

## DOES INTRAGUILD PREDATION ENHANCE PREDATOR PERFORMANCE? A STOICHIOMETRIC PERSPECTIVE

MASAYA MATSUMURA,<sup>1</sup> GENEVIEVE M. TRAFELET-SMITH,<sup>2</sup> CLAUDIO GRATTON,<sup>3</sup> DEBORAH L. FINKE,<sup>4</sup>  
WILLIAM F. FAGAN,<sup>5</sup> AND ROBERT F. DENNO<sup>4,6</sup>

<sup>1</sup>National Agricultural Research Center for Kyushu Okinawa Region, Nishigoshi, Kumamoto, Japan

<sup>2</sup>Old Mill High School, Millersville, Maryland 21108 USA

<sup>3</sup>Department of Entomology, University of Wisconsin, Madison, Wisconsin 53706 USA

<sup>4</sup>Department of Entomology, University of Maryland, College Park, Maryland 20742 USA

<sup>5</sup>Department of Biology, University of Maryland, College Park, Maryland 20742 USA

**Abstract.** Ecological stoichiometry provides a novel context for elucidating the occurrence of intraguild predation. Recent data show that predators on average have a higher nitrogen content and lower C:N ratio than potential herbivorous prey. Thus, many predators may be nitrogen limited, and intraguild predation may allow them to increase their nitrogen intake and growth by supplementing a diet of herbivores with more nitrogen-rich intraguild prey. We tested this hypothesis using an assemblage of salt-marsh-inhabiting arthropods. First, we determined the nitrogen content and C:N ratio of taxa in four trophic groups (plants, herbivores, omnivores, and predators). Second, we fed an intraguild predator, the wolf spider *Pardosa*, one of three diets (herbivores, intraguild prey, or an alternating mix of the two) and measured spider survival, growth, capture rate, and biomass and nitrogen intake.

In general, body nitrogen content increased and C:N ratio decreased from lower to higher trophic levels for marsh-inhabiting species, with predators having a higher nitrogen content and lower C:N ratio than herbivores. Performance experiments showed that in one case *Pardosa* ingested more biomass and nitrogen and grew faster on a diet of intraguild prey (the planthopper egg predator *Tytthus*) than on a diet of herbivores (the planthopper *Prokelisia dolus*). This occurred because *Pardosa* captured more *Tytthus* than *Prokelisia* and not because *Tytthus* (a stoichiometric exception) was higher in nitrogen content. In another case, *Pardosa* grew slower on a diet of intraguild prey (the web-building spider *Grammonota*) than on a planthopper diet even though *Grammonota* was more nitrogen rich, a result we attribute to prey behavior and risk of predation. Mass gain and nitrogen intake in *Pardosa* were highly correlated with the biomass of prey consumed. However, after accounting for the biomass of prey consumed across all diet treatments, we found little evidence that either the nitrogen content or C:N stoichiometry of prey contributed to *Pardosa*'s growth. Thus, there was little support for the hypothesis that the nitrogen stoichiometry of prey directly confers a performance advantage to *Pardosa* and in itself promotes intraguild predation. In this system, characteristics other than the nitrogen stoichiometry of prey play a significant role in prey capture and predator performance. Nonetheless, by supplementing their diet with readily captured intraguild prey, predators such as *Pardosa* can increase their nitrogen intake and performance.

**Key words:** C:N ratio; diet mixing; ecological stoichiometry; intraguild predation; nitrogen content; omnivory; predator performance; prey behavior; prey nutrition; risk of predation; salt marsh; trophic level.

### INTRODUCTION

Omnivory is widespread in terrestrial arthropods, occurring in a diverse group of taxa that occupy both natural and agricultural habitats (Alomar and Wiedenmann 1996, Coll and Guershon 2002). Broadly defined, omnivores feed across two or more trophic levels (Polis and Strong 1996) and include “herbivores” that obtain nutrients from resources other than their host plants (e.g.,

cannibalism), “predators” that feed on certain plant tissues (e.g., pollen, seeds, and meristems) in addition to prey, and predators that feed on herbivores as well as other predators (e.g., intraguild predators) (Coll 1998, Rosenheim 1998, Coll and Guershon 2002, Finke and Denno 2002). Because omnivory is thought to have significant consequences for predator–prey interactions (Rosenheim 1998, Eubanks and Denno 2000a, Finke and Denno 2003), food-web dynamics (Polis and Strong 1996, Fagan 1997, McCann et al. 1998), ecosystem function (Ostrom et al. 1997), and biological control (Rosenheim et al. 1995, Hodge 1999), it becomes paramount to understand factors that promote this feeding strategy.

Manuscript received 22 September 2003; revised 9 January 2004; accepted 26 January 2004. Corresponding Editor: J. T. Cronin.

<sup>6</sup> E-mail: rd12@umail.umd.edu

Ecological stoichiometry, the study of the relative balance of nutrients in organisms from different trophic levels (Elser et al. 1996, 2000, Sterner and Elser 2002), provides a compelling context for elucidating the occurrence of omnivory (Fagan et al. 2002, Denno and Fagan 2003). For example, it has long been recognized that the stoichiometric mismatch in nitrogen content between arthropod herbivores and their host plants ( $C:N_{\text{plants}} \gg C:N_{\text{herbivores}}$ ) imposes tremendous demands for nitrogen and fundamental limitations on insect growth and fitness (McNeill and Southwood 1978, Mattson 1980, White 1993, Awmack and Leather 2002). However, by supplementing a plant diet with additional nitrogen from higher trophic levels, herbivores are able to partially offset this fundamental mismatch and enhance their growth and fitness dramatically (Barros-Bellanda and Zucoloto 2001). Thus, omnivory in "herbivores" may result in part from selective pressures associated with a high nitrogen demand compared to their nitrogen-poor host plants (Denno and Fagan 2003).

Recently, a similar stoichiometric imbalance was documented between higher trophic levels (Fagan et al. 2002). For example, terrestrial arthropod predators have a significantly higher nitrogen content (11.0%) and a lower C:N ratio (5.29) than do herbivores ( $N = 9.6\%$ ,  $C:N = 6.22$ ) (Fagan et al. 2002, Denno and Fagan 2003). Importantly, this difference persists after allometry, gut dilution, phylogeny, and other potentially confounding factors are taken into account (Fagan et al. 2002). Thus, predators that feed exclusively on herbivores are faced with the prospect of nitrogen limitation, especially in specific cases where the contrast in C:N stoichiometry is great (e.g., coccinellids feeding on aphids) (Fagan et al. 2002). Coupled with the knowledge that arthropod predators are often prey limited (Hurd and Eisenberg 1984, Polis and McCormick 1986, Rosenheim et al. 1993, Wise 1993, Hodge 1999, Stamp 2001), predators likely face routine nitrogen shortages, albeit to a lesser degree than herbivores (Denno and Fagan 2003).

Thus, stoichiometric imbalances at higher trophic levels may favor intraguild predation, whereby predators might enhance their nitrogen intake and ultimately their performance by supplementing a diet of herbivores with more nitrogen-rich intraguild prey (Denno and Fagan 2003). Although arthropod predators have been fed diets consisting of herbivores, detritivores, and other predators and have had their performance assessed (Uetz et al. 1992, Li and Jackson 1997, Strohmeyer et al. 1998, Toft and Wise 1999a, Stamp 2001), the relative nitrogen stoichiometries of predators and prey are rarely measured (but see Duval and Williams [2000]). Notably, an explicit link between prey capture, prey stoichiometry, and predator performance has not been established for terrestrial arthropod predators.

Admittedly, variation in prey behavior, toxicity, abundance, and risk of predation may compromise a predator's selection of more nitrogen-rich intraguild prey (Toft 1999, Toft and Wise 1999a, b, Francis et al. 2001, Stamp 2001, Denno and Fagan 2003, Singer and Bernays 2003). Together with the suggestion that stoichiometric effects may attenuate at higher trophic levels (Schindler and Eby 1997, Sterner and Elser 2002, Denno and Fagan 2003), prey behavior and risk of predation may offset any stoichiometric advantage altogether (Singer and Bernays 2003). Attenuation might result from less pronounced stoichiometric mismatches between higher trophic levels (Fagan et al. 2002, Denno and Fagan 2003) or because gross growth efficiencies of higher predators are often low such that assimilate is used largely for maintenance and the stoichiometry of growth becomes less relevant (see Schindler and Eby [1997], Sterner and Elser [2002]). Nonetheless, the extent to which prey behavior and abundance prevail over prey stoichiometry has been largely precluded due to the paucity of data on prey nutrition coupled with controlled experiments (Denno and Fagan 2003). In this multifaceted context, we test the hypothesis that predators will grow more rapidly on a diet of intraguild prey than on one consisting of herbivores because predators on average contain more nitrogen.

The assemblage of arthropods inhabiting the intertidal marshes of North America was used to explore this issue. The top arthropod carnivore is the hunting spider *Pardosa littoralis* that feeds on a diversity of herbivores (planthoppers and leafhoppers) as well as on other predators (mirid bugs and web-building spiders) (Döbel and Denno 1994, Denno et al. 2002, 2003, Finke and Denno 2002, 2003). Notably, intraguild predation by *Pardosa* in this system is frequent and can result in significant reductions in the density of intraguild prey (Denno et al. 2002, *in press*, Finke and Denno 2002, 2003). Thus, our specific objectives were to: (1) determine the nitrogen content and C:N ratio of the common herbivores and predators on the marsh to verify expected trophic differences in nutrient content and (2) compare the survival, growth, capture rate, and nitrogen intake of *Pardosa* when raised on diets of herbivores (planthoppers), intraguild prey (web-building spiders or mirid bugs), and an alternating mix of herbivores and intraguild prey. The mixed-diet treatment was explicitly designed to provide *Pardosa* with the opportunity to supplement an herbivore diet with intraguild prey. Last (3) we determine the overall relationship between *Pardosa* growth and its nitrogen and biomass intake and discuss the extent to which prey behavior might deter the capture of prey independent of potential nutritional benefits. With these experiments we aim to establish a more rigorous link between prey nutrition and predator performance and elucidate the nutritional advantages of an omnivorous feeding strategy.

## METHODS

*Study system*

The vegetation of mid-Atlantic coastal marshes is dominated by perennial cordgrasses (*Spartina*) and sedges (*Scirpus*) that often grow in extensive pure stands (Redfield 1972). In intertidal marshes, the low marsh is occupied by *Spartina alterniflora* whereas *Spartina patens* grows at higher elevations (Bertness 1991). In contrast, upland brackish marshes are covered by *Spartina cynosuroides* and *Scirpus robustus* (Moberley 1956, Redfield 1972).

Although a variety of host-specific herbivorous insects feed on *Spartina*, sap-feeders (planthoppers, leafhoppers, and mirid bugs) are by far the most abundant and diverse guild (Denno 1980, 1983, Denno and Peterson 2000). Of all the sap-feeders on *S. alterniflora*, two phloem-feeding planthoppers, *Prokelisia dolus* and *P. marginata* (Hemiptera: Delphacidae), are by far the most abundant (Denno et al. 2000). Sap-feeders also dominate the herbivore assemblage on *S. patens* where the planthoppers *Delphacodes detecta* and *Tumidagena minuta* abound (Denno 1980).

Wolf spiders, particularly *Pardosa littoralis*, are the most abundant and voracious predators of the active stages of planthoppers (adults and nymphs) in both *Spartina* systems (Döbel et al. 1990, Denno et al. 2002). Other abundant predators of planthoppers include the abundant web-building spider *Grammonota trivitatta*, which feeds on planthopper nymphs and adults (Denno et al. 2002), and the mirid bug *Tytthus vagus*, which selectively consumes planthopper eggs (Finke and Denno 2002, 2003). Notably, *Pardosa* is a voracious intraguild predator of *Tytthus*, and it also consumes other spider species such as *Grammonota* (Finke and Denno 2002, Gratton and Denno 2003; Denno et al., *in press*). Unlike *Pardosa*, *Tytthus* and *Grammonota* rarely engage in intraguild predation. Numerous other arthropod predators occur on the marsh (e.g., spiders, heteropterans, and beetles), but most are relatively uncommon (Denno 1983). True omnivores (sensu Coll and Gueshon 2002) include the longhorn grasshopper *Conocephalus spartinae*, which feeds on the leaves and seeds of both *Spartina* species as well as on planthoppers and other insects, and the coccinellid *Naemia seriata*, which consumes *Spartina* pollen and arthropod prey (Vince et al. 1981; R. F. Denno, *unpublished data*).

*Nitrogen content and C:N stoichiometry of field-collected marsh plants and arthropods*

To determine the nitrogen and carbon content of marsh taxa in four trophic groups (plants, herbivores, true omnivores, and predators) a variety of taxa were collected during July 2002 at two marsh locations in New Jersey, USA (Tuckerton, Ocean County, and Alloway Creek, Salem County). In all, four plant species, eight herbivores, two omnivores, and 21 predators (3–

5 replicates of each taxon) were sampled, kept on ice in the field, and then frozen (see Appendix A). For small arthropods such as planthoppers, 5–10 individuals were pooled to obtain sufficient biomass for analysis, and the sum constituted one replicate. Only one or two individuals of larger arthropods (e.g., wolf spiders) comprised a replicate. All samples were oven dried at 50°C for 48 h before grinding to a powder. Sample aliquots of powder for each replicate (1–3 mg dry mass) were packed into tin capsules that were sent to the Colorado Stable Isotope Laboratory (Northern Arizona University, Flagstaff, Arizona, USA) where percentage of carbon (%C), percentage of nitrogen (%N), and C:N were determined. Samples were analyzed in continuous-flow mode using an isotope-ratio mass spectrometer (Thermo-Quest Finnigan Deltaplus XL, Thermo Electron, Waltham, Massachusetts, USA) interfaced with a Carlo Erba 2100 elemental analyzer (Milan, Italy). The effect of trophic level (plant, herbivore, omnivore, and predator) on %N and C:N was determined using ANOVA, and means were compared using Tukey-Kramer honestly significant difference (hsd) tests.

*Nitrogen limitation and the threshold elemental ratio for Pardosa*

The likelihood that *Pardosa* exhibits reduced growth by feeding on prey (herbivores or predators) with different C:N compositions was estimated using the “threshold elemental ratio” (hereafter TER) developed by Urabe and Watanabe (1992) and further explored by Sterner and Elser (2002). Relative to its own C:N content, the TER identifies the level above which a predator is limited by the C:N ratio of its prey and is thus likely to experience a growth penalty. Expressed in terms of C:N ratios, the TER in a predator–prey interaction is given by

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

where  $\alpha_N$  is the maximum gross growth efficiency for N (i.e., the fraction of ingested N that the predator converts into new biomass),  $\alpha_C$  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 (Fagan et al. 2002, Sterner and Elser 2002, Denno and Fagan 2003). To calculate the TER for *Pardosa*, we used  $\alpha_N = 0.7$  and  $\alpha_C = 0.65$  (see Fagan et al. [2002]). Note that these values imply that *Pardosa* is slightly better at utilizing consumed N than C, but is an imperfect consumer of both (see Nentwig [1987], Riechert and Harp [1987], Fagan et al. [2002]). For further justification and details see Fagan et al. (2002) and Denno and Fagan (2003). The TER of *Pardosa* was then used to determine the C:N ratio of prey above which limited growth occurs and to assess which prey (herbivores, omnivores, or predators) were more likely to confer a growth penalty. The C:N

ratios for *Pardosa* and all potential prey species were determined from field-collected arthropods (Appendix A).

*Survival, growth, capture rate, and nitrogen intake of Pardosa fed diets of herbivores and intraguild prey*

The survival, growth, capture rate, and nitrogen intake of a single *Pardosa* spider (immature) was measured on three diets (herbivores, intraguild prey, or an alternating mix of the two) in plastic tube cages containing a single *Spartina* culm (see Denno et al. [2000] for cage design). Two experiments were conducted in the laboratory. For the first experiment, *Pardosa* was fed a diet of herbivores only (20 last-instar nymphs of the planthopper *Prokelisia dolus*), intraguild prey only (10 immatures of the web-building spider *Grammonota trivittata*), or an alternating mix of the two. In the second experiment, *Pardosa* was fed a diet of herbivores (20 last-instar nymphs of *Prokelisia*), intraguild prey (20 last-instar nymphs of the mirid egg predator *Tytthus vagus*), or a mix. Each diet treatment was replicated 11–13 times. Experimental diets were designed to maintain a nearly constant availability of prey biomass. Thus, because the *Grammonota* spiderlings used as prey in experiment 1 weighed about twice as much ( $1.11 \pm 0.04$  mg wet mass; means  $\pm 1$  SE) as *Prokelisia* nymphs ( $0.53 \pm 0.04$  mg), only half as many were offered as prey (10 vs. 20) to standardize the biomass of prey available to *Pardosa*. This was not an issue in experiment 2 because the *Prokelisia* and *Tytthus* offered were quite similar in size ( $0.48 \pm 0.02$  mg and  $0.41 \pm 0.02$  mg, respectively). The mixed-diet treatment was achieved by alternating herbivore with intraguild prey every 3–5 days. For the mixed treatment in both experiments, *Pardosa* was offered the herbivore first followed by intraguild prey. This resulted in five and four alternating exposure periods to each prey type in experiments 1 and 2, respectively. For all three treatments, prey were replaced every 3–5 days to maintain experimental densities and size classes. Both *Tytthus* and *Grammonota* were selected as intraguild prey because they are so abundant on the marsh and play key roles in interactions with *Pardosa* and *Prokelisia* planthoppers (Döbel and Denno 1994, Denno et al. 2000, Finke and Denno 2002).

For both experiments, single *Pardosa* immatures were raised on one of the three diet treatments and their growth and survival was assessed every 3–5 days by removing and weighing each spider. Thus, body mass (in milligrams), mass gain (in milligrams per day), and survival were assessed repeatedly during the time course of the experiments (10 times over a 45-day period beginning 21 June 2002 and eight times over a 35-day period beginning 22 August for experiments 1 and 2, respectively). Capture rate (number per day) was assessed by counting the number of prey remaining in each cage every 3–5 days and subtracting this count

from the initial number offered. This number was adjusted down by subtracting the number of prey that died in *Pardosa*-free cages (five replicates of each prey treatment), a number that was generally very low. The biomass of prey consumed (in milligrams per day) during each 3–5-day interval was calculated by multiplying capture rate (number per day) by the mean biomass of individual prey offered (*Prokelisia* = 0.53 mg and *Grammonota* = 1.11 mg in experiment 1; *Prokelisia* = 0.48 mg and *Tytthus* = 0.41 mg in experiment 2). Nitrogen intake for *Pardosa* (in milligrams per day) was calculated for each time interval as the product of the wet biomass of prey captured (in milligrams per day), its proportional dry mass, and its mean nitrogen content expressed as a proportion of dry mass. The mean proportional nitrogen content of prey used in these calculations was  $0.114 \pm 0.01$  and  $0.120 \pm 0.01$  for *Prokelisia* and *Grammonota* in experiment 1 and  $0.111 \pm 0.04$  and  $0.098 \pm 0.04$  for *Prokelisia* and *Tytthus* in experiment 2, respectively. Mean dry mass proportions used in the conversions were  $0.219 \pm 0.01$  and  $0.252 \pm 0.03$  for *Prokelisia* and *Grammonota* in experiment 1 and  $0.219 \pm 0.1$  and  $0.279 \pm 0.04$  for *Prokelisia* and *Tytthus* in experiment 2, respectively. *Spartina*, *Prokelisia*, and spiders were cultured and maintained under controlled conditions prior to use in experiments (see Denno et al. [2000]). The nitrogen content and biomass of each prey type was determined from a subset (five replicates) of the same cultured animals used in experiments. Thus, because prey in the same stage class were used and because prey were frequently replaced, neither the biomass nor nitrogen content of prey was likely to change much over the course of the experiment. All cultured arthropods were initially obtained from a *Spartina* marsh near Tuckerton, New Jersey (see Denno et al. [2002]).

Repeated-measures ANOVA was used to test the effects of treatment (herbivore, intraguild prey, or the mix), time (10 or 8 for experiments 1 and 2, respectively), and their interaction on *Pardosa* mass, mass gain, capture rate of prey, biomass of prey consumed, and nitrogen intake (SAS 2001). Non-independence of residual variance across time periods was modeled using either an unstructured or compound symmetry covariance structure (PROC MIXED, SAS 2001). Pairwise comparisons of treatment means were made using *t* tests followed by a Tukey-Kramer adjustment for multiple comparisons. When needed, data were transformed to meet ANOVA assumptions: *Pardosa* mass data were log transformed and capture rate data were square-root transformed. The effects of the three diet treatments on mean *Pardosa* survival were assessed using ANOVA followed by a Tukey-Kramer adjustment for multiple comparisons (JMP version 5, SAS 2001). The nitrogen contents (as percentages) of the herbivore and intraguild prey used in both experiments were compared by ANOVA. Data for experiments 1 and 2 were analyzed separately.

*Relationship between prey biomass and nitrogen intake and the growth and survival of Pardosa*

The relationship between nitrogen intake (in milligrams per day) and mass gain (in milligrams per day) in *Pardosa* was determined by correlating treatment means from experiments 1 and 2. The six diet treatments were: herbivorous prey (*Prokelisia* planthoppers in experiments 1 and 2), intraguild prey in experiments 1 and 2, respectively (*Grammonota* spiders and *Tytthus* egg predators), or an alternating mix of herbivores and intraguild prey in experiments 1 and 2, respectively (*Prokelisia* + *Grammonota* and *Prokelisia* + *Tytthus*). The relationship between prey biomass consumed (in milligrams per day) and both the mass gain and survival of *Pardosa* was determined from the six treatment means, as well as the relationship between prey biomass consumed and nitrogen intake. To assess the effect of prey stoichiometry on mass gain in *Pardosa* independent of the amount of prey consumed, residuals of the relationship between mass gain and biomass consumed were correlated with the nitrogen content (%N) and C:N ratio of the total prey biomass consumed. Relationships were tested using Spearman's rank correlation tests, and residuals were determined from parametric linear correlations (JMP version 5, SAS 2001).

#### RESULTS

*Nitrogen content and C:N stoichiometry of field-collected marsh plants and arthropods*

There was a significant effect of trophic group on both the nitrogen content ( $F_{3,31} = 138.3$ ,  $P < 0.0001$ ) and C:N ratio of salt-marsh organisms ( $F_{3,31} = 239.8$ ,  $P < 0.0001$ ). In general, nitrogen content increased up the food chain from plants ( $1.23 \pm 0.46\%$ ) to predators ( $11.5 \pm 0.2\%$ ) with the largest discrepancy occurring between plants and herbivores ( $9.2 \pm 0.3\%$ ; Fig. 1A). Notably, the nitrogen content of predators was higher than that for herbivores with omnivores falling in between ( $10.5 \pm 0.7\%$ ). The C:N ratio of organisms showed the opposite pattern by decreasing up the food web (Fig. 1B). Plants exhibited the highest values ( $37.6 \pm 1.2$ ), yet herbivores had significantly higher C:N ratios ( $5.6 \pm 0.8$ ) than predators ( $4.3 \pm 0.5$ ), with omnivores again intermediate ( $4.8 \pm 1.6$ ). These data suggest that in general predators feeding on other predators encounter a more nitrogen-rich meal than predators feeding on herbivores. There were trophic exceptions as evidenced by one of our experimental predators *Tytthus* that had a nitrogen content ( $9.3 \pm 0.2\%$ ) lower than that for predators in general ( $11.5 \pm 0.2\%$ ) and similar to that for most herbivores ( $9.2 \pm 0.3\%$ ) (Appendix A). *Grammonota*, our other experimental predator, had a high nitrogen content ( $12.0 \pm 0.1\%$ ), more like that of predators in general.

*Nitrogen limitation and the threshold elemental ratio for Pardosa*

*Pardosa*, with a C:N ratio of 4.02, should experience nitrogen-limited growth ( $TER_{C:N} = 4.32$ ) when feeding

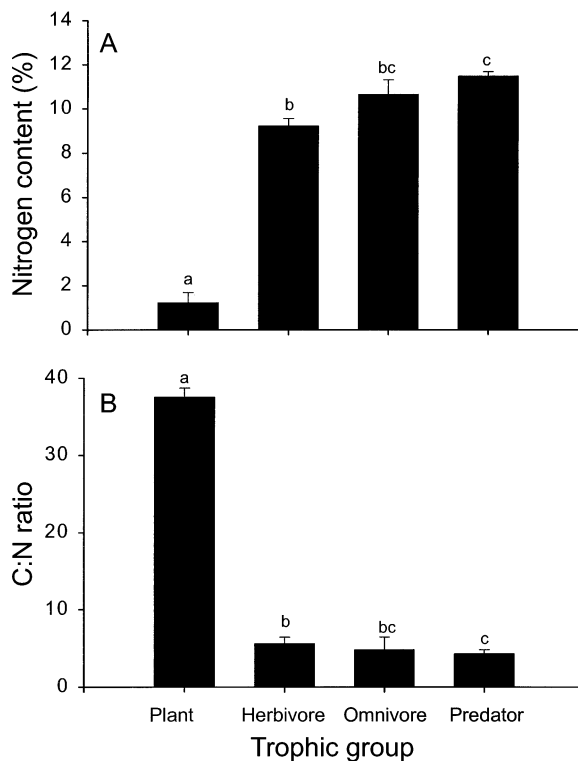


FIG. 1. (A) Nitrogen content and (B) C:N ratio of salt marsh plants and associated arthropods (herbivores, omnivores, and predators). All taxa were collected from *Spartina* marshes near Tuckerton and Alloway Creek, New Jersey, USA. Means (+ SE) with different letters are significantly different (ANOVA followed by Tukey-Kramer hsd test,  $P < 0.05$ ). See Appendix A for specific taxa analyzed.

on prey with a C:N ratio  $\geq 4.32$ . Thus, feeding exclusively on any marsh herbivore (C:N =  $5.6 \pm 0.8$ , range = 4.5–6.4) or omnivore (C:N =  $4.8 \pm 1.6$ , range = 4.6–5.0) has potential adverse growth consequences (see Appendix A). By feeding on marsh predators (C:N =  $4.3 \pm 0.5$ , range = 3.5–5.3), nitrogen-limited growth should be less likely for *Pardosa*. For the prey species used in our experiments, and all else being equal, *Pardosa* should experience growth penalties when feeding exclusively on *Prokelisia dolus* (C:N =  $5.3 \pm 0.2$ ) and *Tytthus* (C:N =  $5.2 \pm 0.1$ ), but not when consuming *Grammonota* (C:N =  $4.0 \pm 0.04$ ).

*Survival, growth, capture rate, and nitrogen intake of Pardosa fed diets of herbivores and intraguild prey*

In the first experiment, *Pardosa* survived and performed better on the herbivore diet than a diet of intraguild prey (Fig. 2) despite the higher nitrogen content of the intraguild prey (*Grammonota* =  $12.0 \pm 0.1\%$ , *Prokelisia* =  $11.4 \pm 0.1\%$ ;  $F_{1,6} = 24.4$ ,  $P = 0.003$ ). For example, there was a significant effect of diet on survival ( $F_{2,30} = 5.09$ ,  $P = 0.013$ ), with *Pardosa* exhibiting significantly higher survival on a diet of

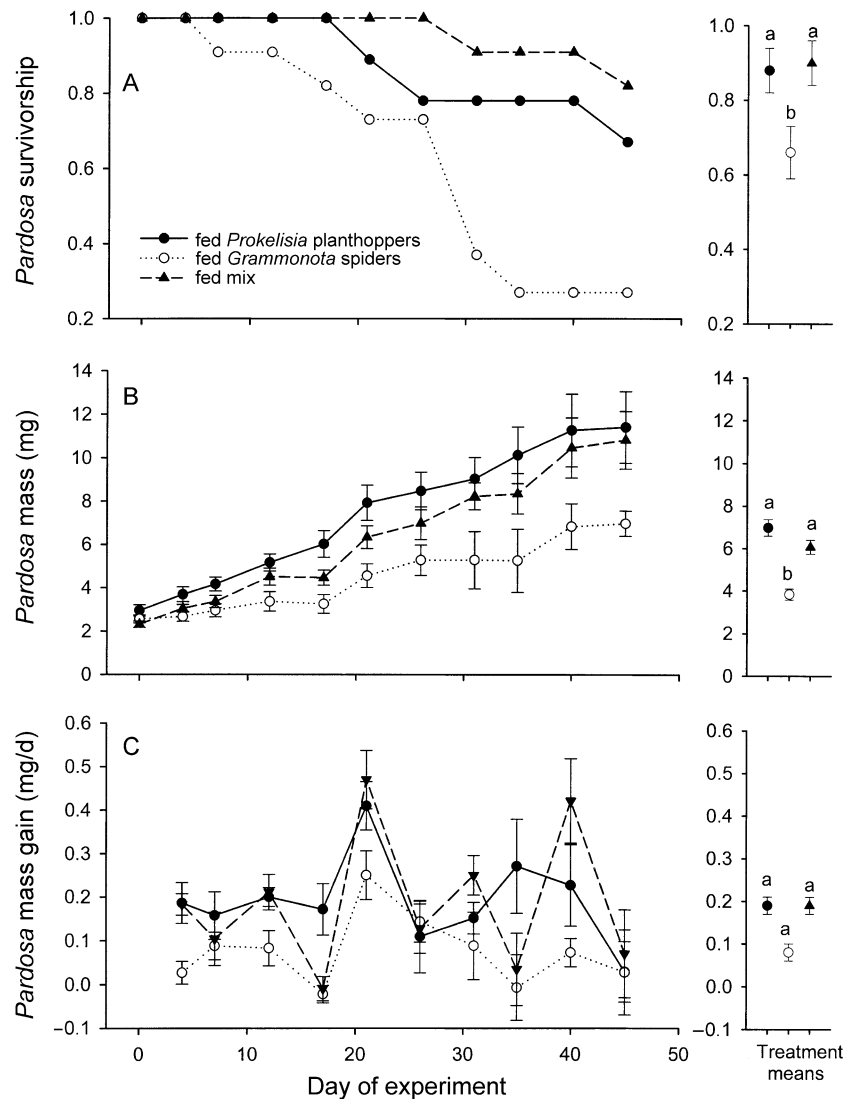


FIG. 2. (A) Survivorship (as a proportion), (B) mass, and (C) mass gain of *Pardosa* wolf spiders fed one of three diets for 45 days: *Prokelisia* planthoppers (herbivores), *Grammonota* spiders (intraguild prey), or an alternating mix of planthoppers and spiders. For the mixed-diet treatment, herbivores were always offered first in the alternating sequence and were switched with intraguild prey every 3–5 days. In the right panels, overall treatment means ( $\pm$  SE) with different letters are significantly different (Tukey-Kramer comparison,  $P < 0.05$ ).

*Prokelisia* planthoppers and the mixed diet than when fed only *Grammonota* spiders (Fig. 2A). Similarly, there was a significant effect of diet and its interaction with time on the mass of *Pardosa* (Appendix B). *Pardosa* fed *Prokelisia* planthoppers or the alternating mix of prey were significantly heavier than those fed *Grammonota* (Fig. 2B). Fed an alternating mixed diet, *Pardosa* gained mass more during periods when it was fed *Prokelisia* than when it was fed exclusively *Grammonota* (Fig. 2C). This alternating pattern of mass gain is supported by a significant diet by time interaction (Appendix B).

In experiment one, *Pardosa* captured more prey, consumed more prey biomass, and therefore consumed

more nitrogen when fed a diet of herbivores than intraguild prey or the mix (Fig. 3). For instance, there was a significant effect of diet and its interaction with time on the number of prey captured (Appendix B); on average, *Pardosa* captured 2–3 times as many *Prokelisia* per unit time as it did *Grammonota* (Fig. 3A). The fluctuating pattern of prey capture when fed the alternating mix emphasizes the ease with which *Pardosa* captured the herbivore compared to intraguild prey (Fig. 3A). This pattern undoubtedly contributed to the significant interactive effect of diet with time on prey capture (Appendix B). There was also a significant effect of diet and its interaction with time on the biomass of prey consumed and on nitrogen intake, with *Pardosa*

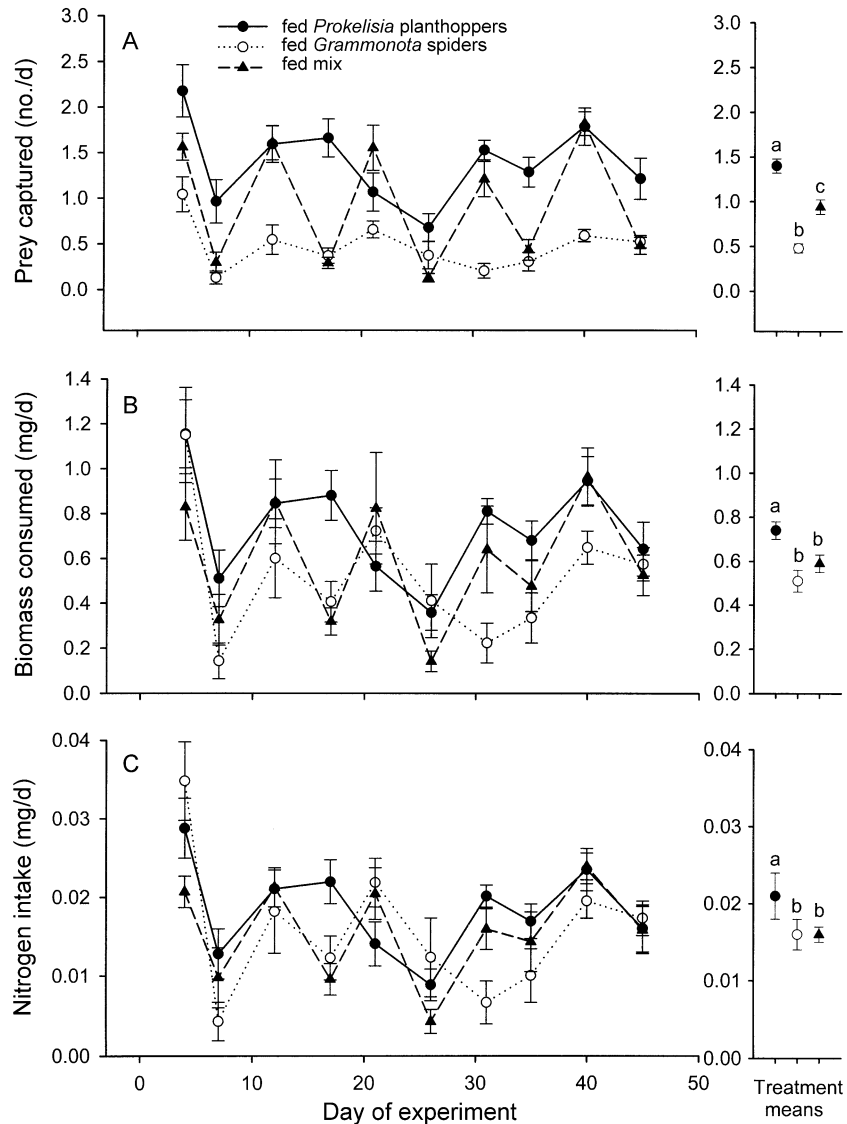


FIG. 3. (A) Number of prey captured, (B) prey biomass consumed, and (C) nitrogen intake of *Pardosa* wolf spiders fed one of three diets for 45 days: *Prokelisia* planhoppers (herbivores), *Grammonota* spiders (intraguild prey), or an alternating mix of planhoppers and spiders. For the mixed-diet treatment, herbivores were always offered first in the alternating sequence and were switched with intraguild prey every 3–5 days. In the right panels, overall treatment means ( $\pm$  SE) with different letters are significantly different (Tukey-Kramer comparison,  $P < 0.05$ ).

consuming the most prey biomass (Fig. 3B) and nitrogen (Fig. 3C) when fed a diet of *Prokelisia* (Appendix B). Again, a fluctuating pattern of biomass consumption and nitrogen intake was evident when *Pardosa* was fed the alternating mix of prey (Fig. 3B, C).

Results from the second experiment showed that *Pardosa* survived equally well on diets of *Prokelisia* planhoppers, *Tytthus* predators, and an alternating mix of the two ( $F_{2,24} = 0.66$ ,  $P = 0.53$ ; Fig. 4A). This result occurred even though *Prokelisia* was slightly more nitrogen rich ( $11.1 \pm 0.4\%$  nitrogen) than *Tytthus* ( $9.8 \pm 0.4\%$ ;  $F_{1,8} = 5.8$ ,  $P = 0.042$ ). However, by all other measures, *Pardosa* performed best on a diet of *Tytthus*.

For example, there were significant effects of diet and its interaction with time on the mass of *Pardosa* and on its daily mass gain (Appendix B). In general, *Pardosa* grew to a larger size and gained mass most rapidly on a diet of *Tytthus* compared to *Prokelisia* with intermediate performance on the mixed diet (Fig. 4B, C). When fed the alternating mix, a fluctuating pattern was evident with *Pardosa* gaining more mass when exposed to *Tytthus* than *Prokelisia* (Fig. 4C). Thus, supplementing a diet of herbivores with intraguild prey enhanced the growth of *Pardosa* (Fig. 4B, C).

Diet and its interaction with time significantly affected *Pardosa*'s capture rate of prey, with more *Tyt-*

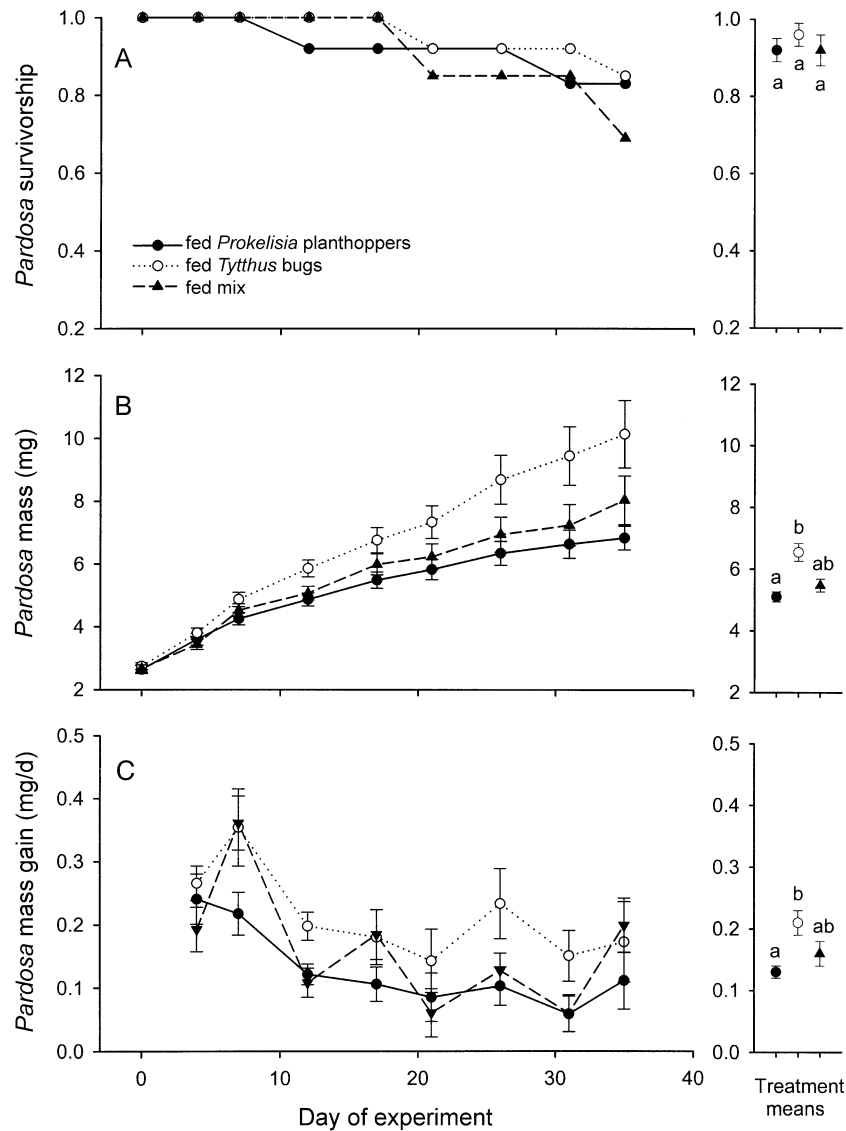


FIG. 4. (A) Survivorship (as a proportion), (B) mass, and (C) mass gain of *Pardosa* wolf spiders fed one of three diets for 35 days: *Prokelisia* planthoppers (herbivores), *Tytthus* bugs (intraguild prey), or an alternating mix of planthoppers and bugs. For the mixed-diet treatment, herbivores were always offered first in the alternating sequence and were switched with intraguild prey every 3–5 days. In the right panels, overall treatment means ( $\pm$  SE) with different letters are significantly different (Tukey-Kramer comparison,  $P < 0.05$ ).

thus taken per unit time than *Prokelisia* (Fig. 5A, Appendix B). A fluctuating pattern of prey capture was seen on the mixed diet with higher capture rates during periods of exposure to *Tytthus* than *Prokelisia* (Fig. 5A), a pattern supported by the significant diet by time interaction (Appendix B). Diet had no significant effect on the biomass of prey consumed, although there was a trend for increased consumption of *Tytthus* (Fig. 5B, Appendix B). However, there was a significant effect of diet on the amount of nitrogen consumed (Appendix B), with *Pardosa* consuming more nitrogen per unit time when fed *Tytthus* than *Prokelisia* and with nitrogen intake intermediate on the mixed diet (Fig. 5C).

#### Relationship between prey biomass and nitrogen intake and the growth and survival of *Pardosa*

There was a significant positive relationship between nitrogen intake and mass gain in *Pardosa* across the six diet combinations ( $r = 0.83$ ,  $P = 0.04$ ; Fig. 6A). Moreover, both mass gain ( $r = 0.83$ ,  $P = 0.04$ ; Fig. 6B) and survivorship in *Pardosa* were significantly related to the biomass of prey consumed ( $r = 0.80$ ,  $P = 0.05$ ; Fig. 6C). *Pardosa* grew most rapidly and survived best on a diet of *Tytthus* where its daily acquisition of nitrogen was highest. *Pardosa* exhibited moderate performance on a diet of planthoppers or on a mixed diet of intraguild prey and planthoppers and growth and

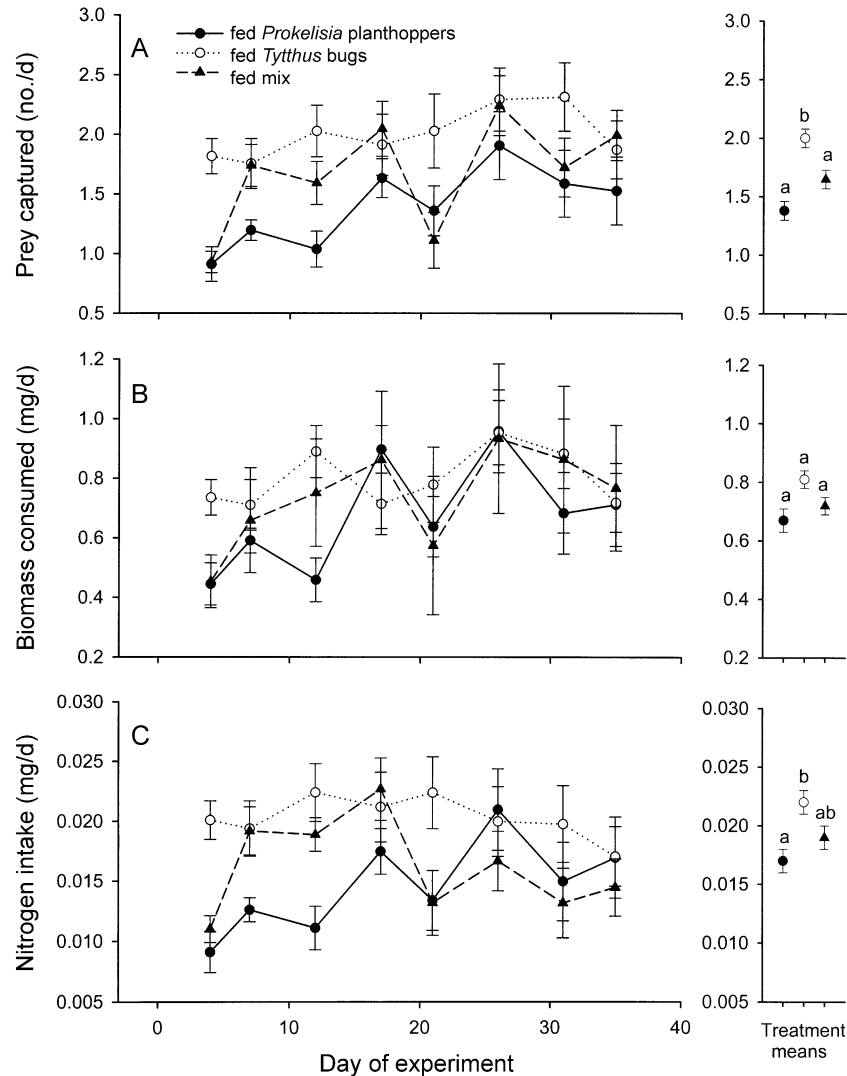


FIG. 5. (A) Number of prey captured, (B) prey biomass consumed, and (C) nitrogen intake of *Pardosa* wolf spiders fed one of three diets for 35 days: *Prokelisia* planthoppers (herbivores), *Tytthus* bugs (intraguild prey), or an alternating mix of planthoppers and bugs. For the mixed-diet treatment, herbivores were always offered first in the alternating sequence and were switched with intraguild prey every 3–5 days. In the right panels, overall treatment means ( $\pm$  SE) with different letters are significantly different (Tukey-Kramer comparison,  $P < 0.05$ ).

survival were most impaired on a *Grammonota* diet. Overall, nitrogen intake was highly correlated with the biomass of prey consumed ( $r = 0.92$ ,  $P < 0.01$ ; Fig. 6D). Thus, to extract the effect of prey stoichiometry on mass gain in *Pardosa* while controlling for the biomass of prey consumed, we correlated the residuals of the relationship between mass gain and prey biomass consumed (Fig. 6B) with the mean nitrogen content (as a percentage) and C:N ratio of the six prey diets. However, we found no relationship between the residuals of mass gain and either the nitrogen content (Fig. 7A;  $r = 0.09$ ,  $P = 0.87$ ) or C:N ratio of prey biomass (Fig. 7B;  $r = 0.03$ ,  $P = 0.96$ ). Thus, variation in *Pardosa*'s performance and nitrogen intake across the different prey diets results from differences in capture rate and

biomass consumption rather than prey stoichiometry. Nonetheless, feeding on intraguild prey enhanced nitrogen intake and growth in one case (*Tytthus*) but severely hampered it in another (*Grammonota*).

#### DISCUSSION

Overall, salt marsh arthropods displayed the same trophic pattern of nitrogen stoichiometry as that exhibited by arthropods at large (Fagan et al. 2002, Denno and Fagan 2003), namely that predators in general have a higher nitrogen content and lower C:N ratio than herbivores (Fig. 1). Reasons for the elevated nitrogen content of predators compared to herbivores are several (Fagan et al. 2002). First, predators may consume food with higher nitrogen content than herbivores. Second,

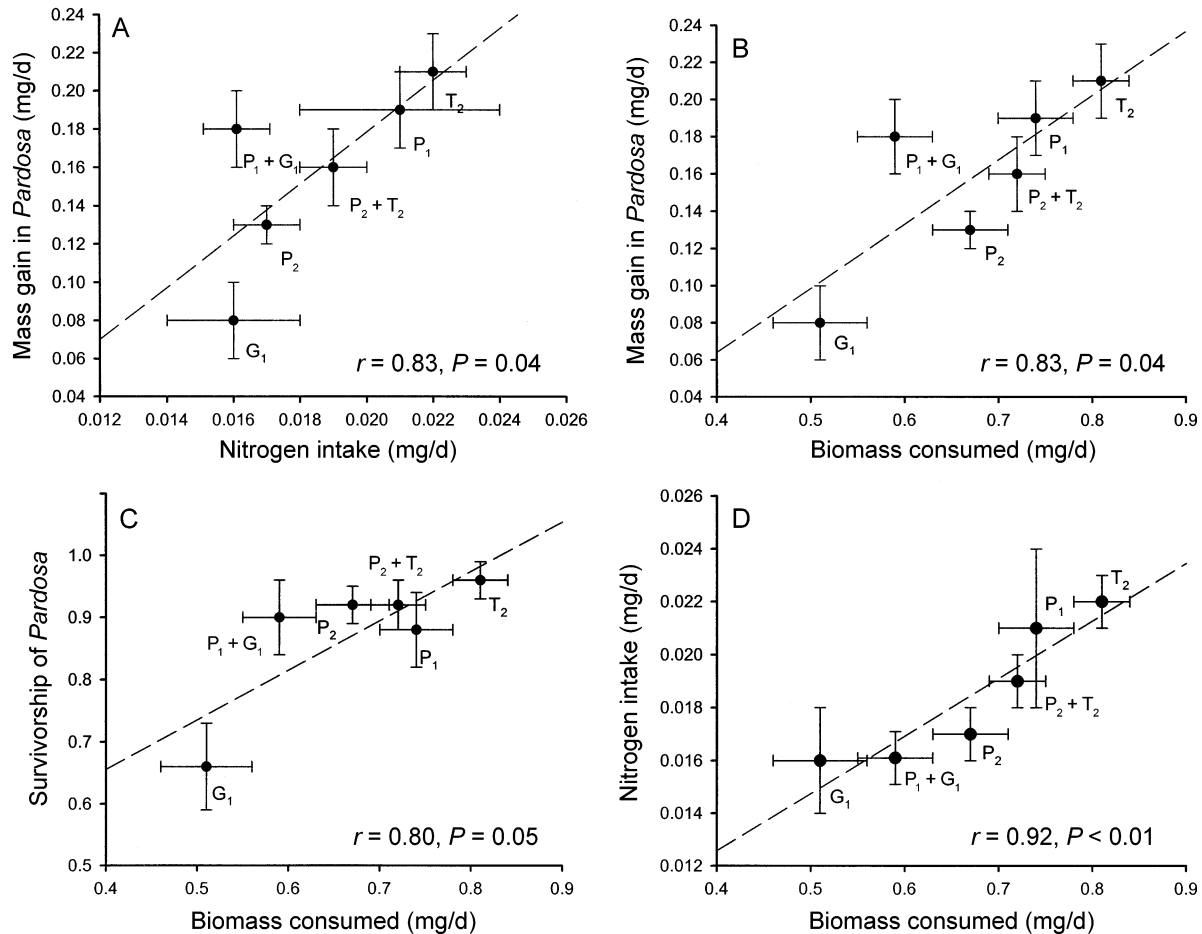


FIG. 6. Relationship between (A) mass gain and nitrogen intake, (B) mass gain and prey biomass consumed, (C) survivorship and prey biomass consumed, and (D) nitrogen intake and prey biomass consumed in the wolf spider *Pardosa* fed one of six diets in two experiments: herbivorous prey (*Prokelisia* planthoppers in experiments 1 [ $P_1$ ] and 2 [ $P_2$ ]), intraguild prey in experiments 1 and 2 (*Grammonota* spiders [ $G_1$ ], *Tytthus* egg predators [ $T_2$ ]), or an alternating mix of herbivores and intraguild prey in experiments 1 and 2, respectively ( $P_1 + G_1$ ,  $P_2 + T_2$ ). Treatment means  $\pm$  SE are shown.

selection may act in response to the dietary scarcity of nitrogen such that herbivores substitute low-nitrogen materials in constructing certain body parts. Last, herbivory and predation might select for different allocations to high- and low-nitrogen structures such as muscle vs. exoskeleton. Regardless of the underlying cause, however, there is a clear difference in the nitrogen content between herbivorous and predaceous arthropods on the marsh.

Using estimates of a predator's nitrogen requirements and its efficiency in retaining carbon and nitrogen from ingested food, Fagan et al. (2002) showed that the disparity in nitrogen content between predators and their prey places predators at risk for nitrogen limitation and accompanying growth penalties. Using the same stoichiometric approach and calculating the "threshold elemental ratio" for *Pardosa* ( $TER_{C:N} = 4.32$ ) above which growth penalties occur (Urabe and Watanabe 1992), we show that this predator is more likely to incur growth penalties by feeding exclusively

on marsh-inhabiting herbivores and omnivores than by feeding on many predator species. In further support of nitrogen limitation in predators, we found a significant positive relationship between nitrogen intake and mass gain in *Pardosa* (Fig. 6A). Other empirical data also support this notion. For example, the addition of amino acids to the diet of wolf spiders enhanced their growth and survivorship (Mayntz and Toft 2001), and nutrient amendments to standard fruit fly media resulted in increased developmental rates and survival in spiders feeding on the flies (Toft 1999). Predatory stinkbugs also grew faster on herbivores fed a protein-rich diet (Strohmeyer et al. 1998). Also, web reclamation and recycling of protein-rich silk by spiders and the consumption of exuviae following molting by some invertebrate predators and omnivores have been linked to nitrogen limitation (Peakall 1971, Lewis 1981, Opell 1998).

Thus, solely from the perspective of nitrogen stoichiometry, generalist predators such as *Pardosa* should

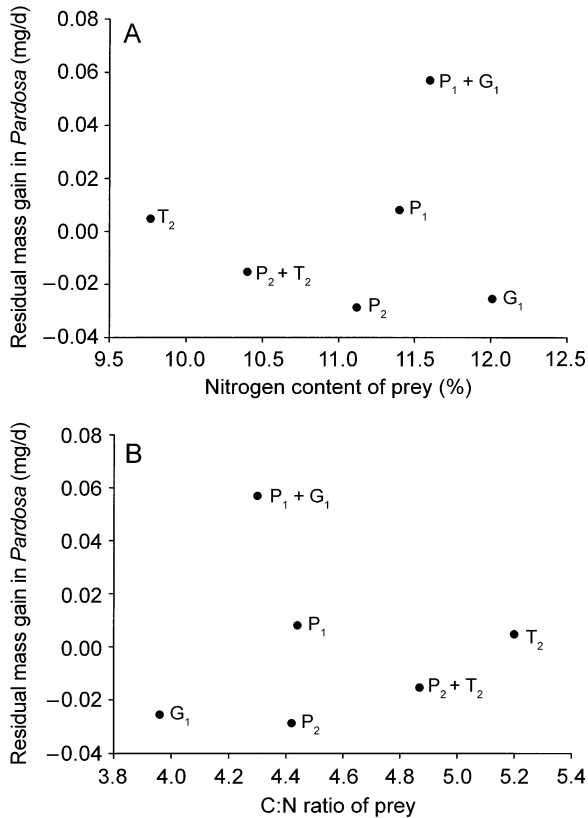


FIG. 7. Residuals of the relationship between mass gain in *Pardosa* and the biomass of prey consumed (see Fig. 5B) plotted against the (A) nitrogen content and (B) C:N ratio of prey. The six prey diets taken from two experiments were: herbivorous prey (*Prokelisia* planthoppers in experiments 1 [P<sub>1</sub>] and 2 [P<sub>2</sub>]), intraguild prey in experiments 1 and 2 (*Grammonota* spiders [G<sub>1</sub>], *Tytthus* egg predators [T<sub>2</sub>]), or an alternating mix of herbivores and intraguild prey in experiments 1 and 2 (P<sub>1</sub> + G<sub>1</sub>, P<sub>2</sub> + T<sub>2</sub>). No significant correlation exists between residual mass gain and either the nitrogen content or the C:N ratio of prey ( $P > 0.05$ ).

benefit by including intraguild prey in their diet rather than restricting their diet to herbivores. Our results suggest that some but not all instances of exposure to intraguild prey result in increased nitrogen intake and enhanced predator performance. *Pardosa*, for example, consumed more nitrogen and grew best on a diet of *Tytthus* compared to when it was fed exclusively herbivorous planthoppers (Figs. 4B, C, 5C). Moreover, *Pardosa* exhibited enhanced performance when it supplemented a diet of planthoppers with *Tytthus*. By contrast, this result did not occur when *Pardosa* was fed a diet of *Grammonota* spiders on which it consumed less prey biomass and nitrogen (Fig. 3B, C), survived poorly (Fig. 2A), and grew slowly (Fig. 2B, C) compared to when it was fed *Prokelisia* prey.

Notably, *Pardosa* grew faster on a diet of *Tytthus*, not because this intraguild prey contained more nitrogen than *Prokelisia*, but because it captured *Tytthus* more readily than planthoppers (Fig. 5A) and thus was

able to enhance its nitrogen intake (Fig. 5C). In fact, *Tytthus* is exceptional in that it contains less nitrogen ( $9.3 \pm 0.2\%$ ) than most marsh predators ( $11.5 \pm 0.2\%$ ) and is closer in nitrogen content to the herbivore mean ( $9.2 \pm 0.3\%$ ), perhaps reflecting its taxonomic affinity to a clade of relatively nitrogen-poor herbivores, namely the Miridae (Fagan et al. 2002). *Grammonota* is far more representative of marsh predators, with a nitrogen content of  $12.0 \pm 0.1\%$ , and it is more nitrogen rich than *Prokelisia* ( $11.4 \pm 0.1\%$ ). Yet, *Pardosa* performed poorly on this more nitrogen-rich intraguild prey because *Grammonota* was less readily captured (Fig. 3A). After accounting for growth due to overall prey biomass intake, we found little evidence that either the nitrogen content or C:N stoichiometry of prey contributed to *Pardosa*'s growth. For example, residuals of the relationship between mass gain and biomass intake in *Pardosa* were uncorrelated with either the %N or C:N ratio of prey. In short, we found little support for the hypothesis that the nitrogen stoichiometry of prey directly confers a performance advantage to *Pardosa* and thus in itself promotes intraguild predation. In this case, factors other than the nitrogen stoichiometry of prey played a significant role in prey capture and predator performance.

Although most intraguild prey are more nitrogen rich than herbivore prey ( $C:N_{\text{herbivore}} > C:N_{\text{predator}}$ ; Appendix A), they are also less abundant, a pattern that results from a fundamental trade-off between resource quantity and quality that exists across trophic levels in food webs (Denno and Fagan 2003). We controlled for the biomass of prey offered in our experiments, but in the field *Pardosa* encounters *Prokelisia* planthoppers ( $>1000$  adults/m<sup>2</sup>,  $>50,000$  nymphs/m<sup>2</sup>) far more frequently than *Tytthus* (200–400 *Tytthus*/m<sup>2</sup>) or *Grammonota* (300–600 *Grammonota*/m<sup>2</sup>), even though these are among the most abundant arthropod predators on the marsh (Denno et al. 2000, Finke and Denno 2002, Gratton and Denno 2003). Nonetheless, the intraguild predation of *Tytthus* by *Pardosa* is sufficiently frequent in certain habitats on the marsh to relax predation on *Prokelisia* and prevent its suppression by the predator complex at large (Finke and Denno 2002, 2003).

Prey behavior (e.g., mobility and defense), size, and toxicity can also influence risk of predation (Endo and Endo 1994, Jackson et al. 1998, Toft 1999, Toft and Wise 1999b, Eubanks and Denno 2000b, Stamp 2001, Singer and Benays 2003) independent of prey nitrogen content. In fact, the behavior of both *Tytthus* and *Grammonota* alters their risk of *Pardosa* attack relative to what one would predict based solely on their nitrogen stoichiometry. Wolf spiders are visually orienting predators that detect their prey by movement and vibrations (Uetz 1992, Samu 1993, Döbel and Denno 1994). Compared to relatively sessile planthoppers, *Tytthus* predators are active foragers that scurry along leaves in search of planthopper eggs and are more susceptible to movement-orienting wolf spiders (Finke and Denno

2002). Thus, despite the similar nutrition and size of *Tytthus* and *Prokelisia*, the behavior of *Tytthus* predisposes it to *Pardosa* attack. By contrast, *Grammonota* is a sit-and-wait predator that builds aerial sheet webs near the marsh surface where it can detect both prey and approaching predators via web vibrations (Döbel et al. 1990). The combination of a sit-and-wait foraging behavior coupled with its aggressive behavior and ability to detect and avoid an intraguild predator (Denno et al., *in press*) likely contributes to its reduced vulnerability to *Pardosa*.

Thus, prey characteristics such as behavior or toxicity may compromise a predator's ability to capture potentially more nitrogen-rich intraguild prey (Toft 1999, Toft and Wise 1999a, b, Francis et al. 2001, Stamp 2001, Denno and Fagan 2003, Singer and Bernays 2003). For example, instances exist in which intraguild predation or cannibalism do not enhance predator performance (Toft and Wise 1999a). Moreover, other cases like ours occur where predators or omnivores do not choose the most nitrogen-rich prey item (Duval and Williams 2000, Eubanks and Denno 2000b) or they specialize on poor quality prey (Rotheray and Gilbert 1989). In most of these examples the nutritional advantage of feeding on intraguild prey is offset in part by feeding on herbivorous prey that are more abundant, more noticeable, less toxic, or more vulnerable to attack (Dixon 1998, Eubanks and Denno 2000b, Denno and Fagan 2003). In contrast, cases certainly exist in which invertebrate predators do benefit by feeding on other predators. For example, jumping spiders survive best when provisioned with a spider diet than with a mix of nitrogen-poor herbivorous insects (Li and Jackson 1997). There are even cases in which predators specialize on other predators, such as araneophagic spiders (Jackson 1992, Li and Jackson 1997) and some fireflies (Eisner et al. 1997). In numerous instances, cannibalism (the ultimate match in predator-prey stoichiometry) results in enhanced predator survival and performance (Spence and Carcamo 1991, Wissinger et al. 1996, Snyder et al. 2000).

Other adaptations may allow predators to exist on diets comprised largely of herbivores (Denno and Fagan 2003). When faced with a nitrogen-poor diet, predators might increase feeding rate (Simpson and Simpson 1990) or enhance the efficiency of nutrient extraction from prey (Cohen 1995, Furrer and Ward 1995, Toft 1999). However, there can be penalties associated with feeding compensation such as toxin accumulation or limitations on gut throughput (Sih 1987, Slansky and Wheeler 1992).

Given the potential drawbacks of a diet composed exclusively of herbivores, Denno and Fagan (2003) argued that dietary supplementation via intraguild predation should remain as one option for predators to meet their high nitrogen demands. In fact, intraguild predation is common among terrestrial arthropod pred-

ators (Polis et al. 1989, Rosenheim 1998, Hodge 1999, Finke and Denno 2002).

The problem has been, and continues to be, isolating factors that promote intraguild predation. In most performance studies of invertebrate predators, however, prey nutrition is not explicitly measured, but it is often implicated as a key determinant of success (e.g., Polis et al. 1989). Our research showed that predator performance and nitrogen intake are clearly associated (Fig. 6A), but not in ways necessarily linked to the nitrogen content of the prey. Even in cases where predator performance is linked to prey nutrition (e.g., Li and Jackson 1997), there is little reason to expect generalist predators to restrict their foraging to the most nitrogen-rich prey (Singer and Bernays 2003). Rather, selective pressures associated with a high nitrogen demand in predators should promote dietary supplementation including bouts of intraguild predation (Denno and Fagan 2003). Indeed, many predators are opportunistic in their foraging strategy and do not exhibit strong prey preferences (Marshall and Rypstra 1999, Nyffeler 1999, Toft 1999, Denno and Fagan 2003), although toxicity and size can influence prey selection (Polis et al. 1989, Hodge 1999, Theodoratus and Bowers 1999, Toft 1999). Moreover, evidence suggests that some omnivores and intraguild predators perform best on mixed prey diets (Uetz et al. 1992, Coll 1998, Toft and Wise 1999a), a feeding strategy that is consistent with the argument that supplemental feeding on intraguild prey allows predators to meet their nitrogen demands (Denno and Fagan 2003). Likewise, our experiments showed that *Pardosa* was able to increase its nitrogen intake, growth, or survival by augmenting an herbivore diet with intraguild prey (Figs. 2A, B, 4B, 5C). In no case, however, did *Pardosa* perform best on the mixed diet (Figs. 2–5) calling into question the benefits of dietary complementation per se for this predator (see Singer and Bernays [2003]).

Dissecting out the relative contribution of the nitrogen content of prey to predator performance and the occurrence of intraguild predation remains a challenge. The challenge is further exacerbated because stoichiometric constraints tend to attenuate at higher trophic levels, both because stoichiometric mismatches between trophic levels are less pronounced and because gross growth efficiencies of higher predators are often low due to large body size and prey limitation (see Schindler and Eby 1997, Fagan et al. 2002, Sterner and Elser 2002, Denno and Fagan 2003). Thus, maintenance plays a predominant role in overall predator metabolism making the impacts of mismatched prey stoichiometry on growth more difficult to detect. We argue that detecting a stoichiometric signal using visually searching predators such as *Pardosa* is even more difficult due to the greater potential for the offsetting effects of prey behavior. Although our experiments were among the first to specifically measure prey nitrogen content and assess predator performance on diets of

herbivores and intraguild prey, we were unable to control for other prey-specific traits such as mobility and defense that also affected risk of capture and predator performance. In this context, we found little support for the hypothesis that prey stoichiometry underlies intraguild predation in this system. Nonetheless, we found a positive relationship between nitrogen intake and growth rate across the different diet treatments offered to *Pardosa* (Fig. 6A), a relationship that results in large part from enhanced biomass consumption (Fig. 6D). Moreover, we show a clear increase in the growth of *Pardosa* that results from the intraguild predation of *Tytthus*. This result supports the view that obtaining supplemental nitrogen from higher trophic levels, especially when intraguild prey is easily captured, can indeed benefit predators and promote intraguild predation despite the nitrogen stoichiometry of prey. Because of the important consequences of omnivory and intraguild predation for food-web dynamics and biocontrol (Rosenheim et al. 1995, Polis and Strong 1996, Rosenheim 1998, Finke and Denno 2003), elucidation of the manner in which predator and prey behaviors interface with their nitrogen stoichiometry to promote intraguild predation is crucial.

#### ACKNOWLEDGMENTS

Jim Elser and two anonymous reviewers provided insightful comments or reviews of an earlier draft of this report. Ken Able and Bobbie Zlotnik of the Rutgers University Marine Station facilitated our research at the Tuckerton field site and Ken Strait and PSEG provided access to the Alloway Creek site. Michael Draney identified several spider taxa. Rick Doucett (Stable Isotope Laboratory, Northern Arizona University) assisted with the nitrogen and carbon analysis of taxa. We are most grateful to these colleagues for their advice and support. This research was supported by a fellowship from the Organization for Economic Co-operation and Development Research Programme (Biological Resource Management for Sustainable Agriculture Systems) to M. M., an NSF Grant (DEB-9903601) to R. F. D. with RET supplement to G. M. T., and a NJ and MD Sea Grant (MERP) to C. G. and R. F. D.

#### LITERATURE CITED

- Alomar, O., and R. N. Wiedenmann. 1996. Zoophytophagous Heteroptera: implications for life history and integrated pest management. Proceedings, Thomas Say Publications in Entomology. Entomological Society of America, Lanham, Maryland, USA.
- Awmack, C. S., and S. R. Leather. 2002. Host plant quality and fecundity in herbivorous insects. *Annual Review of Entomology* **47**:817–844.
- Barros-Bellanda, H. C. H., and F. S. Zucoloto. 2001. Influence of chorion ingestion on the performance of *Ascia monuste* and its association with cannibalism. *Ecological Entomology* **26**:557–561.
- Bertness, M. D. 1991. Zonation of *Spartina patens* and *Spartina alterniflora* in a New England salt marsh. *Ecology* **72**:138–148.
- 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. 1980. Ecotope differentiation in a guild of sap-feeding insects on the salt marsh grass, *Spartina patens*. *Ecology* **61**:702–714.
- Denno, R. F. 1983. Tracking variable host plants in space and time. Pages 291–341 in R. F. Denno and M. S. McClure, editors. *Variable plants and herbivores in natural and managed systems*. Academic Press, 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.
- Denno, R. F., C. Gratton, H. Döbel, and D. L. Finke. 2003. Predation risk affects relative strength of top-down and bottom-up impacts on insect herbivores. *Ecology* **84**:1032–1044.
- 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.
- Denno, R. F., M. S. Mitter, G. A. Langellotto, C. Gratton, and D. L. Finke. *In press*. Interactions between hunting spiders and web-builders: consequences of intraguild predation and cannibalism for prey suppression. *Ecological Entomology*.
- Denno, R. F., and M. A. Peterson. 2000. Caught between the devil and the deep blue sea, mobile planthoppers elude natural enemies and deteriorating host plants. *American Entomologist* **46**:95–109.
- Denno, R. F., M. A. Peterson, C. Gratton, J. Cheng, G. A. Langellotto, A. F. Huberty, and D. L. Finke. 2000. Feeding-induced changes in plant quality mediate interspecific competition between sap-feeding herbivores. *Ecology* **81**:1814–1827.
- 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.
- Döbel, H. G., R. F. Denno, and J. A. Coddington. 1990. Spider community structure in an intertidal salt marsh: differences along an elevational gradient. *Environmental Entomology* **19**:1356–1370.
- 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* **94**:9723–9728.
- Elser, J. J., D. Dobberfuhl, N. A. MacKay, and J. H. Schampel. 1996. Organism size, life history, and N:P stoichiometry: towards a unified view of cellular and ecosystem processes. *Bioscience* **46**:674–684.
- Elser, J. J., et al. 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. 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., 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.
- Finke, D. L., and R. F. Denno. 2002. Intraguild predation diminished in complex-structured vegetation: implications for prey suppression. *Ecology* **83**:643–652.
- Finke, D. L., and R. F. Denno. 2003. Intraguild predation relaxes natural enemy impacts on herbivore populations. *Ecological Entomology* **28**:67–73.
- 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.
- Gratton, C., and R. F. Denno. 2003. Seasonal shift from top-down to bottom-up impact in phytophagous insect populations. *Oecologia* **134**:487–495.
- Hodge, M. A. 1999. The implications of intraguild predation for the role of spiders in biological control. *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.
- Jackson, R. R. 1992. Eight-legged tricksters: spiders that specialize in catching other spiders. *Bioscience* **42**:590–598.
- Jackson, R. R., D. Li, N. Fijn, and A. Barrion. 1998. Predator–prey interactions between aggressive-mimic jumping spiders (Salticidae) and araneophagic spitting (Scytodidae) from the Philippines. *Journal of Insect Behavior* **11**:319–342.
- Lewis, J. G. E. 1981. The biology of centipedes. Cambridge University Press, Cambridge, UK.
- 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.
- Marshall, S. D., and A. L. Rypstra. 1999. Spider competition in structurally simple ecosystems. *Journal of Arachnology* **27**:334–350.
- 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.
- Mobberley, D. G. 1956. Taxonomy and distribution of the genus *Spartina*. *Iowa State College Journal of Science* **30**:471–574.
- Nentwig, W. 1987. *Ecophysiology of spiders*. Springer-Verlag, New York, New York, USA.
- Nyffeler, M. 1999. Prey selection of spiders in the field. *Journal of Arachnology* **27**:317–324.
- 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.
- Peakall, D. B. 1971. Conservation of web proteins in the spider *Araneus diadematus*. *Journal of Experimental Zoology* **178**:257–264.
- 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.
- Redfield, A. C. 1972. The development of a New England salt marsh. *Ecological Monographs* **42**:201–237.
- 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.
- Rosenheim, J. A. 1998. Higher-order predators and the regulation of insect populations. *Annual Review of Entomology* **43**:421–447.
- 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., 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 Linnean Society* **95**:29–70.
- Samu, F. 1993. Wolf spider feeding strategies: optimality of prey consumption in *Pardosa hertensis*. *Oecologia* **94**:139–145.
- SAS. 2001. SAS/STAT software: changes and enhancements. Release 8.2. SAS Institute, Cary, North Carolina, USA.
- Schindler, D. E., and L. A. Eby. 1997. Stoichiometry of fishes and their prey: implications for nutrient recycling. *Ecology* **78**:1816–1831.
- 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.
- Singer, M. S., and E. A. Bernays. 2003. Understanding omnivory needs a behavioral perspective. *Ecology* **84**:2532–2537.
- 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., and J. J. Elser. 2002. *Ecological stoichiometry*. Princeton University Press, Princeton, New Jersey, USA.
- Strohmeier, 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.
- Theodoratus, D. H., and M. D. Bowers. 1999. Effects of sequestered iridoid glycosides on prey choice of the prairie wolf spider, *Lycosa carolinensis*. *Journal of Chemical Ecology* **25**:283–295.
- Toft, S. 1999. Prey choice and spider fitness. *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. 1992. Foraging strategies of spiders. *Trends in Ecology and Evolution* **7**:155–159.
- Uetz, G. W., J. Bishoff, and J. Raven. 1992. Survivorship of wolf spiders (Lycosidae) reared on different diets. *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.
- Vince, S. W., I. Valiela, and J. M. Teal. 1981. An experimental study of the structure of herbivorous insect communities in a salt marsh. *Ecology* **62**:1662–1678.
- White, T. C. R. 1993. *The inadequate environment: nitrogen and the abundance of animals*. Springer-Verlag, New York, New York, USA.
- 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.

#### APPENDIX A

A table presenting carbon and nitrogen content and C:N ratio of mid-Atlantic salt marsh taxa (plants, herbivores, omnivores, and predators) is available in ESA's Electronic Data Archive: *Ecological Archives* E085-078-A1.

#### APPENDIX B

A table presenting analysis of variance results for the effect of diet (herbivore prey, intraguild prey, or a mix of the two), time, and their interaction on *Pardosa* mass, mass gain, capture rate of prey, biomass of prey consumed, and nitrogen intake is available in ESA's Electronic Data Archive: *Ecological Archives* E085-078-A2.