

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

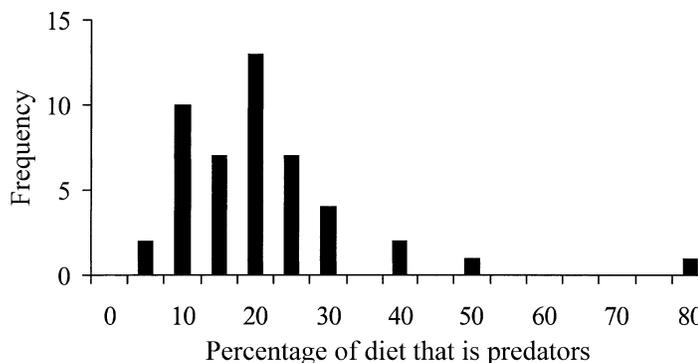
For our consideration of omnivory, we focus on the contribution of nitrogen (N) limitation to feeding strategies in terrestrial arthropods. We adopt a broad view in which omnivory is defined as feeding on two or more trophic levels (Menge and Sutherland 1987, Polis and Strong 1996), a definition that 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-

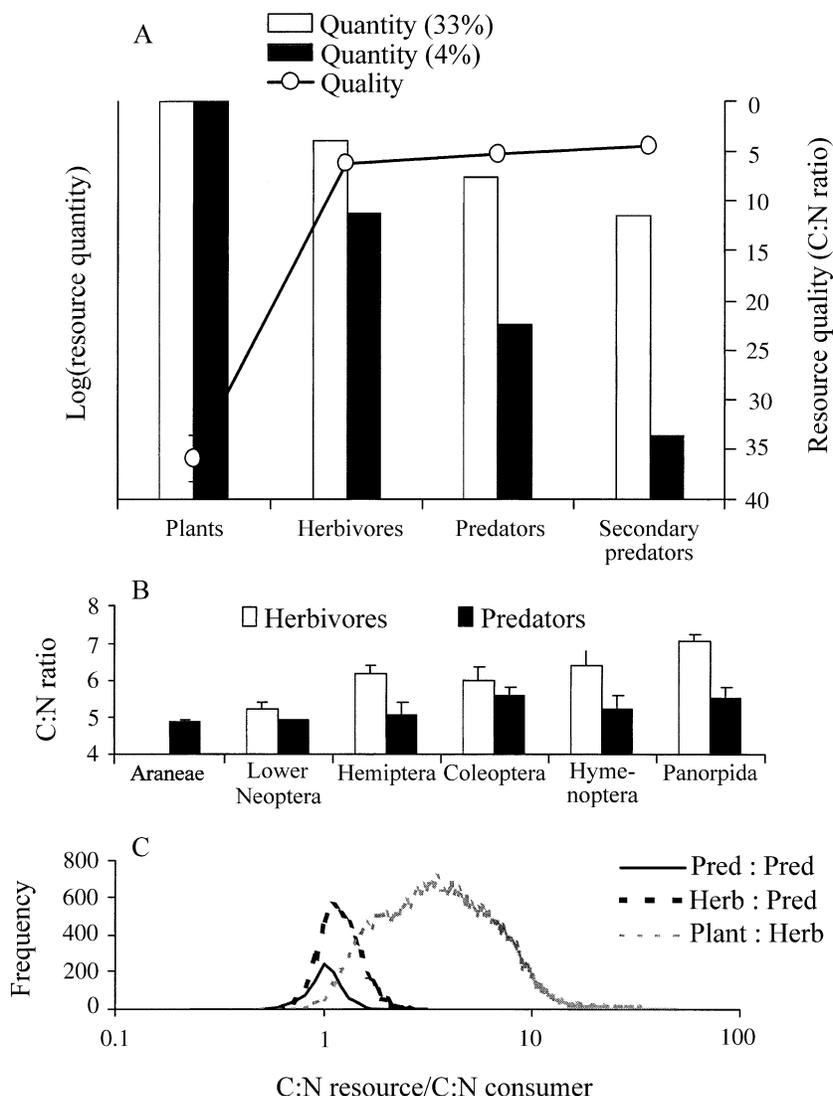


FIG. 2. Ratio of carbon to nitrogen (C:N) content across trophic levels, among taxa, and between potential resource-consumer pairs. Panel (A) outlines a trade-off between decreasing resource availability (standing crop biomass, on a logarithmic axis) and increasing resource quality (i.e., decreasing 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-

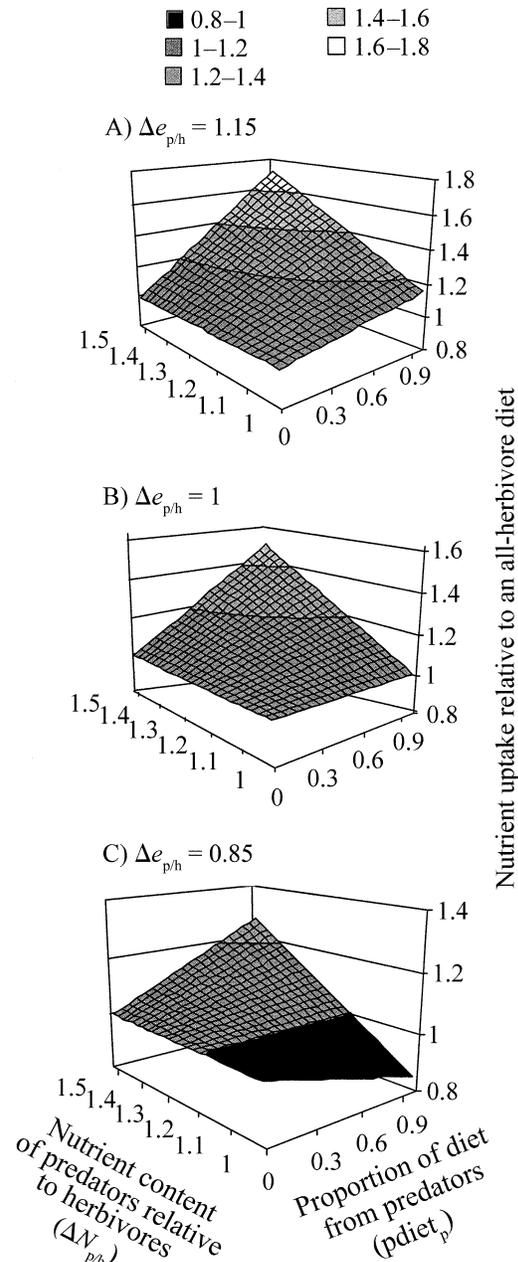


FIG. 3. Nutrient uptake for omnivores with mixed diets of herbivores and predators. Panel (A) depicts the case in which predators more quickly or efficiently take up nutrients from other predators. In (B), nutrient uptake rates from predators and herbivores are equal, whereas in (C), uptake rates from 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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