model I	Model II	Model III
Resource renewal	$\rho(R, K, B, N, P)$	$1 - \frac{R}{K}$	$1 - \frac{R}{K}$	$1 - \frac{R}{\min\left[K, \frac{(B - q_N N - q_P P)}{q_{R\min}}\right]}$
Functional response of N feeding on R	$a_{RN}(R, P)$	$\frac{a_{RN}R}{1 + cP}$	$a_{RN}R$	$\frac{a_{RN}R}{1 + a_{RN}h_{RN}R}$
Functional response of P feeding on R	$a_{RP}(R, N)$	$a_{RP}R$	$a_{RP}R$	$\frac{a_{RP}R}{1 + a_{RP}h_{RP}R + a_{NP}h_{NP}N}$
Functional response of P feeding on N	$a_{NP}(R, N)$	0	$a_{NP}N$	$\frac{a_{NP}N}{1 + a_{RP}h_{RP}R + a_{NP}h_{NP}N}$
Conversion of R into N	$e_{RN}(B, R, N, P)$	e_{RN}	e_{RN}	$e_{RN} \left\{ \min \left[1, \frac{(B - q_N N - q_P P)}{q_N R} \right] \right\}$
Conversion of R into P	$e_{RP}(B, R, N, P)$	e_{RP}	e_{RP}	$e_{RP} \left\{ \min \left[1, \frac{(B - q_N N - q_P P)}{q_P R} \right] \right\}$
Conversion of N into P	$e_{NP}(q_N, q_P)$	0	e_{NP}	$e_{NP} \left\{ \min \left[1, \frac{q_N}{q_P} \right] \right\}$

Note: For definitions of parameters see Table 2.

to nonequilibrium systems will be briefly addressed in the *Discussion*.

SCENARIO 1: RESOURCE COMPETITION WITH AND WITHOUT INTERFERENCE COMPETITION IN A SYSTEM WITH FIXED RESOURCE QUALITY

Scenario 1 assumes that the precursor to an omnivory system is a competitive system with fixed resource

quality. These assumptions can be included in the general model by setting the attack rate of consumer P on consumer N to zero and the conversion efficiencies of consumed resources R into consumer biomass to constant values (Model I in Table 1). Because an omnivore must be able to harm its prey, I also investigate the situation in which one of the consumers is already physically superior to the other consumer. Such phys-

TABLE 2. Definitions of model parameters.

Parameter	Definition	Units
a_{RN}	search and attack rate of N on R	area per biomass of N per time
a_{RP}	search and attack rate of P on R	area per biomass of P per time
a_{NP}	search and attack rate of P on N	area per biomass of P per time
B	total nutrient content in system	mass of nutrient per area
c	per capita interference effect of P on N	per biomass of P
e_{RN}	conversion of R into N	dimensionless number between 0 and 1
e_{RP}	conversion of R into P	dimensionless number between 0 and 1
e_{NP}	conversion of N into P	dimensionless number between 0 and 1
h_{RN}	handling time of N feeding on R	time \times biomass of N per biomass of R
h_{RP}	handling time of P feeding on R	time \times biomass of R per biomass of P
h_{NP}	handling time of P feeding on N	time \times biomass of P per biomass of N
K	carrying capacity of R	biomass of R per area
m_N	biomass loss rate of N	per time
m_P	biomass loss rate of P	per time
$q_{R\min}$	minimal nutrient quota per biomass of R	mass of nutrient per biomass of R
q_N	nutrient quota per biomass of N	mass of nutrient per biomass of N
q_P	nutrient quota per biomass of P	mass of nutrient per biomass of P
r	maximum specific growth rate of R	per time
ρ	fraction of r attained by R	dimensionless number

Note: The definitions assume that the densities of R , N , and P are expressed in biomass per unit area.

ical asymmetry can be included in the model by assuming unidirectional, behavioral interference between consumers. To tilt the balance as much as possible in favor of the inferior resource competitor P , I assume that interference behavior incurs no cost to the “donor” of interference (consumer P), whereas the “receiver” of interference (consumer N) suffers a proportional reduction $1/(1 + cP)$ in its attack rate on the resource (Model I in Table 1).

It is a well-established result that stable coexistence of two consumers limited by a single, homogeneous resource of constant quality is impossible and that the consumer which can maintain a population at the lowest level of the resource will competitively exclude the other consumer, if competition is purely exploitative (Armstrong and McGehee 1980). This can be illustrated with plots of zero-net-growth isoclines of Model I (with the interference constant c set to zero) in the RN - and RP -subsystems. The superior exploitative competitor (assumed to be N) can always invade a system in which the inferior exploitative competitor (assumed to be P) is at equilibrium with the resource (Fig. 1B). Once established, N will quickly drive the resource to levels where the population growth rate of P becomes negative and P goes extinct. Conversely, P is unable to invade a system in which N is at equilibrium with the resource (Fig. 1A).

The outcome of competition may change, if the two consumers also engage in interference and if there is a trade-off between exploitation and interference abilities. If the inferior exploitative competitor P is superior in interference competition, the superior exploitative competitor N may be unable to invade an RP system at equilibrium. This scenario is only possible in sufficiently productive systems. If the carrying capacity of the resource is high, interference from a high density of P at the RP equilibrium will cause an invading population of N to decline (Fig. 1B). Because interference does not convey any direct benefit to P , it does not, however, enhance the ability of P to increase from low densities in an RN system at equilibrium. Thus, in sufficiently productive systems, invasion of a single consumer-resource system at equilibrium by the respective other consumer is impossible (Fig. 1A, B) and the system settles either to an RN or an RP equilibrium, depending on initial conditions. Stable coexistence of two consumers sharing a single resource is thus impossible also in the case of unidirectional interference competition. These results are robust against the inclusion of nonlinear functional responses of the consumers (Appendix A) and extend to situations where interference between consumers is mutual (Amarasekare 2002).

SCENARIO 2: FOOD CHAIN WITH AND WITHOUT OMNIVORY IN A SYSTEM WITH FIXED RESOURCE QUALITY

Scenario 2 assumes that the precursor to an omnivory system is a linear food chain with fixed resource qual-

ity. These assumptions can be included in the general model by setting the attack rate of consumer P on the resource to zero and the conversion efficiencies of consumed food into consumer biomass to constant values (Model II in Table 1).

In contrast to a purely competitive system, stable coexistence of two consumers depending on a single resource is possible, if the species are arranged in a linear food chain and if the resource at the base of the food chain has a sufficiently high carrying capacity (Oksanen et al. 1981, DeAngelis 1992). This can again be illustrated with an isocline plot in the RN subsystem (an RP subsystem does not exist, because P does not feed on the resource). If the carrying capacity of the resource is high, a sufficient density of intermediate consumers N is maintained in an RN system so that invading top consumers P can increase from low densities (Fig. 1C). In the case of linear functional responses (Fig. 1C), invasibility of an RN system by P also guarantees the existence of a globally stable equilibrium of the food chain.

A linear food chain thus clearly fulfills the basic condition that the three species must be able to coexist prior to the evolution of omnivory. If costs of diet generalization are low, selection should then favor the inclusion of the resource in the top consumer's diet, in particular in habitats with high resource carrying capacity K . In the latter situation, the intermediate consumer will, however, be frequently driven to extinction, as can be seen in the plane of the RP subsystem (Fig. 2B). As K increases, the increasingly abundant and productive alternative food source R sustains an increased predation pressure from the top consumer on the intermediate consumer. Mutual invasibility and coexistence of the two consumers is therefore often limited to a relatively narrow range of resource carrying capacities (Fig. 2A–C; Diehl and Feiel 2000, 2001, Mylius et al. 2001). This poses a dynamical constraint on the maintenance of omnivory. At resource carrying capacities for which the intermediate consumer goes extinct, omnivory is not expressed and the former top consumer should evolve into a specialist consumer of the resource.

The destabilizing effect of a high resource carrying capacity can, however, be completely neutralized by low resource quality (low conversion efficiency e_{RP} of resources into top consumer biomass). Whenever the combination of parameters allows stable persistence of an omnivory system at some K , three-species persistence is possible also at infinitely high K if e_{RP} is lower than a threshold value (Figs. 2D–F, 3). This is shown in Appendix B, where the threshold conversion efficiency is given in Eq. B9. Fig. 3 illustrates how stable coexistence of the intermediate consumer with an omnivorous top consumer depends on the balance of resource carrying capacity (K) and resource quality (e_{RP}). When resource quality is high (here, $e_{RP} > 0.3$) coexistence is impossible. With decreasing resource qual-

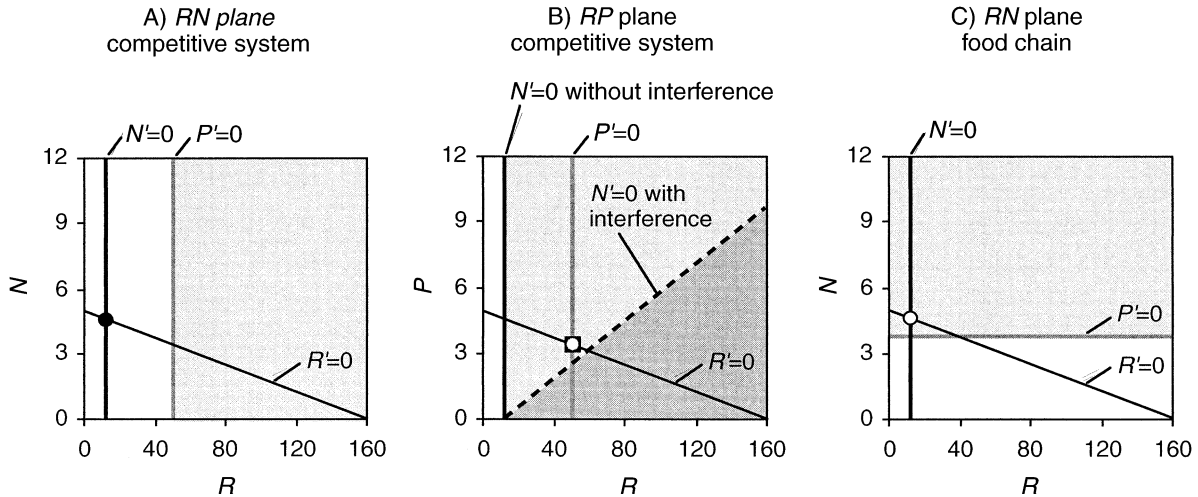


FIG. 1. Invasibility of boundary equilibria in a competitive system with and without interference and in a food chain. Panel A shows zero-net-growth isoclines in the RN plane (i.e., $P = 0$) of a system where N and P are exploitative competitors (Model I). Panel B shows zero-net-growth isoclines in the RP plane (i.e., $N = 0$) of a system where N and P are exploitative competitors and P may additionally interfere with N (Model I). Panel C shows zero-net-growth isoclines in the RN plane (i.e., $P = 0$) of a system where P feeds on N but not on R (Model II). In panels A and C, the gray areas mark conditions under which P can increase (i.e., $P' > 0$) from low densities in an RN -system. If the intersection of the R and N isoclines is in the gray area, then P can invade an RN system at equilibrium. Likewise, the gray areas in panel B mark the conditions under which N can increase (i.e., $N' > 0$) from low densities in an RP system. The dark gray area applies to a system with unidirectional interference of P against N . In the absence of interference, $N' > 0$ in the entire gray area. In the example, N can invade an RP system at equilibrium only in the absence of interference (panel B). Invasibility of boundary equilibria: filled circle = noninvasive; open circle = invasive; open square = noninvasive with interference, invasive without interference. Default parameter values are $a_{RN} = 0.1$, $a_{RP} = 0.1$, $a_{NP} = 0.14$, $m_N = 0.15$, $m_P = 0.5$, $e_{RN} = 0.12$, $e_{RP} = 0.1$, $e_{NP} = 0.9$, $K = 160$, $r = 0.5$. In panels A and B, $a_{NP} = 0$ and $e_{NP} = 0$; in panel C, $a_{RP} = 0$ and $e_{RP} = 0$.

ity, coexistence becomes first possible over a narrow range of relatively low resource carrying capacities. With further decreases in resource quality, the coexistence region extends to ever increasing resource carrying capacities. Below the threshold conversion efficiency (here $e_{RP} < 0.0706$), stable persistence of the omnivory system is possible at infinite K .

SCENARIO 3: RESOURCE COMPETITION AND OMNIVORY IN A SYSTEM WITH DYNAMICALLY FLEXIBLE RESOURCE QUALITY

Scenario 3 assumes that the precursor to an omnivory system is a competitive system with flexible resource quality. In scenarios 1 and 2, food quality was modeled phenomenologically as constant conversion efficiencies of consumed food into consumer biomass. The nutritional quality of many plants (and some animals) can, however, be a dynamic trait related to flexible tissue contents of essential components (e.g., mineral nutrients, vitamins, fatty acids) or toxic compounds. Here, I focus on mineral nutrient to biomass stoichiometry as a broadly relevant, mechanistic representation of food quality (Elser et al. 2000). I consider a system consisting of a plant species R with flexible nutrient stoichiometry and two herbivorous consumers N and P with fixed stoichiometry and explore the possibilities for three-species coexistence with and without an additional omnivorous feeding link between the consumers.

The model is an extension of the one-resource–two-consumer model of Loladze et al. (*in press*; see also Loladze et al. 2000), to which I have added the possibility of predation by consumer P on consumer N (Model III in Table 1). At any given time, plant production is assumed to be limited either by a mineral nutrient or by some other resource (e.g., light, space). The total amount of nutrient in the system is given by B , whereas the supply of other limiting plant resources is implicitly modeled as a carrying capacity K . The limiting nutrient occurs in the system only in organic form, i.e., incorporated in plant and consumer biomass. This corresponds to the assumption that there is no storage pool of the limiting nutrient, as is approximately true for, e.g., pelagic aquatic systems. Any nutrient excreted by consumers or lost in dead consumer bodies is assumed to be instantly mineralized and incorporated into plant biomass. Thus, the specific nutrient content q_R of plant biomass is dynamic and given by

$$q_R = \frac{B - q_N N - q_P P}{R} \tag{2}$$

where q_N and q_P are the specific nutrient contents per biomass of consumer N and P . I assume q_N and q_P to be constant, although these ratios may vary somewhat in practice (DeMott et al. 1998, Sterner and George 2000). The nutrient content of plants has a physiologically set lower bound q_{Rmin} . Plant growth is limited by

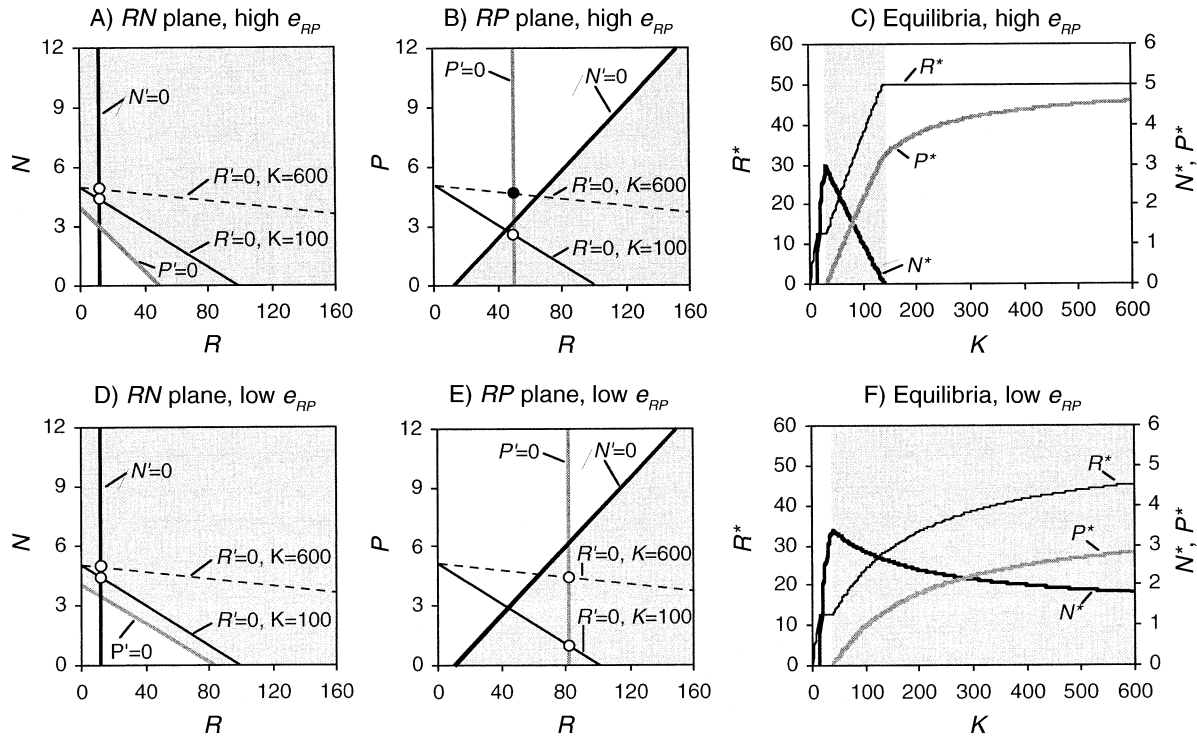


FIG. 2. Invasibility of boundary equilibria and sequence of equilibrium biomasses along a gradient of resource carrying capacities K for different conversion efficiencies e_{RP} of resources into omnivores in Model II. Panels A and D show zero-net-growth isoclines in the RN plane (i.e., $P = 0$) for two different carrying capacities ($K = 100$ and $K = 600$). Panels B and E show the corresponding zero-net-growth isoclines in the RP plane (i.e., $N = 0$). In panels A and D, the gray areas mark conditions under which the omnivore can increase (i.e., $P' > 0$) from low densities in an RN system. Likewise, the gray areas in panels B and E mark the conditions under which the intermediate consumer can increase (i.e., $N' > 0$) from low densities in an RP system. In the example, the omnivore can always invade an RN system (panels A, D). In contrast, at high resource quality (high e_{RP}), an increase in K must eventually lead to noninvasibility of the RP system by the intermediate consumer, because the intersection of the N and P isoclines is below the intersection of the R isocline with the ordinate (panel B). Consequently, stable persistence of an omnivory system is restricted to a narrow range of carrying capacities (gray area in panel C). At low resource quality (low e_{RP}), the intersection of the N and P isoclines occurs at higher values of P (panel E), and the intermediate consumer will be able to invade an RP system also at infinitely high K (gray area in panel F). At sufficiently low carrying capacities, the R and N isoclines may intersect in the lower left corners (white areas) of panels A and D, and the omnivore cannot invade an RN system at equilibrium. Invasibility of boundary equilibria: filled circle = noninvasible; open circle = invulnerable. Parameter values are as in Fig. 1 (default values). In panels A–C, $e_{RP} = 0.1$; in panels D–F, $e_{RP} = 0.06$.

the nutrient when the following inequality is fulfilled (as follows from substitution of Eq. 2 into the expression for resource renewal ρ in Model III [Table 1]):

$$\frac{q_{R\min}}{q_R} > \frac{R}{K}. \quad (3)$$

When Eq. 3 is reversed, plant growth is limited by intraspecific competition for other limiting resources. The transition between the two forms of limitation shows as a bend in the plant (R) isocline (Fig. 4).

With nutritional quality of plants being dynamic, efficiencies for the conversion of plant biomass into consumer biomass are no longer constant. Following Loladze et al. (*in press*), a simple rule is adopted to calculate these conversion efficiencies. When the specific nutrient content of a food species is larger than the specific nutrient content of consumer biomass (i.e., $q_i > q_p$, where i is the food and j is the consumer), con-

version efficiency is set to its maximum value e_{ij} . Conversely, when a food species is nutrient deficient compared to its consumer, only a fraction q_i/q_j of e_{ij} is realized. In this case, consumer growth is limited by the nutrient content rather than the carbon content of its food. An important final assumption is that consumers have saturating functional responses.

Loladze et al. (*in press*) have shown that stable coexistence of two consumers limited by a single plant is possible, if plant quality is dynamic. This can be illustrated with isocline plots in the RN and RP subsystems (Fig. 4A, B). Plant quality q_R is a decreasing function of plant and consumer densities (Eq. 2). The plant and consumer densities for which $q_R = q_j$ form a straight line with negative slope. To the left of that line, consumer growth is limited by the carbon content of plants ($q_R > q_j$) and consumer isoclines are straight vertical lines as in systems with constant resource qual-

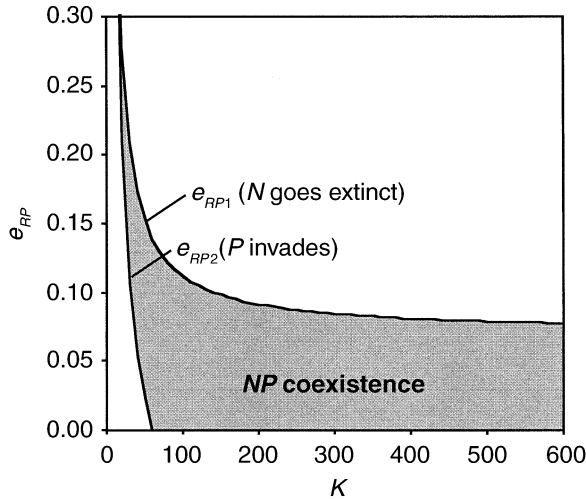


FIG. 3. Combinations of resource carrying capacities K and conversion efficiencies e_{RP} of resources into omnivores for which omnivores P and intermediate consumers N coexist stably in Model II. Coexistence is possible in the gray area bounded by e_{RP1} and e_{RP2} . Parameter values are as in Fig. 2; e_{RP1} asymptotes at 0.0706. A three-species equilibrium with omnivory is feasible whenever e_{RP} is high enough to allow P to invade an RP system at equilibrium (i.e., $e_{RP} > e_{RP2}$) but low enough to not drive N extinct (i.e., $e_{RP1} > e_{RP}$) (see Appendix B).

ity. To the right of the $q_R = q_j$ line, consumer growth is limited by the nutrient content of plants ($q_R < q_j$). Here, any increase in plant density R is more than compensated for by a concomitant decrease in food quality q_R ; i.e., the consumers' nutrient intake rates and, consequently, their growth rates decrease with increasing R and consumer isoclines have negative slopes in the region where $q_R < q_j$ (Fig. 4A, B). If the equilibria of both the RN and the RP subsystems lie in this region of low plant quality, mutual invasibility is possible and a globally stable equilibrium with both competitors may exist (Fig. 4A, B). At the resulting three-species equilibrium, both consumers are limited by plant quality q_R rather than plant quantity R (Loladze et al., *in press*).

A competitive system with flexible plant quality thus also fulfills the condition that the three species must be able to coexist prior to the evolution of omnivory. If costs of diet generalization are low, selection should then favor the inclusion of the competitor in the subsequent top consumer's diet. This evolutionary scenario may indeed lead to a stable omnivory system. After the inclusion of a feeding link from consumer P on consumer N in the competitive system depicted in Fig. 4A, B, mutual invasibility and stable three-species coexistence are still possible (Figs. 4C, D, 5).

In the numerical example, I have assumed a tradeoff between the omnivore's capacities to feed on plants vs. intermediate consumers. Compared to the intermediate consumer N , the omnivore P has a lower maximum conversion efficiency e_{Rj} and a longer handling time h_{Rj}

when feeding on plants. Nevertheless, because P has a lower mortality rate than N , the former is actually the superior competitor in situations where plant quality is high. This can be seen by comparison of the vertical parts of the consumer isoclines in the purely competitive system. At high plant quality ($q_R > q_j$), P requires a lower plant density than does N to achieve zero net population growth (Fig. 4A, B). Thus, when plant quality is dynamic, competitive ranking may change with changing plant quality and stable coexistence of a three-species omnivory system may be possible, even if the omnivore is the superior competitor under some environmental conditions. In the example, P can invade the system at a lower plant carrying capacity than can N (Fig. 5A). This is in stark contrast to a fundamental coexistence requirement in more traditional models (e.g., Model II). When the quality of the basal resource is fixed, stable coexistence of a three-species omnivory system is only possible if the intermediate consumer is the superior resource competitor under all environmental conditions, which implies that it can invade the system at a lower resource carrying capacity than can the omnivore (Fig. 2; Polis and Holt 1992, Holt and Polis 1997).

Fig. 5A also illustrates how plant quality and quantity interact in determining coexistence of the omnivore with the intermediate consumer. As plant carrying capacity K increases, plant quality at equilibrium $q_R(R^*)$ decreases. Because the intermediate consumer is the superior resource competitor at low resource quality, it may eventually invade the system. At even higher K , all species may be so strongly nutrient limited that their densities become independent of further increases in K . In this case, three-species coexistence is possible also at infinitely high K . This result seems to recover the similar result from the model with fixed quality of the basal resource (Fig. 3). Still, the influence of plant quality and quantity on consumer coexistence is more complex when plant quality is dynamic, because the productive capacity of plants now depends on two limiting resources (modeled as K and B). For example, if the productive capacity of plants is varied through variation in the total amount of nutrient in the system B , three-species coexistence is, again, possible only at relatively low plant quality (Fig. 5B). At still lower levels of plant quality (at levels of B , where plant biomass is kept below the carrying capacity set by other limiting resources), however, none of the consumers can exist at all (Fig. 5B).

Fig. 5B indicates that dynamic flexibility in resource quality may lead to complex patterns of species coexistence and abundance along environmental gradients. These patterns include multiple stable states (e.g., at $B > 0.31$, there is an alternative stable state with only R and P) and unstable dynamics (e.g., at $B > 0.38$, the R - P system starts to oscillate). A detailed analysis of Model III is, however, beyond the scope of this paper. The main point of the limited numerical analysis

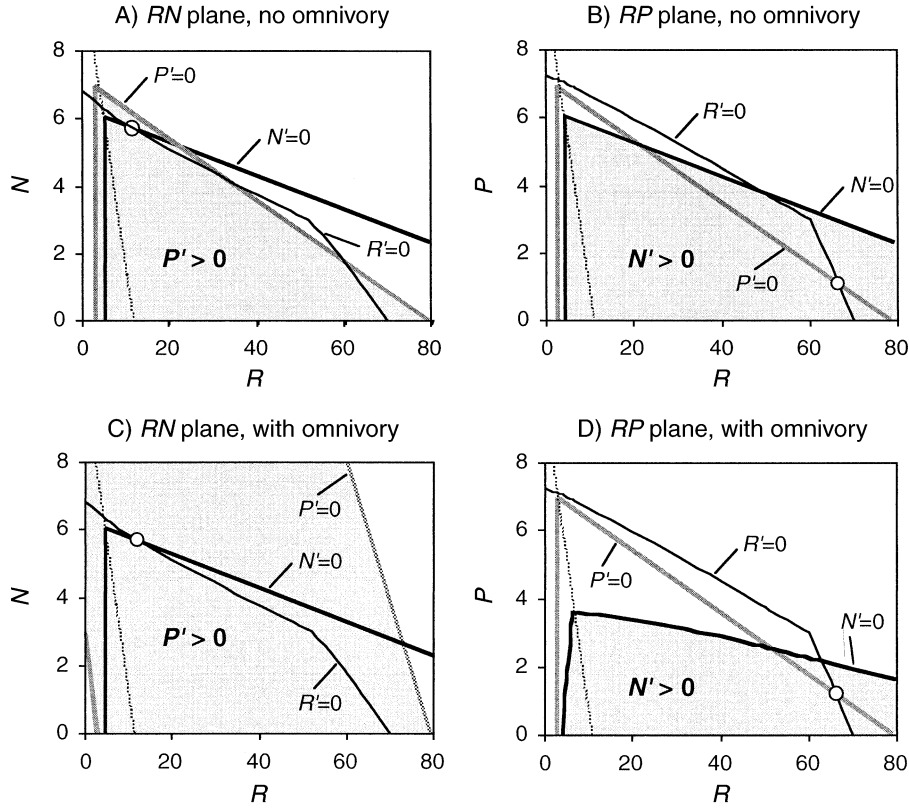


FIG. 4. Invasibility of boundary equilibria (open circles) in a competitive system without (A, B) and with (C, D) omnivory in Model III. Panels A and C show zero-net-growth isoclines in the RN plane (i.e., $P = 0$). Panels B and D show the corresponding zero-net-growth isoclines in the RP plane (i.e., $N = 0$). Moving from left to right along the plant isocline ($R' = 0$), a transition from nutrient limitation of plant growth to limitation by other resources (which determine the plant carrying capacity K) occurs at the bend. Consumer isoclines have negative slopes where plant quality is low (i.e., consumer growth is limited by the nutrient density rather than the carbon density of the plant). This occurs to the right of the thin dotted line where $q_R = q_N = q_P$. Gray areas mark conditions under which the respective missing consumer can increase (i.e., $P' > 0$ or $N' > 0$) from low densities. In the example, mutual invasibility (and stable NP coexistence) is possible in both a purely competitive system and an omnivory system. Parameter values are $a_{RN} = 0.085$, $a_{RP} = 0.08$, $B = 0.3$, $m_N = 0.25$, $m_P = 0.15$, $e_{RN} = 0.8$, $e_{RP} = 0.66$, $e_{NP} = 0.9$, $h_{RN} = 0.16$, $h_{RP} = 0.4$, $K = 70$, $q_{Rmin} = 0.003$, $q_N = 0.03$, $q_P = 0.03$, $r = 0.58$. In panels A and B, $a_{NP} = 0$. In panels C and D, $a_{NP} = 0.05$, and $h_{NP} = 0.5$.

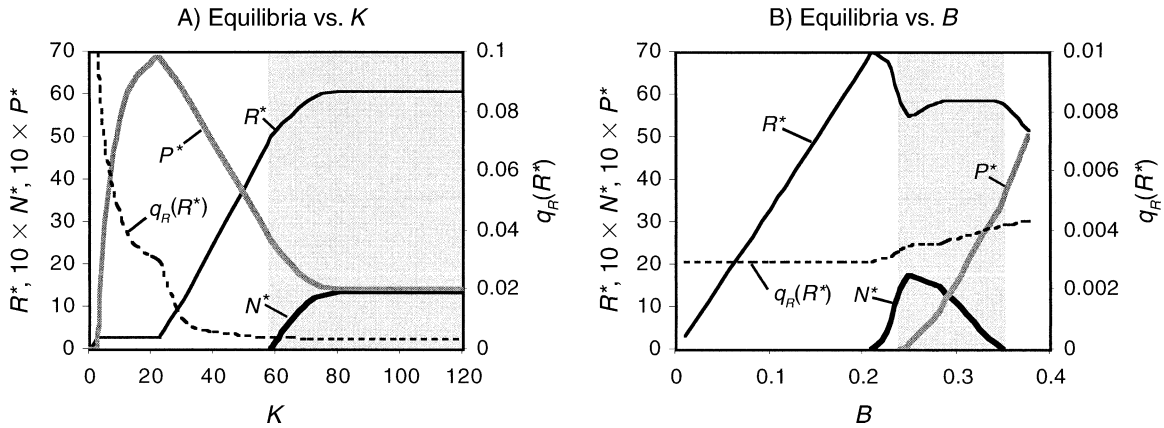


FIG. 5. Sequence of equilibrium biomasses and of the nutrient quota per biomass of resource at equilibrium $q_R(R^*)$ along a gradient of resource carrying capacities K (panel A) and a gradient of total nutrient content B in the system (panel B) in Model III. Stable persistence of an omnivory system is possible in the gray areas. Parameter values are as in Fig. 4 C, D. In panel B, $K = 70$. Initial conditions were $R = 58.5$, $N = 1.07$, $P = 1.6$. In panel B, for $B > 0.38$, the RP system starts to oscillate.

of Model III was to demonstrate, that the evolution of omnivory from a purely competitive system is theoretically possible and that the interplay of resource quality and quantity may, again, play a key role in the evolution and maintenance of omnivory.

DISCUSSION

Intuitively, interference among resource competitors seems to be a plausible avenue for the evolution of omnivory. A hypothetical progression has been proposed starting from exploitation competition, followed by aggression to monopolize local resources, eventually leading to intraguild predation (Polis 1988). The analysis of Model I suggests, however, that omnivory is unlikely to evolve from a competitive system with a single, homogeneous resource of constant quality, because stable persistence of two competitors is then impossible even if consumers exhibit a trade-off between resource exploitation and interference abilities (see also Case and Gilpin 1974, Briggs 1993, Amarasekare 2002). Clearly, such an evolutionary scenario requires an additional stabilizing mechanism.

The analysis of Model II shows that omnivory can evolve from a food chain, but that persistence of an omnivory system and, thus, the maintenance of omnivory, is dynamically constrained. Stable persistence is impossible or limited to a narrow range of resource carrying capacities, if resource quality is high (Fig. 3), but may occur over much broader ranges of resource carrying capacities, if resource quality is low. The latter situation is encountered by many omnivores feeding on both plant and animal material. Compared to animal prey, plant abundance is usually much higher, but the quality of most plant tissues is rather low (Mattson 1980, DeVries and Stein 1992, White 1993, Whitman et al. 1994, Elser et al. 2000). It is, for example, not uncommon that exclusive plant feeding only delays starvation but does not allow reproduction of zoophytophagous insects (Naranjo and Gibson 1996). In this case, the omnivore cannot persist on the plant alone, and exclusion of the intermediate consumer (which is needed to transform low quality plant tissue into high quality animal tissue) by the omnivore becomes impossible even in the most productive environments (J. van de Koppel and P. M. J. Herman, *unpublished manuscript*).

Loladze et al. (*in press*) have shown that low resource quality may also enable stable coexistence of two herbivores competing for a single plant with flexible nutrient content (see Fig. 4A, B). In their model, nutrients bound up in herbivore biomass are not available to plants, and herbivores may, in turn, be limited by the nutrient content of their food. This creates competition for limiting nutrients among herbivores and plants and stable coexistence of the two herbivores is only possible, if all three species are nutrient limited. Thus, low nutrient content in plant biomass is a prerequisite for the evolution of omnivory from a com-

petitive system with dynamic plant quality. Stable coexistence of competing herbivores requires furthermore that their competitive ranking depends on plant quality; i.e., the species that is superior at high plant quality must be inferior at low plant quality and vice versa.

Building on the model of Loladze et al., I have shown that evolution of omnivory from a competitive system is indeed feasible, if the quality of the shared plant is affected by plant and consumer densities (Model III). The competitive ranking of consumers may also in this case vary with plant quality, creating the intriguing possibility of stable persistence of a herbivore with an omnivore, in spite of the latter being superior in exploitative competition under some environmental conditions. Low plant quality may be important also for the maintenance of omnivory in such a system, as indicated by strongly negative correlations between resource quality $q(R^*)$ and equilibrium density of the intermediate consumer N in presence of the omnivore P (Fig. 5A and B). It seems that N can only coexist with P at low plant quality, i.e., under conditions where N was assumed to be superior in exploitative competition. Given the limited analysis of Model III, it is not possible to generalize these observations. The numerical examples do, however, clearly indicate that an explicit treatment of flexible resource stoichiometry broadens the possibilities for the evolution of omnivory, at least at the plant-herbivore interface.

Model III makes the simplifying assumption that consumers metabolize carbon and nutrients in the same proportions as found in their body tissues. Under the more realistic assumption that carbon is disproportionately metabolized to meet maintenance needs (Sternler 1997, Kooijman 2000) the boundary between carbon and nutrient limitation of consumer growth (thin dotted lines in Fig. 4) would be moved towards lower nutrient quota per plant biomass (i.e., to the right). This would limit the conditions for coexistence of the herbivores to a smaller area in parameter space. Possibly more restrictive is the assumption that a sufficiently large amount of nutrients can be bound in herbivore biomass to affect the nutrient stoichiometry of plants. This may be realistic in, e.g., pelagic aquatic systems (to which the model of Loladze et al. was originally applied), but is less likely in terrestrial arthropod systems, where plants are big compared to herbivores and the nutrient content of plant tissues is usually scarcely affected by the amount of nutrients stored in herbivores. Terrestrial plant quality may, however, vary in response to herbivore densities because of inducible plant defenses (Agrawal and Karban 1999). It is quite conceivable that the effects of density-dependent variation in defensive plant chemicals are similar to the effects of variation in plant nutrient content, because increases in herbivore densities should, in both cases, negatively affect the growth rates of both plants and herbivores.

For simplicity, I have limited the analysis of the roles of resource quality and abundance to stable precursor

systems. A nonequilibrium scenario may, however, open up the possibility that omnivory evolves from a competitive system with fixed resource quality. Unstable coexistence of two consumers on a single resource is possible, with the two consumer populations fluctuating in synchrony (Armstrong and McGehee 1980, Abrams and Holt 2002). Whether evolution of omnivory from such a system is a likely scenario will depend on the balance of two opposing tendencies. On the one hand, selection pressure towards feeding on the competitor may be especially high during troughs of the resource population. On the other hand, however, the victim of intraguild predation may not be able to withstand additional mortality during such population troughs and go extinct, in which case omnivory is not maintained. The result that low resource quality stabilizes omnivory systems is, in any case, consistent with the more general notion that weaker flows of energy and nutrients from the resource to the omnivore can help maintain omnivory in both equilibrium and nonequilibrium systems (McCann and Hastings 1997, McCann et al. 1998). Essentially, weak flows from the resource to the omnivore reduce the risk that a sufficiently large omnivore population is sustained to drive the intermediate consumer to extinction. The stabilizing effect of low resource quality is therefore highly likely to extend to nonequilibrium systems.

It must be pointed out that in all numerical examples of Models I–III the omnivore always has a higher growth rate when feeding on both food types than when feeding on either the resource or the intermediate consumer alone. This is an important requirement for the evolution and maintenance of omnivory, because, otherwise, the omnivore should evolve into a specialist consumer of the more profitable food type. Still, the present analysis mainly delineates conditions for the population dynamical feasibility of evolutionary pathways towards omnivory. Whether these pathways are evolutionary likely should be investigated with models, in which traits affecting the capacity to feed on more than one trophic level (e.g., conversion efficiencies) evolve dynamically in response to costs and benefits of diet generalization vs. specialization.

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LITERATURE CITED

Abrams, P. A., and R. D. Holt. 2002. The impact of consumer–resource cycles on the coexistence of competing species. *Theoretical Population Biology* **62**:281–295.

- Agrawal, A. A., and R. Karban. 1999. Why induced defenses may be favored over constitutive strategies in plants. Pages 45–61 in R. Tollrian and C. D. Harvell, editors. *The ecology and evolution of inducible defenses*. Princeton University Press, Princeton, New Jersey, USA.
- Amarasekare, P. 2002. Interference competition and species coexistence. *Proceedings of the Royal Society of London B* **269**:2541–2550.
- Armstrong, R. A., and R. McGehee. 1980. Competitive exclusion. *American Naturalist* **115**:151–170.
- Briggs, C. J. 1993. Competition among parasitoid species on a stage-structured host and its effect on host suppression. *American Naturalist* **141**:372–397.
- Case, T. J., and M. E. Gilpin. 1974. Interference competition and niche theory. *Proceedings of the National Academy of Sciences (USA)* **71**:3073–3077.
- Cohen, A. C. 1996. Plant feeding by predatory Heteroptera: evolutionary and adaptational aspects of trophic switching. Pages 1–17 in O. Alomar and R. N. Wiedenmann, editors. *Zoophytophagus Heteroptera: implications for life history and integrated pest management*. Entomological Society of America, Lanham, Maryland, USA.
- Coll, M., and M. Guershon. 2002. Omnivory in terrestrial arthropods: mixing plant and prey diets. *Annual Review of Entomology* **47**:267–297.
- DeAngelis, D. L. 1992. *Dynamics of nutrient cycling and food webs*. Chapman and Hall, London, UK.
- DeMott, W. B., R. Gulati, and K. Siewertsen. 1998. Effects of phosphorus deficient diets on the carbon and phosphorus balance of *Daphnia magna*. *Limnology and Oceanography* **43**:1147–1161.
- Denno, R. F., and W. F. Fagan. 2003. Might nitrogen limitation promote omnivory among carnivorous arthropods? *Ecology* **84**:2522–2531.
- DeVries, D. R., and R. A. Stein. 1992. Complex interactions between fish and zooplankton: quantifying the role of an open water planktivore. *Canadian Journal of Fisheries and Aquatic Sciences* **49**:1216–1227.
- Diehl, S. 1993. Relative consumer sizes and the strengths of direct and indirect interactions in omnivorous feeding relationships. *Oikos* **68**:151–157.
- Diehl, S., and M. Feiel. 2000. Effects of enrichment on 3-level food chains with omnivory. *American Naturalist* **155**:200–218.
- Diehl, S., and M. Feiel. 2001. Intraguild prey suffer from enrichment of their resources: a microcosm experiment with ciliates. *Ecology* **82**:2977–2983.
- Droop, M. R. 1974. The nutrient status of algal cells in continuous culture. *Journal of the Marine Biology Association UK* **54**:825–855.
- Elser, J. J., W. F. Fagan, R. F. Denno, D. R. Dobberfuhl, A. Folarin, A. Huberty, S. Inderlandi, S. S. Kilham, E. McCauley, K. I. Schulz, E. H. Siemann, and R. W. Sterner. 2000. Nutritional constraints in terrestrial and freshwater food webs. *Nature* **408**:578–580.
- Eubanks, M. D., and R. F. Denno. 1999. The ecological consequences of variation in plants and prey for an omnivorous insect. *Ecology* **80**:1253–1266.
- Eubanks, M. D., J. D. Styrsky, and R. F. Denno. 2003. The evolution of omnivory in heteropteran insects. *Ecology* **84**:2549–2556.
- Hairston, N. G. Jr., and N. G. Hairston, Sr. 1993. Cause–effect relationships in energy flow, trophic structure, and interspecific interactions. *American Naturalist* **142**:379–411.
- Hastings, H. M., and M. Conrad. 1979. Length and evolutionary stability of food chains. *Nature* **282**:838–839.
- Holt, R. D., and G. A. Polis. 1997. A theoretical framework for intraguild predation. *American Naturalist* **149**:745–764.

- Hutson, V., and R. Law. 1985. Permanent coexistence in general models of three interacting species. *Journal of Mathematical Biology* **21**:285–298.
- Kooi, B. W., L. D. J. Kuijper, M. P. Boer, and S. A. L. M. Kooijman. 2002. Numerical bifurcation analysis of a tri-trophic food web with omnivory. *Mathematical Biosciences* **177/178**:201–228.
- Kooijman, S. A. L. M. 2000. *Dynamic energy and mass budgets in biological systems*. Second edition. Cambridge University Press, Cambridge, UK.
- Loladze, I., Y. Kuang, and J. J. Elser. 2000. Stoichiometry in producer–grazer systems: linking energy flow with element cycling. *Bulletin of Mathematical Biology* **62**:1137–1162.
- Loladze, I., Y. Kuang, J. J. Elser, and W. F. Fagan. *In press*. Coexistence of two predators on one prey mediated by stoichiometry. *Theoretical Population Biology*.
- Mattson, W. J. 1980. Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics* **11**: 119–161.
- McCann, K., and A. Hastings. 1997. Re-evaluating the omnivory-stability relationship in food webs. *Proceedings of the Royal Society London B* **264**:1249–1254.
- McCann, K., A. Hastings, and G. R. Ruxel. 1998. Weak trophic interactions and the balance of nature. *Nature* **395**: 794–798.
- Mylius, S. D., K. Klumpers, A. M. de Roos, and L. Persson. 2001. Impact of intraguild predation and stage structure on simple communities along a productivity gradient. *American Naturalist* **158**:259–276.
- Naranjo, S. E., and R. L. Gibson. 1996. Phytophagy in predacious Heteroptera: effects on life history and population dynamics. Pages 57–93 in O. Alomar and R. N. Wiedenmann, editors. *Zoophytophagus Heteroptera: implications for life history and integrated pest management*. Entomological Society of America, Lanham, Maryland, USA.
- Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemelä. 1981. Exploitation ecosystems in gradients of primary productivity. *American Naturalist* **118**:240–261.
- Pimm, S. L., and J. H. Lawton. 1978. On feeding on more than one trophic level. *Nature* **275**:542–544.
- Polis, G. A. 1988. Exploitative competition and the evolution of interference, cannibalism and intraguild predation in age/size structured populations. Pages 185–202 in B. Ebenman and L. Persson, editors. *Size structured populations: ecology and evolution*. Springer-Verlag, New York, New York, USA.
- Polis, G. A., and R. D. Holt. 1992. Intraguild predation: the dynamics of complex interactions. *Trends in Ecology and Evolution* **7**:151–154.
- Polis, G. A., C. A. Myers, and R. D. Holt. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics* **20**:297–330.
- Sterner, R. W. 1997. Modelling interactions of food quality and quantity in homeostatic consumers. *Freshwater Biology* **38**:473–481.
- Sterner, R. W., and N. B. George. 2000. Carbon, nitrogen, and phosphorus stoichiometry of cyprinid fishes. *Ecology* **81**:127–140.
- White, T. C. R. 1993. *The inadequate environment: nitrogen and the abundance of animals*. Springer-Verlag, New York, New York, USA.
- Whitman, D. W., M. S. Blum, and F. Slansky, Jr. 1994. Carnivory in phytophagous insects. Pages 161–205 in T. N. Ananthakrishnan, editor. *Functional dynamics of phytophagous insects*. Science Publications, Lebanon, New Hampshire, USA.

APPENDIX A

The derivations of the stability of the three-species equilibrium of a two-consumer–one-resource system with unidirectional consumer interference and of the criteria for mutual invasion of the two consumers are available in ESA's Electronic Data Archive: *Ecological Archives* E084-064-A1.

APPENDIX B

The derivation of the coexistence region in e_{RP} - K space for model II with omnivory is available in ESA's Electronic Data Archive: *Ecological Archives* E084-064-A2.