

PREDATION RISK AFFECTS RELATIVE STRENGTH OF TOP-DOWN AND BOTTOM-UP IMPACTS ON INSECT HERBIVORES

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Abstract. Elucidating the relative strength of top-down and bottom-up forces in communities of phytophagous insects has been a major historical focus. Current consensus is that both forces play a role, but it is poorly known if these forces act differently on herbivores in the same assemblage and what factors underlie this variation. Using manipulative experiments with an assemblage of sap-feeding phytophagous insects (six species of planthoppers, leafhoppers, and heteropteran bugs) inhabiting intertidal *Spartina* marshes, we examined the association between herbivore behavior, risk of predation, and ultimately the relative impact of top-down (wolf spider predation) and bottom-up (host-plant nutrition) factors on the population density of each sap-feeding herbivore.

A factorial experiment on open *Spartina* islets in the field (two levels of plant nutrition crossed with two levels of spider predation) showed that bottom-up and top-down manipulations differentially affected the various sap-feeders. Overall, bottom-up effects dominated in this sap-feeder community, whereby the density of all six sap-feeders increased when the nitrogen content of *Spartina* was elevated. By contrast, wolf-spider addition significantly suppressed populations of only the *Prokelisia* species and had little impact on the other four sap-feeder species in the community. Functional-response experiments and behavioral studies revealed that certain species (*Prokelisia* planthoppers) were at much higher risk of attack by wolf spiders than other sap-feeders in the assemblage and that risk of predation was associated with a species' particular "escape/defensive behavior." Moreover, risk of spider predation was roughly linked to the strength of top-down impacts in the field, because species with ineffective escape behaviors and a high risk of spider attack (*Prokelisia* planthoppers) were the only sap-feeders whose populations were suppressed by spider predation in the field. Thus, specific behavioral characteristics of the sap-feeders on *Spartina* influenced risk of predation and the relative strength of top-down and bottom-up impacts on their population dynamics.

Notably, all herbivores in this system were positively influenced by elevated plant nutrition, only the common sap-feeder species (*Prokelisia* planthoppers) were adversely affected by spider predation, and it was the rarer sap-feeders in the assemblage that were least impacted by predation. These results call into question the overall pervasiveness of top-down forces and underscore the primacy of basal resources in structuring this community of phytophagous insects.

Key words: *bottom-up vs. top-down impact; phytophagous insect community; planthopper; plant nutrition; population suppression; predation; Prokelisia; risk of predation; sap-feeding insects; Spartina alterniflora; spider; trophic cascades.*

INTRODUCTION

Ecologists now agree that both top-down and bottom-up forces interact in complex ways to collectively impact populations of phytophagous insects (Price et al. 1980, Denno and McClure 1983, Hunter and Price 1992, Stiling and Rossi 1997, Forkner and Hunter 2000, Denno et al. 2002). An important recent emphasis, however, has been to identify those factors that alter the relative strength of natural-enemy and host-plant effects on herbivores (Moran et al. 1996, Beck-

erman et al. 1997, Schmitz et al. 1997, Denno and Peterson 2000, Forkner and Hunter 2000, Roda et al. 2000), and to elucidate conditions that promote or diminish the cascading consequences of bottom-up and top-down forces on food-web structure (Polis and Strong 1996, Fagan 1997, Moran and Hurd 1998, Rosenheim 1998, Pace et al. 1999, Schmitz et al. 2000, Halaj and Wise 2001). For example, habitat structure, physical disturbance, allochthonous resources, and invasive species are all known to either directly or indirectly change the strength of bottom-up or top-down impacts on herbivorous insects (Riechert and Bishop 1990, Polis and Hurd 1996, Schoener and Spiller 1999, Denno et al. 2002). Also, there have been numerous studies demonstrating that plants, either by virtue of their productivity, nutrition, or structure can mediate the strength of top-down forces (Faeth 1985, Hunter et

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al. 1997, Polis et al. 1998, Forkner and Hunter 2000, Denno et al. 2002). Moreover, interactions among species at higher trophic levels such as omnivory, intraguild predation, and predator facilitation can either moderate or enhance top-down impacts (Moran et al. 1996, Fagan 1997, Losey and Denno 1998, Rosenheim 1998, Sih et al. 1998). There are also several recent studies showing that structural features of host plants can temper intraguild predation (Roda et al. 2000, Norton et al. 2001, Finke and Denno 2002), thus demonstrating the complex and interactive impacts of bottom-up and top-down forces on phytophagous insect populations.

Historically, there has been less emphasis on the herbivorous insects themselves and how their behavior (e.g., escape response) or life history strategy (e.g., dispersal ability) might alter the relative strength of natural-enemy and host plant-related forces, although the potential importance of herbivore identity certainly has been acknowledged (Polis 1999, Forkner and Hunter 2000). Recent studies in both terrestrial and aquatic systems strongly suggest that herbivore behavior can either alter the strength of top-down and bottom-up impacts or influence their cascading effects (Beckerman et al. 1997, Schmitz et al. 1997, Peckarsky and McIntosh 1998, Denno and Peterson 2000, Denno et al. 2002). In most of these studies, however, the focus was on the behavioral response of a single insect herbivore to manipulated predation and/or plant-resource factors and not on the responses of the community of herbivores at large. It is known that phytophagous insects in the same assemblage can be affected differentially by natural enemies and host-plant resources (Karban 1989, Denno and Peterson 2000). What is poorly understood is how behavioral differences among herbivores might influence their risk of predation, and interact with host-plant variability to ultimately dictate the relative strength of top-down and bottom-up impacts for each herbivore in the assemblage. The extent to which the various herbivores in a community respond similarly to top-down and bottom-up forces bears directly on the predominance of natural-enemy vs. plant-resource control in a system, the nature of reticulate interactions among players, and the probability that top-down or bottom-up effects will cascade throughout the food web (see Polis 1999, Schmitz et al. 2000).

Using manipulative experiments with an assemblage of sap-feeding phytophagous insects (planthoppers, leafhoppers, and heteropteran bugs) inhabiting coastal salt marshes, we examined the interaction between risk of predation and response to variable plant quality in order to assess the relative strength of top-down and bottom-up impacts for each herbivore. We selected a wolf-spider species as our focal predator because hunting spiders are the most abundant and consequential natural enemies in this estuarine system (Denno 1983, Döbel and Denno 1994, Denno et al. 2002). We chose

plant nutrition as our bottom-up variable because sap-feeding herbivores often, but not always, show dramatic population increases on nitrogen-subsidized host plants (White 1993, Denno et al. 2002). Risk of spider predation (proportion captured across a range of prey densities) was assessed for each sap-feeder by conducting functional response experiments in the laboratory. Risk of predation was then linked to herbivore behavior by measuring differences in the "escape response" among sap-feeders to an advancing spider. A manipulative factorial experiment was subsequently conducted in the field to assess the relative impact of spider predation and host-plant nutrition on the population density of each sap-feeding herbivore. We hypothesized that bottom-up impacts would be generally stronger than top-down effects for sap-feeders with an effective escape response and thus a lowered risk from spider predation. By focusing on the herbivores themselves and behaviors that alter their risk of predation, we aim to advance our knowledge of the factors that determine the overall strength and extent of top-down and bottom-up impacts in phytophagous insect communities.

METHODS

Study site and the cordgrass-herbivore-predator system

Our field experiment was conducted on an expansive intertidal marsh in the Great Bay-Mullica River estuarine system at the end of Great Bay Boulevard and just north of the Rutgers University Marine Station, Tuckerton, Ocean County, New Jersey, USA. The vegetation on this and most other mid-Atlantic coastal salt marshes is dominated by the perennial cordgrass *Spartina alterniflora*, where it grows in extensive pure stands within the intertidal zone (Denno 1983, Gallagher et al. 1988). Within the intertidal zone, however, the structure and nutrition (nitrogen content) of *Spartina* vary tremendously due to differences in nutrient subsidy, soil drainage, salinity, and evaporation (Denno 1983, Gallagher et al. 1988). Along an elevational gradient from low-marsh (tidal creek banks) to high-marsh habitats (meadows and mud flats), *Spartina* plants generally decrease dramatically in stature and nitrogen content (Denno 1983, Ornes and Kaplan 1989, Denno et al. 2002).

Sap-feeders are by far the most abundant and diverse guild of phytophagous insects on *Spartina* (Denno 1983, Denno and Peterson 2000). Of all the sap-feeders, two phloem-feeding planthoppers, *Prokelisia marginata* and *P. dolus* (Hemiptera: Delphacidae), dominate the assemblage with densities often exceeding several thousand adults per square meter (Denno et al. 2000). Two other delphacid planthoppers, *Delphacodes penedetecta* and *Megamelus lobatus* are far less abundant (<100 adults/m²) (Denno 1983). The two *Prokelisia* species and *D. penedetecta* are trivoltine at mid-At-

lantic latitudes, have similar generation times (~ 40 d), and overwinter as nymphs in leaf litter (Denno 1983, 1994). By contrast, *M. lobatus* is bivoltine and overwinters in the egg stage (Denno 1994). All four planthopper species are similar in size (~ 3 mm in body length) and insert their eggs in leaf blades (*Prokelisia*) or blades, sheaths, and tillers (*D. penedetecta* and *M. lobatus*) (Denno 1994). The *Prokelisia* species feed primarily on the basal portion of leaf blades in the canopy of *Spartina*, whereas *D. penedetecta* and *M. lobatus* occur in the crown where they feed on stems and tillers respectively.

The planthopper species are wing dimorphic with both migratory adults (macropters with fully developed wings) and flightless adults (brachypters with reduced wings) occurring in the same population (Denno et al. 1996, Denno and Peterson 2000). However, mid-Atlantic populations of these species differ dramatically in their wing-form composition and thus the incidence of dispersal. Most adults of *P. marginata* are macropterous ($>95\%$), whereas far fewer macropters occur in populations of *P. dolus* ($\sim 30\%$), *D. penedetecta* ($<5\%$), and *M. lobatus* ($<3\%$) (Denno et al. 1991, 1996).

Two other sap-feeders are moderately abundant (up to 100 adults/m²) on mid-Atlantic marshes, the phloem-feeding leafhopper *Sanctanus aestuarium* (Hemiptera: Cicadellidae) and the mesophyll-feeding bug *Trigonytulus uhleri* (Hemiptera: Miridae) (Denno 1983). Both of these sap-feeders feed in the canopy of *Spartina*, particularly *T. uhleri* that feeds on the tips of leaf blades (Vince et al. 1981, Denno 1983). Both species are fully flight capable (all adults are macropterous), larger than planthoppers (4–6 mm in length), bivoltine, and overwinter as eggs embedded in plant tissues (Denno 1983). All six sap-feeders are monophagous and feed exclusively on *Spartina* (Denno 1983).

Wolf spiders (Araneae: Lycosidae) are the major natural enemies of planthoppers on mid-Atlantic salt marshes (Döbel et al. 1990, Döbel and Denno 1994). Of the hunting spider species on the marsh, *Pardosa littoralis* (5–6 mm) is the most abundant, with densities frequently exceeding 200 individuals/m². *Pardosa* is a voracious predator with a per capita consumption rate of 70 planthoppers/d (Döbel and Denno 1994). *Prokelisia* planthoppers typically comprise 61% of the diet of *Pardosa*, but other arthropods including various sap-feeders can be attacked as well (Döbel and Denno 1994). Parasitoids, although present on mid-Atlantic marshes, inflict far less mortality on sap-feeders than do invertebrate predators (Denno 1983).

Risk of spider predation for sap-feeders

Two functional response experiments were conducted in laboratory mesocosms to assess the relative risk of the various sap-feeders to wolf spider (*Pardosa*) predation. The first experiment compared the relative susceptibility of the two *Prokelisia* planthoppers to spi-

der predation by assessing mortality across a range of prey densities. Because *P. marginata* is primarily macropterous and *P. dolus* is largely brachypterous (Denno et al. 1996), both wing forms of each species were tested separately to isolate the effects of species and wing form on risk of predation. A second experiment was conducted to compare risk of spider predation among the other sap-feeders (*P. marginata*, *D. penedetecta*, *S. aestuarium*, and *T. uhleri*). *M. lobatus* was too rare to obtain a sufficient number of individuals necessary to assess its susceptibility to spider predation.

The first experiment employed a full factorial design with four prey types (macropters and brachypters of *P. marginata* and *P. dolus*) offered at seven prey densities (5, 10, 20, 40, 60, 80, and 120 adults per mesocosm) to a *Pardosa* wolf spider (adult female, 25–40 mg). Each treatment combination was replicated three times. The body lengths of *P. marginata* and *P. dolus* used in this experiment were 2.5 ± 0.3 mm (mean ± 1 SE) and 2.4 ± 0.3 mm, respectively. After a 2-h settling period for the prey, a single *Pardosa* wolf spider (starved for 48 h) was added to each mesocosm. Spiders and prey interacted for 24 h, after which we determined the number and proportion of prey captured by subtracting the number of remaining insects (living and intact dead individuals) from the density of prey offered. Predation-related mortality was easily distinguished from other sources of death because spiders leave a small pellet of exsanguinated exoskeleton following feeding. Three predator-free controls were also established for each prey type (20 adults per mesocosm) to assess background levels of mortality.

The second experiment used a factorial design with four prey species (*P. marginata*, *D. penedetecta*, *S. aestuarium*, and *T. uhleri*) offered at four densities (8, 15, 30, and 60 adults per mesocosm) to a single *Pardosa* wolf spider. The body lengths of the sap-feeders used in this experiment were: *P. marginata* (2.5 ± 0.3 mm), *D. penedetecta* (2.8 ± 0.3 mm), *S. aestuarium* (4.0 ± 0.5 mm), and *T. uhleri* (6.0 ± 0.4 mm). Replication and protocols for this experiment were otherwise identical to the first experiment.

Mesocosms used for both experiments consisted of plastic tube cages (7.5 cm diameter \times 30 cm in height) made of cellulose butyrate and topped with an organdy-mesh cover. Mesocosms were pressed into sand-filled pots (9 cm diameter) containing either three (Experiment 1) or five *Spartina* transplants (Experiment 2) ~ 20 cm in height. All arthropods and *Spartina* transplants used in these experiments were obtained from our field site at Tuckerton, New Jersey. For details concerning the set-up and maintenance of *Spartina* and arthropod cultures, consult Denno et al. (2000).

Logistic regression was used to determine the relationship between prey density and the proportion of prey taken (Juliano 1993, SAS 2001). Initially a full model was constructed to examine the effect of Den-

sity, Density², Species, and Wing-Form (Experiment 1 only) on the proportion of prey taken (logit). Nonsignificant effects and interactions were dropped from the final models using the Wald chi-square statistic. Thus, the final model for Experiment 1 included all main effects (Density, Density², Species, Wing-Form), whereas for Experiment 2, the final model included only Density and Species effects (Juliano 1993). Differences in susceptibility among species (i.e., intercepts) were evaluated by comparing the overlap of 95% confidence intervals of the Species effect parameter estimates.

Escape responses of sap-feeders

Insight into the mechanism underlying the relative susceptibility of the various sap-feeders to spider predation was gained by determining their behavioral responses to an advancing artificial spider. The escape responses of the five sap-feeders (*P. marginata*, *P. dolus*, *D. penedetecta*, *S. aestuarium*, and *T. uhleri*) were determined by placing a single adult sap-feeder on potted *Spartina* (3 plants/pot), thrusting an artificial spider toward the "prey," and measuring its reaction. The rapid thrust was intended to mimic the natural attack behavior of a pouncing *Pardosa*, but at the same time controlled for the direction and pace of the approach. Sap-feeder responses were divided into four discrete categories: (1) remaining in place, (2) descending down the plant into the crown, (3) "squirreling" behind a leaf or stem, and (4) jumping off the plant altogether.

The artificial predator consisted of a dead *Pardosa* wolf spider glued to the end of a green, plastic-coated wire (0.5 mm diameter \times 30 cm in length). The spider was thrust horizontally and rapidly to within 1 cm of the settled sap-feeder, and its response was scored within 5 s of the approach. Approximately 50 individuals were tested for each sap-feeder species except for *S. aestuarium* for which only 32 individuals were available. Sap-feeders were caged over the potted *Spartina* plants for 24 h before the cage was gently removed and the test performed.

A *G* test was used to detect differences in response profiles (number of counts in each of the four response categories) among the five sap-feeders (Sokal and Rohlf 1995, Zar 1996). Subsequently, for each species a series of three multinomial logistic regressions were performed to determine if one or more behaviors occurred significantly more frequently than others (SAS 2001). For each regression, a different behavior was used as the reference to which the other three behaviors were contrasted (Allison 1999). *P* values from logistic regressions were corrected for multiple comparisons using a Bonferroni adjustment (Westfall et al. 1999).

Relative strength of top-down and bottom-up forces on sap-feeder population growth

To test for the effects of plant nutrition, spider predation, and their interaction on sap-feeder population

growth in the field, we conducted a manipulative experiment on an archipelago of small, uncaged *Spartina* islets located in a flooded mudflat area on the high marsh at the Tuckerton field site (see Denno et al. 2000). Islets averaged 1.85 ± 0.13 m² in area and were separated from each other by 1–3 m. In all, two plant nutrition treatments (fertilized islets and nonfertilized islets) were each crossed with two spider-predation treatments (spiders added vs. withheld). Fertilized islets were replicated nine times and nonfertilized islets were replicated four times for a total of 26 islets.

To achieve high and low levels of plant nutrition, *Spartina* islets were either fertilized or not on 21 May 1999 with a 3:1 mixture of granular ammonium nitrate (N-P-K: 34-0-0) and phosphoric acid (0-46-0). Each "high-quality islet" received eight applications of the fertilizer mixture at a rate of 60 g·m⁻²·date⁻¹, applied biweekly from 21 May to 15 July. Because high-marsh *Spartina* generally has a low-nitrogen content (Denno 1983, Ornes and Kaplan 1989), "low-quality islets" were achieved by withholding fertilizer.

Prior to the application of the spider treatment, all islets were defaunated three times (10, 16, and 25 June) to remove ambient herbivores and spiders and to equalize initial arthropod densities among treatments. Using a D-vac suction sampler (D-Vac, Ventura, California, USA), each islet was vacuumed for 10 min to achieve nearly complete defaunation (Denno et al. 2000). The spider augmentation treatment was initiated on 30 June and was applied on five subsequent dates as well (8, 15, 21, 28 July and 3 August) to insure intended density levels despite emigration. On each date, *Pardosa* wolf spiders were applied at a rate of 100 individuals/m² to those islets calling for spiders. Spiders (large immatures) for this treatment were obtained by vacuuming neighboring *Spartina* meadows with a D-vac suction sampler (Denno et al. 2000).

Sap-feeders could freely colonize all islets following the final defaunation on 25 June, and all treatments were in place by 30 June. Subsequently, the effect of the treatments on sap-feeder population size (number per square meter) was assessed on two dates during the next 6-wk period (28 July and 17 August). Populations of sap-feeders and spiders were censused using a D-vac vacuum sampler (Denno et al. 2000). One sample was taken on each islet on each sampling date and consisted of two 10-s placements of the sampling head on the marsh surface such that 0.2 m² of *Spartina* was vacuumed. Arthropods were killed in an ethyl-acetate jar, transferred to 95% ethanol sample bottles, and returned to the laboratory where they were counted.

To confirm the effectiveness of the fertilizer treatment, the aboveground biomass (in grams of dry mass per square meter) and nitrogen content (percentage) of *Spartina* were assessed once (25 August) on each islet. One vegetation sample was taken on each islet by clipping all aboveground biomass within a 0.047-m² wire frame (Denno et al. 2002). Living vegetation was sep-

arated from dead plant material and the living fraction was oven dried at 80°C for 24 h before weighing. The nutritional content of the live fraction was determined by grinding each dried sample to a powder in a Wiley mill, passing it through a 1-mm mesh screen, and analyzing it for percentage nitrogen using a CHN automated analyzer (Leco, St. Joseph, Michigan, USA) located in the University of Maryland Soils Testing Laboratory.

Treatment effects on the final population density of sap-feeders were assessed on 17 August using ANOVA. Treatment effects on the density of stocked wolf spiders were assessed on samples taken one date earlier on 28 July to coincide with their peak seasonal abundance and when planthopper nymphs were large and most vulnerable to spider predation (see Döbel et al. 1990, Döbel and Denno 1994). Also, assessing the abundance of stocked spiders on this earlier date reflected a more robust assessment of the predation pressure that potentially influenced the final density of sap-feeders on 17 August.

A within-subjects ANOVA was used to test the effects of host-plant nutrition (fertilized and nonfertilized islets) and predation (wolf spiders added vs. withheld) on the final population density ($\log[N + 1]/\text{m}^2$) of six sap-feeder species (*P. marginata*, *P. dolus*, *D. penedetecta*, *M. lobatus*, *S. aestuarium*, and *T. uhleri*) (PROC MIXED, SAS 2001). For this analysis, density assessments for the six species were made on each islet and thus individual islets were treated as subjects (nested within fertilization and spider-addition treatments), fertilization and spider effects were the between-subjects factors, and species was the within-subject factor. Denominator degrees of freedom were estimated using the Kenward-Roger calculation (PROC MIXED, SAS 2001). Preplanned contrasts were used to test the effect of the top-down and bottom-up treatments on the population density of each species separately (from species \times fertilizer and species \times spider interactions). For the entire sap-feeder community, treatment effects were calculated from the overall ANOVA (between-subjects effects, Table 2). Treatment effects on plant parameters and wolf-spider density were examined using ANOVA for each dependent variable: nitrogen (angular-transformed percentage), live biomass (log-transformed gram per square meter), and spider density ($\log[N + 1]/\text{m}^2$). Untransformed means (± 1 SE) are reported.

The magnitude of bottom-up and top-down treatment effects (fertilization and spider addition) on the density of each species was calculated as the natural log of the ratio of the mean treatment density over the mean control density (Effect size_{BU or TD} = $\ln[\text{Treatment density}/\text{Control density}]$) (Fig. 4). Values of 0 indicate that herbivore density was equal in treatment and controls, positive values suggest that the treatment had a positive effect on population density, whereas negative effect sizes indicate that the treatment had an adverse impact on herbivore density. Thus, the expectation was for

fertilization to have a positive effect and for spider addition to have a negative effect on herbivore population size. The relative strength of the bottom-up (plant nutrition) compared to the top-down treatment (spider predation) or the relative effect size was indexed as the natural log of the ratio of the two effect sizes (Relative effect size = $\ln[|\text{Effect size}_{\text{BU}}|/|\text{Effect size}_{\text{TD}}|]$). A value of 0 indicates that herbivore density was influenced equally by bottom-up and top-down treatments, positive values indicate that bottom-up effects had a relatively greater impact on herbivore density than top-down effects, and negative values indicate that top-down effects were stronger than bottom-up impacts.

RESULTS

Risk of spider predation for sap-feeders

Functional response experiments strongly suggest that the two *Prokelisia* planthoppers (*P. marginata* and *P. dolus*) are similarly vulnerable to *Pardosa* spider predation and that they are at a much higher risk of predation than the other sap-feeder species. For the *Prokelisia* species, spiders captured similar numbers of each species across the entire range of prey densities offered (compare Fig. 1A with C). Logistic regression found a significant effect of both prey Density² ($\chi^2 = 71.26$, $P < 0.0001$) and prey Density ($\chi^2 = 41.58$, $P < 0.0001$) on the proportion of planthoppers killed indicating a type III functional response. There was no effect of either Species ($\chi^2 = 0.36$, $P = 0.55$) or its interaction with Density² ($\chi^2 = 0.17$, $P = 0.17$) on the proportion taken (Fig. 1B and D). There was, however, a significant effect of Wing form on the proportion of prey captured ($\chi^2 = 14.68$, $P < 0.0001$) with brachypters being captured at a slightly higher frequency than macropters for both species (Fig. 1B and D). Because brachypters dominate populations of *P. dolus* and macropters are the frequent wing form in *P. marginata* populations (Denno et al. 1996), *P. dolus* may be slightly more vulnerable to spider predation than *P. marginata*.

Although the two *Prokelisia* species were at a high risk of predation from *Pardosa*, this was not the case for the other sap-feeders in the guild. Far more *P. marginata* were captured across a range of prey densities than were *T. uhleri*, *D. penedetecta*, or *S. aestuarium* (Fig. 2A). Logistic regression found a significant effect of Density ($\chi^2 = 92.17$, $P < 0.0001$) and sap-feeder Species ($\chi^2 = 88.55$, $P < 0.0001$) on the proportion of prey taken, but their interaction was not significant ($\chi^2 = 1.94$, $P = 0.58$) (Fig. 2B). This result suggested a type II functional response with homogeneous slopes across species but with different intercepts. A comparison of overlap in 95% confidence intervals associated with species-effect estimates (intercepts) showed that a significantly higher proportion of *P. marginata* was captured (intercept $\pm 95\%$ confidence limit =

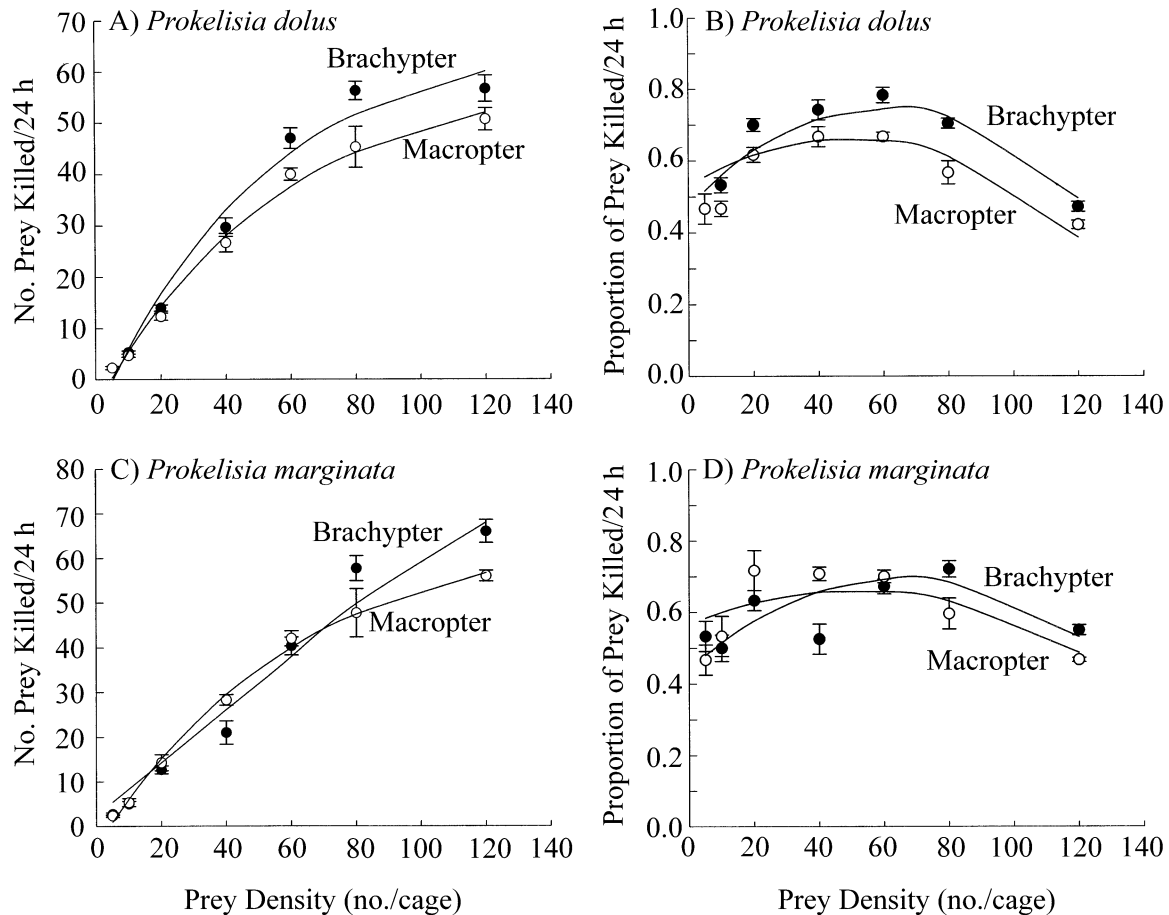


FIG. 1. Functional response of the wolf spider *Pardosa littoralis* to increasing densities of the planthoppers *Prokelisia marginata* and *P. dolus*. The number (A and C) and proportion (B and D) of flight-capable macropterous adults (open circles) and flightless brachypterous adults (solid circles) captured by a single wolf spider in 24 h are shown. Although both planthopper species were attacked and killed at a similar rate (logistic regression; $\chi^2 = 0.36$, $P = 0.55$), brachypterous adults were slightly more susceptible to spider predation than macropters ($\chi^2 = 14.68$, $P < 0.0001$). Means ± 1 SE are shown.

1.206 ± 0.218) than either *T. uhleri* (0.213 ± 0.288) or *D. penedetcta* (0.115 ± 0.249), which did not differ. A significantly lower proportion of *S. aestuarium* (-0.805 ± 0.315) was captured than any of the other sap-feeders. For both functional response experiments, $<5\%$ of sap-feeder mortality was attributable to causes other than predation.

Escape responses of sap-feeders

When under simulated attack by an artificial spider, the five sap-feeder species differed dramatically in their "escape-response behaviors" (frequency of responses in each of four response categories: remaining in place, descending down the plant, squirreling behind leaf or stem, and jumping off the plant; $\chi^2 = 150.87$, $P < 0.0001$) (Table 1). The most prevalent response for both *P. marginata* and *T. uhleri* to an approaching predator was to "remain in place" although some movement occurred (twitching or advancing a few steps). This behavior occurred significantly more frequently than

all other behaviors for *T. uhleri* and more often than "squirreling behind leaves" for *P. marginata* (Table 1). For *P. dolus*, all four responses occurred with similar frequency, although there was a nonsignificant trend for individuals to either "descend down the plant" or remain in place. In contrast, *D. penedetcta* was most likely to "squirrel behind the stem" out of sight, and *S. aestuarium* most frequently "jumped off the plant" altogether (Table 1).

Relative strength of top-down and bottom-up forces on sap-feeder population growth

Our nutrient subsidy manipulation successfully increased both the biomass and nutritional quality of *Spartina*. Fertilization significantly increased above-ground live biomass from 417 ± 105 g/m² (islets without spider supplement) and 359 ± 52 g/m² (islets with spider supplement) on nonsubsidized islets to 964 ± 63 g/m² (islets without spider supplement) and 975 ± 56 g/m² (islets with spider supplement) on subsidized

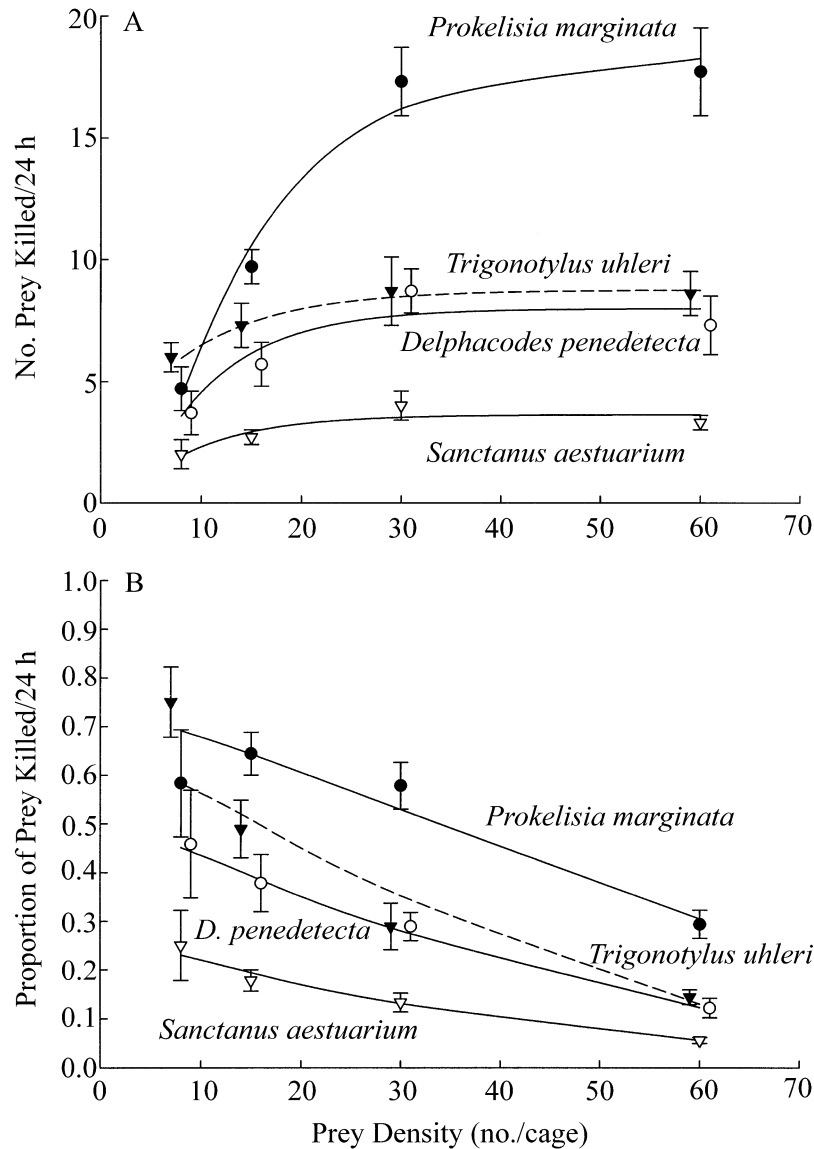


FIG. 2. Functional response of the wolf spider *Pardosa littoralis* to increasing densities of the planthoppers *Prokelisia marginata* (solid circles), *Delphacodes penedetector* (open circles), the mirid bug *Trigonotylus uhleri* (solid triangles), and the leafhopper *Sanctanus aestuarium* (open triangles). (A) The number and (B) the proportion of adults captured by a single wolf spider in 24 h are shown. Significantly more *P. marginata* were taken than either *T. uhleri* or *D. penedetector*, which were taken more frequently than *S. aestuarium* (logistic regression; $\chi^2 = 88.55$, $P < 0.0001$). Means \pm 1 SE are shown.

TABLE 1. Behavioral responses of five sap-feeding herbivores resting on their *Spartina* host plant to a simulated spider attack.

Sap-feeder taxon (n)	Remaining	Descending	Squirreling	Jumping
<i>Prokelisia marginata</i> (47)	0.40 ^a (19)	0.26 ^{ab} (12)	0.11 ^b (5)	0.23 ^{ab} (11)
<i>Prokelisia dolus</i> (50)	0.28 ^a (14)	0.34 ^a (17)	0.14 ^a (7)	0.24 ^a (12)
<i>Delphacodes penedetector</i> (49)	0.10 ^a (50)	0.08 ^a (4)	0.70 ^b (34)	0.12 ^a (6)
<i>Sanctanus aestuarium</i> (32)	0.00 ^a (0)	0.03 ^a (1)	0.38 ^{ab} (12)	0.59 ^b (19)
<i>Trigonotylus uhleri</i> (56)	0.79 ^a (44)	0.07 ^b (4)	0.12 ^b (7)	0.02 ^b (1)

Notes: The proportion and frequency (in parentheses) of responses in each of four "escape categories" (remaining in place, descending down the plant, squirreling behind leaf or stem, and jumping off the plant) are shown. Frequencies marked with different letters (within-row comparisons only) are significantly different (logistic regression, $P < 0.05$).

TABLE 2. Results of within-subjects ANOVA testing the effects of host-plant nutrition (fertilized and nonfertilized islets) and predation (wolf spiders added vs. withheld) on the final population density ($\log[N + 1]/\text{m}^2$) of six sap-feeder species (*Prokelisia marginata*, *P. dolus*, *Delphacodes penedetector*, *Megamelus lobatus*, *Sanctanus aestuarium*, and *Trigonotylus uhleri*) after two months of population growth on open islets of *Spartina alterniflora* at Tuckerton, New Jersey.

Source of variation	df†	F	P
Between subjects			
Fertilization	1, 32	67.91	<0.0001
Spider addition	1, 32	6.29	0.017
Fertilization × Spider addition	1, 32	0.36	0.552
Within subjects			
Species	5, 75	341.37	<0.0001
Species × Fertilization	5, 75	4.84	0.001
Species × Spider addition	5, 75	2.29	0.054
Species × Fertilization × Spider addition	5, 75	1.29	0.278

Notes: Islets were treated as subjects (nested within fertilization and spider-addition treatments), fertilization and spider effects were between-subjects factors, and species was the within-subject factor. P values in bold highlight significant treatment effects ($P < 0.05$).

† Numerator, denominator degrees of freedom (Kenward-Roger calculation; PROC MIXED, SAS 2001).

islets ($F_{1,22} = 83.16$, $P < 0.0001$). Spider addition had no direct ($F_{1,22} = 0.18$, $P = 0.68$) or interactive effect with fertilization on plant biomass ($F_{1,22} = 0.31$, $P = 0.58$). Similarly, fertilization enhanced the nitrogen content of *Spartina* from $1.5 \pm 0.1\%$ (islets without spiders) and $1.5 \pm 0.1\%$ (islets with spiders) on non-subsidized plots to $2.3 \pm 0.1\%$ (islets without spiders) and $2.4 \pm 0.1\%$ (islets with spiders) on subsidized islets ($F_{1,22} = 59.90$, $P < 0.0001$). Spider augmentation had neither a direct ($F_{1,22} = 0.02$, $P = 0.90$) nor interactive effect on nitrogen content ($F_{1,22} = 0.02$, $P = 0.88$).

Spider augmentation was effective in enhancing the density of *Pardosa* wolf spiders on treatment islets. Spider density was significantly higher on islets stocked with spiders (483 ± 52 spiders/ m^2 and 109 ± 6 spiders/ m^2 on fertilized and nonfertilized islets, respectively) than on islets where spiders were not added (142 ± 30 spiders/ m^2 and 13 ± 5 spiders/ m^2 on fertilized and nonfertilized islets, respectively) ($F_{1,22} = 68.76$, $P < 0.0001$). A significant Fertilizer effect was also evident with spider density generally higher on islets subsidized with nitrogen ($F_{1,22} = 81.10$, $P < 0.0001$).

Certain sap-feeders were far more abundant (*P. marginata* and *P. dolus*) than others in the community (significant Species effect on population density, Table 2, Fig. 3). Although nitrogen fertilization generally increased sap-feeder abundance (significant Fertilizer effect), and spider augmentation reduced sap-feeder density (significant Spider Addition effect), sap-feeder species responded very differently to the bottom-up and top-down manipulations (significant interactive effects of Species × Fertilizer and Species × Spider Addition on population density, Table 2, Fig. 3).

Tests of treatment effects on individual species found that only *Prokelisia* planthoppers were impacted significantly by both enhanced plant nutrition and spider

augmentation (Fig. 4). Adults of both *P. marginata* and *P. dolus* were far more abundant on fertilized islets than on nonfertilized ones (Fig. 3A and B). Notably, adults of *P. marginata* erupted from ~ 500 adults/ m^2 on nonfertilized islets to nearly 3000 adults/ m^2 on fertilized *Spartina*. There was also a significant adverse impact of the spider-addition treatment on the density of *P. marginata* and *P. dolus* (Fig. 4), whereby spiders reduced populations of *P. marginata* by 66% (Fig. 3A) and populations of *P. dolus* by 38% (Fig. 3B). In stark contrast to the *Prokelisia* planthoppers, populations of the other sap-feeders were impacted significantly only by enhanced plant nutrition (Fig. 4). The planthoppers *D. penedetector* and *M. lobatus*, the leafhopper *S. aestuarium*, and the mirid bug *T. uhleri* all achieved significantly higher densities on fertilized islets and spider addition had no significant negative effect on population size (Figs. 3C–F and 4).

Although nitrogen subsidy promoted significant population increases in all sap-feeders, effect sizes ($\ln[\text{Treatment density}/\text{Control density}]$) suggest that certain species (*T. uhleri*, *M. lobatus*, *P. marginata*, and *D. penedetector*; effect size ≥ 1.5) responded far more positively than others (*P. dolus* and *S. aestuarium*; effect size < 1.5 ; Fig. 4; Table 2, Species × Fertilizer effect). In addition, a significant Species × Spider interaction (Table 2) indicated that the effect of predation was more pronounced for some species than others. In particular, *P. marginata* and especially *P. dolus* (effect size = -0.5 and -1.6 , respectively, $P < 0.05$) were adversely impacted by spider augmentation, whereas the other four sap-feeders were little affected by this treatment (effect sizes ≤ -0.5 , $P > 0.05$; Fig. 4).

Overall, bottom-up effects dominated over top-down impacts in this sap-feeder community (mean effect size_{BU} = 1.5, mean effect size_{TD} = -0.4 , respectively;

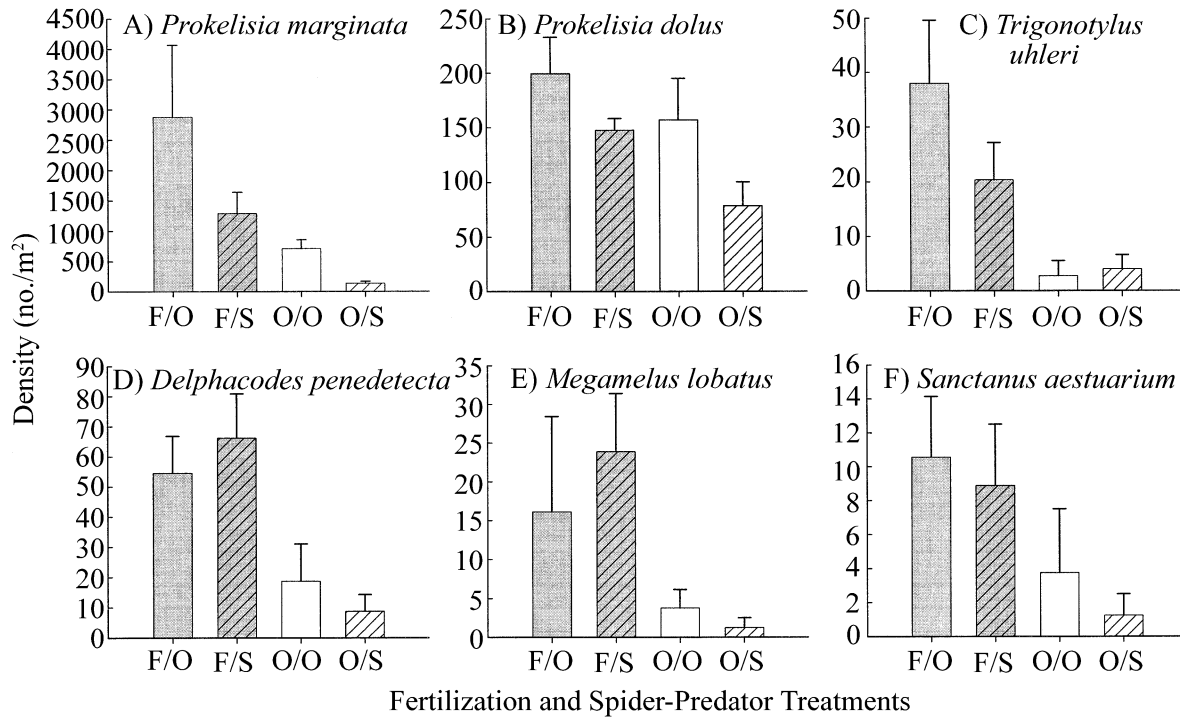


FIG. 3. Effects of nutrient subsidy (fertilization) and spider augmentation on the adult density of six sap-feeding herbivores: (A) *Prokelisia marginata*, (B) *P. dolus*, (C) *Trigonotylus uhleri*, (D) *Delphacodes penedetector*, (E) *Megamelus lobatus*, and (F) *Sanctanus aestuarium* on experimental *Spartina* islets on a salt marsh at Tuckerton, New Jersey. Islets were either fertilized (gray bars) or not (white bars), and spiders were either added (hatched bars), resulting in four treatment combinations: fertilized islets without spiders (F/O), fertilized islets with spiders (F/S), nonfertilized islets without spiders (O/O), and nonfertilized islets with spiders (O/S). Means + 1 SE are shown.

Fig. 4). For example, the relative effect of nitrogen subsidy was greater than the impact of spider predation (relative effect size = $\ln[|\text{Effect size}_{\text{BU}}|/|\text{Effect size}_{\text{TD}}|]$) for most species (>0.5) (Fig. 4). However, there was considerable variation in the relative strength of these two forces across species. Bottom-up impacts were relatively much greater than top-down effects for *D. penedetector* and *M. lobatus* (relative effect size >2.0) followed by *T. uhleri*, *S. aestuarium*, and *P. marginata* (<0.5 – 2.0). Only for *P. dolus* did the adverse effects of spider predation on population size outweigh the positive effects of enhanced plant quality (relative effect size = -0.2), but the effects of the two forces were quite similar (mean effect size_{BU} = 0.4 and mean effect size_{TD} = -0.5 ; Fig. 4). In general however, the relative strength of bottom-up effects in the assemblage of sap-feeders at large was very high (relative effect size = 1.3, Fig. 4).

DISCUSSION

Bottom-up and top-down forces differentially affected the various species of herbivores on *Spartina*. This pattern resulted even though the herbivores in the system were of similar size, members of the same sap-feeding guild, and phylogenetically related. Overall, bottom-up effects dominated in this sap-feeder com-

munity, whereby the density of all six sap-feeders (planthoppers, leafhoppers, and mirid bugs) increased when the nitrogen content of their *Spartina* host plant was elevated to a naturally occurring high level via fertilization (Figs. 3 and 4). In contrast to the widespread effects of plant nutrition on the herbivore assemblage, wolf-spider (*Pardosa littoralis*) addition significantly suppressed populations of only *Prokelisia* planthoppers (*P. marginata* and *P. dolus*), but had little impact on the other four sap-feeder species in the community (Figs. 3 and 4). Thus, the relative contribution of plant-related factors and natural enemies to herbivore population dynamics is very much herbivore species dependent in this system.

The differential susceptibility of the sap-feeders to wolf-spider predation was documented independently with functional response experiments in the laboratory. Results from these experiments showed that the two *Prokelisia* species were similarly vulnerable to wolf-spider predation, with *P. dolus* being slightly more at risk than *P. marginata* due to the predominance of flightless adults in populations (Fig. 1). This subtle difference in risk, however, did not translate into a higher absolute impact of spider predation on *P. dolus* populations in the field (Figs. 3 and 4). Also, these two planthoppers were much more likely to be attacked and

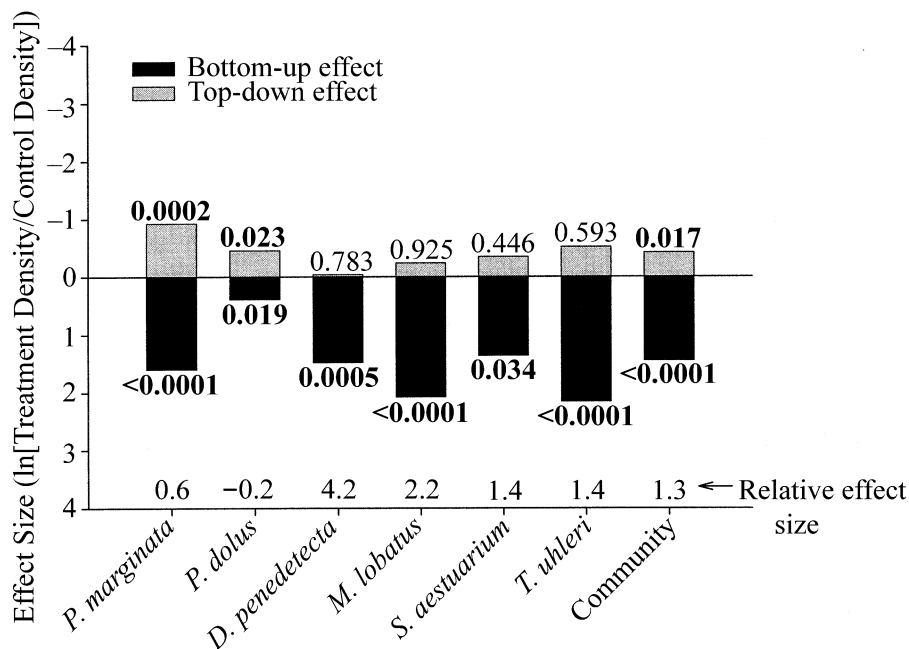


FIG. 4. Effect size ($\ln[\text{treatment density}/\text{control density}]$) of the bottom-up (plant-nutrition) and top-down (spider-predation) treatments on the final population density of six sap-feeding herbivores (log-transformed number of adults/ per square meter) and the pooled sap-feeder community after two months of population growth on open islets of *Spartina alterniflora* at Tuckerton, New Jersey. *P* values above and below bars indicate the significance of the top-down and bottom-up treatments relative to controls for each sap-feeder species (preplanned contrasts) and for the community at large. Values in bold highlight significant effect sizes ($P < 0.05$). Numbers above the abscissa specify the relative strength of the bottom-up compared to the top-down treatment on population density (relative effect size = $\ln[|\text{effect size}_{\text{BU}}|/|\text{effect size}_{\text{TD}}|]$) for each species and for the sap-feeder community at large. A relative effect size value of 0 indicates that herbivore density was influenced equally by bottom-up and top-down treatments, positive values indicate that bottom-up effects had a relatively greater impact on herbivore density than top-down effects, and negative values indicate that top-down effects were stronger than bottom-up impacts.

killed by wolf spiders than the other sap-feeders in the assemblage (Fig. 2). Thus, the only two sap-feeders suffering strong top-down effects from wolf-spider predation in the field were the two species shown to be most at risk from spider predation in laboratory experiments.

The behavior of each sap-feeder was roughly linked to its risk of spider predation and ultimately to the strength of top-down impacts in the field. Least susceptible to spider attack was the leafhopper *S. aestuarium* (Fig. 2), a species whose most frequent behavioral response to an advancing spider was to jump off the plant altogether (Table 1). Notably, top-down impacts on this leafhopper were negligible in the field (Fig. 3F). The planthopper *D. penedetecta* responded to a simulated spider attack primarily by squirreling behind stems where it remained hidden (Table 1), although it was shown to be a bit more vulnerable to spider predation in the laboratory than the leafhopper (Fig. 2). Nonetheless, top-down effects from wolf spiders were minimal on this planthopper in the field (Fig. 3D). Most susceptible to spider attack were the *Prokelisia* species (Figs. 1 and 2), two planthoppers whose most frequent response to an advancing spider was to either remain in place while twitching slightly or to

descend slowly down the plant in plain sight of the predator (Table 1). Wolf spiders are visually orienting predators that detect their prey by movement (Uetz 1991, Samu 1993, Döbel and Denno 1994). Thus, small-scale movements that attract attention but do not result in rapidly abandoning the plant or relocating out of sight, apparently predispose *Prokelisia* planthoppers to attack. The mirid *T. uhleri* was an apparent exception to this pattern in that its primary response to an advancing spider was to remain in place (Table 1), yet it was only moderately vulnerable to spider attack in the laboratory (Fig. 2) and was little affected by the spider-addition treatment in the field (Fig. 3C). The key to this apparent dilemma is found in the different microhabitats these sap-feeders exploit. *T. uhleri* feeds exclusively on the tips of leaf blades in the upper canopy of *Spartina* where it escapes most ground-foraging spiders like *Pardosa* (Vince et al. 1981). By contrast, all the other sap-feeders feed and reproduce in the middle or basal portion of *Spartina* where *Pardosa* and other hunting spiders abound (Vince et al. 1981, Döbel and Denno 1994). Thus, this mirid rarely encounters *Pardosa* and its behavior does not predispose it to wolf spider attack. Moreover, *T. uhleri* is slightly larger than

the other sap-feeders and may thus fend off attack with slightly greater success than the smaller planthoppers.

Additionally, it could be argued that abundance and not behavior is the major factor underlying differences in risk of predation and top-down control among the various sap-feeders. Recall that it was the uncommon planthoppers and leafhoppers in this system that were least affected by the spider addition treatment (Figs. 3C–F and 4). If abundance were key, however, one would have expected spider impacts to be greater for these sap-feeders on fertilized islets where they were significantly more abundant than on nonfertilized controls. In fact, this did not occur for three out of the four uncommon species in the guild (*D. penedetector*, *M. lobatus*, and *S. aestuarium*) where spider impacts appeared to be less on fertilized islets than on nonfertilized ones (Fig. 3D–F). Thus, we argue that herbivore behavior has a relatively greater effect on risk of predation than does outright abundance, although we do not deny its possible role.

Behavior has been shown to influence the risk of predation in a variety of herbivores in other systems, both terrestrial (Beckerman et al. 1997, Schmitz et al. 1997, Denno and Peterson 2000) and aquatic (Sih 1987, Peckarsky and McIntosh 1998). In several cases, predator-induced changes in herbivore behavior resulted in effects that cascaded to primary producers where either biomass or plant-species diversity were affected (Schmitz et al. 1997, Peckarsky and McIntosh 1998, Schmitz 1998). In the *Spartina* system, jumping or hiding behaviors diminished the risk of attack, and species exhibiting these behaviors were not heavily impacted by spider predation in the field. Herbivores lacking such escape behaviors or employing them infrequently (e.g., *Prokelisia* planthoppers), were the most adversely impacted by spider predation in the field. Thus, herbivore behavior has the potential to influence the strength of top-down impacts and promote trophic cascades, underscoring the important link between behavioral ecology and food web-level interactions (Schmitz 1998).

Despite differences in the strength of top-down impacts among the sap-feeders on *Spartina*, bottom-up forces dominated in this system. Other studies have predicted (Hunter and Price 1992) and documented (Stein and Price 1995, Denno and Peterson 2000, Forkner and Hunter 2000) the primacy of bottom-up effects in phytophagous arthropod communities. Moreover, when top-down forces are important in the *Spartina* system, their impact is often mediated by plant resources. For example, complex vegetation with leaf litter promotes the aggregation of wolf spiders and enhances their ability to suppress *Prokelisia* populations (Döbel and Denno 1994, Denno et al. 2002). The predominance of bottom-up forces in this system is further supported when one compares the relative strength of plant nutrition and spider predation on the common and scarce sap-feeders in the assemblage. Notably, it

was the abundant species (*Prokelisia* planthoppers) that were most impacted by spider predation and not the less common (*T. uhleri*, *M. lobatus*, *D. penedetector*) or scarce sap-feeders (*S. aestuarium*) (Fig. 3). Were natural enemies generally important in suppressing herbivores, and thus primarily responsible for species abundance patterns (sensu Hairston et al. 1960), one would have predicted the opposite pattern.

Our results suggest the general importance of plant nutrition as a major driver of the population dynamics of the sap-feeding herbivores on *Spartina*. The well-documented stoichiometric mismatch between the carbon to nitrogen content (C:N) of plants (35–40) and that for herbivorous insects (5–7) underscores the limiting nature of nitrogen for herbivorous insects, and accounts for the multitude of ecological and physiological adaptations that have evolved in herbivores that help offset this inherent discrepancy (McNeill and Southwood 1978, Mattson 1980, White 1993, Denno and Fagan, *in press*). Thus, it was not surprising to see populations of all six sap-feeders increase on nitrogen-enriched *Spartina*, albeit to varying degrees. Population responses to enhanced plant nitrogen were particularly strong for the planthopper *P. marginata* and the mirid bug *T. uhleri*, whose populations exploded on fertilized islets of *Spartina* (compare spider-free treatments in Fig. 3A and C). The combination of extraordinary dispersal capability (most adults macropterous) and high realized fecundity on nitrogen-enriched host plants (Vince et al. 1981, Denno 1994, Denno and Peterson 2000) undoubtedly promoted the rapid colonization and population increase of these two sap-feeders on fertilized *Spartina* islets. Less mobile species (most adults brachypterous) exhibited more variable responses to fertilized *Spartina*, with *P. dolus* showing a moderate population increase, and *D. penedetector* and *M. lobatus* showing larger increases (Fig. 3B, D, and E). Differences in fecundity and feeding compensation among these sap-feeders most likely contributed to their variable responses to enhanced plant quality (see Denno 1994, Denno et al. 2000).

Specific behavioral and life history characteristics of the sap-feeders on *Spartina* influenced the relative strength of top-down and bottom-up forces on their population dynamics, a point that has been emphasized by others (Polis 1999, Forkner and Hunter 2000, Denno et al. 2002). Toward making some general predictions, species with effective escape or hiding behaviors were least susceptible to spider predation, were affected little by top-down forces in the field, and were influenced largely by enhanced plant nutrition. Sap-feeders with less effective escape behaviors were impacted relatively more by top-down forces in the field. At a broader spatial scale, high mobility also appears to promote bottom-up control because it facilitates the location and colonization of nitrogen-rich *Spartina* and because such patches often occur in habitats where invertebrate predators are initially rare (Denno and Peterson 2000,

Denno et al. 2002). Spatial and temporal heterogeneity in the biomass and quality of basal resources sets the stage for strong bottom-up control in many communities of phytophagous insects (Denno and McClure 1983, Hunter and Price 1992, Denno et al. 2002). Nonetheless, in certain habitats and for particular herbivores, top-down impacts can be strong, and we argue that both herbivore behavior and life history strategy including dispersal are important contributors to the relative roles that plant resources and natural enemies play in the population dynamics of herbivorous insects.

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