COMMUNITY ECOLOGY - ORIGINAL RESEARCH

Predator hunting mode influences patterns of prey use from grazing and epigeic food webs

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Abstract Multichannel omnivory by generalist predators, especially the use of both grazing and epigeic prey, has the potential to increase predator abundance and decrease herbivore populations. However, predator use of the epigeic web (soil surface detritus/microbe/algae consumers) varies considerably for reasons that are poorly understood. We therefore used a stable isotope approach to determine whether prey availability and predator hunting style (active hunting vs. passive web-building) impacted the degree of multichannel omnivory by the two most abundant predators on an intertidal salt marsh, both spiders. We found that carbon isotopic values of herbivores remained constant during the growing season, while values for epigeic feeders became dramatically more enriched such that values for the two webs converged in August. Carbon isotopic values for both spider species remained midway between the two webs as values for epigeic feeders shifted, indicating substantial use of prey from both food webs by both spider species. As the season progressed, prey abundance in the grazing food web increased while prey abundance in the epigeic web remained constant or declined. In response, prey consumption by the web-building spider shifted toward the grazing web to a much greater extent than did consumption by the hunting spider, possibly because passive web-capture is more responsive to changes in prey availability. Although both generalist predator species engaged in multichannel omnivory, hunting mode influenced the extent to which these predators used prey from the grazing and epigeic food webs, and could thereby influence the strength of trophic cascades in both food webs.

Keywords Multichannel omnivory · Detritus · Predation · Stable isotopes · Trophic interactions

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Introduction

Multichannel omnivory, the consumption of resources from more than one food web, can have profound effects on ecosystems (Polis and Strong 1996). Multichannel omnivory by a generalist predator can affect system

stability (Anderson and Polis 2004; McCann et al. 1998, 2005), prey suppression in both food webs, including the initiation of trophic cascades (Oelbermann and Scheu 2009; Polis and Strong 1996; von Berg et al. 2010), level of cannibalism by the predator (Chen and Wise 1999; von Berg et al. 2010), and decomposition rates (Leroux and Loreau 2010; Wise et al. 1999). A common form of multichannel omnivory is the use of prey from both the aboveground grazing food web and the soil-surface or epigeic food web (Polis and Strong 1996), but the extent to which generalist predators use both grazing and epigeic prey varies considerably in both time and space, for reasons that are not well understood (Bell et al. 2008; Halaj and Wise 2002; Pace et al. 1999; Wise et al. 1999). (We use the term epigeic food web to collectively refer to species that feed on plant detritus, associated microbes, and algae found at the soil surface.) Previous studies have found that generalist predator populations may be sustained early in the growing season by prey from the epigeic food web, and in turn depress populations of grazing herbivores later in the growing season (e.g., Settle et al. 1996). In many instances, however, the addition of epigeic prey increases the abundance of generalist predators without impacting grazing prey (Birkhofer et al. 2008; Halaj and Wise 2002; Miyashita et al. 2003; Wise et al. 2006).

Variation in the use of epigeic and grazing prey by generalist predators has primarily been attributed to the relative availability of prey from the two webs (Miyashita and Takada 2007; Shimazaki and Miyashita 2005). Given that predator habitat domain and hunting style can influence prey capture (Schmitz 2007; Sih et al. 1998; Woodcock and Heard 2011), functional characteristics of generalist predators may also influence the use of grazing and epigeic prey. For example, predators that are restricted to a narrow habitat domain in the lower canopy may be more likely to encounter epigeic prey, and predators with an active hunting strategy (as opposed to sit-and-wait or sit-and-pursue; sensu Schmitz 2007) might be more likely to encounter both epigeic and grazing prey by moving throughout the canopy. Thus, the relative abundance of predators with different foraging behaviors, rather than prey availability per se, could explain variation in top–down effects across systems.

Previous studies have found that stable isotopes provide a powerful tool for understanding how generalist predator diets change with the availability of epigeic and grazing prey (Halaj et al. 2005; Kuusk and Ekbom 2010; McNabb et al. 2001; Wise et al. 2006). We therefore used stable isotopes of carbon to assess the level of multichannel omnivory over the course of a summer by the two most abundant generalist predators (a hunting and a web-building spider) in a salt marsh on the east coast of North America. Previous studies in agricultural systems have

demonstrated that spiders feed on both epigeic and grazing prey (Settle et al. 1996; Wise et al. 1999, 2006), and this type of multichannel omnivory can lead to a trophic cascade in the grazing food web. Three features of these salt marshes therefore provide opportunities to investigate factors that may contribute to variation in multichannel omnivory by generalist predators. First, there is a temporal shift in the relative abundance of basal resources in the food webs over the course of the summer. Detrital and algal resources on the marsh tend to decline during the growing season (Pickney and Zingmark 1993; Sullivan and Moncreiff 1988), while live plant resources tend to increase in availability during the growing season (Denno 1976; Vince and Valiela 1981). Thus, the grazing food web may become more important to spiders as summer progresses, as was found in a terrestrial grassland (Shimazaki and Miyashita 2005). Second, the two most abundant spiders differ in hunting mode, which may influence their use of prey. The wolf spider *Pardosa littoralis* (henceforth *Pardosa*) is an active hunting spider, so it does not use a web to capture prey, and has previously been thought to rely primarily on the grazing food web (Döbel and Denno 1994; Döbel et al. 1990). In contrast, the linyphiid spider *Grammonota trivittata* (henceforth *Grammonota*) is a sit-and-pursue predator that captures prey in a sheet web built close to the marsh surface. Due to their narrow habitat domain in the lower canopy, linyphiid spiders are generally considered to be members of the epigeic food web (McNabb et al. 2001; Shimazaki and Miyashita 2005), so the epigeic web may be more important for *Grammonota* than for *Pardosa*. Third, the relative abundance of prey in grazing and epigeic food webs may be driven by spatial variation in epigeic and grazing prey resources among marsh grass species. Marsh vegetation is dominated by two species of cordgrass that grow in contiguous monospecific patches, which differ markedly in the abundance and condition of their detrital layers. One grass, *Spartina patens*, supports an abundant thatch layer 5–20 cm deep, whereas thatch in the other grass, *S. alterniflora*, is rarely more than a few centimeters deep (Denno 1977). As a result, the marsh surface under *S. alterniflora* receives more light, permitting greater algal abundance (Redfield 1972), and may thus support higher densities of epigeic feeders. The difference in thatch accumulation between the two grasses is partially caused by faster microbial decomposition in *S. alterniflora* (Denno 1977), and epigeic feeders may respond positively to the associated increase in microbial abundance. Both these factors suggest higher densities of epigeic feeders in *S. alterniflora* than in *S. patens* and greater dependence on epigeic feeders by spiders. However, herbivore densities are also commonly higher in *S. alterniflora* than in *S. patens* (Lewis and Denno 2009). We therefore expected spider use of the food webs

to differ between the two grass habitats only if the herbivore-to-epigeic feeder ratio differed substantially between grasses.

Elucidating the factors that modify spider use of the grazing and epigeic food webs in natural systems will increase our understanding of herbivore suppression, including pest control in agroecosystems. Spiders can play an important role in suppressing agricultural pests (Symondson et al. 2002) and their ability to capitalize on the epigeic food web can increase their efficacy (Settle et al. 1996), but may also decrease spider efficacy in suppressing pests when epigeic prey are preferred (Wise et al. 2006). Notably, both *Pardosa* and *Grammonota* are capable of reducing herbivore densities on the marsh (Denno et al. 2004), and the effect of *Pardosa* on herbivores has been shown to cascade to benefit *Spartina* (Finke and Denno 2006). Therefore, an understanding of the role of spider functional characteristics on consumption from the epigeic and grazing food webs may increase our understanding of the factors that drive trophic cascades in the grazing food web.

We measured densities and isotopic values of spiders, herbivores, and epigeic feeders in both *S. patens* and *S. alterniflora* during June, July, and August 2005. We had four objectives. First, to determine the extent to which marsh spiders engaged in multichannel omnivory. Second, to determine whether *Grammonota* relied on epigeic prey to a greater extent than did *Pardosa*, as suggested by its hunting mode and the documented tendencies of other Linyphiids. *Grammonota* are rare in *S. patens*, so this test was carried out only in *S. alterniflora*. Third, to test whether temporal changes in the herbivore-to-epigeic feeder ratio affected spider diet composition. Our final objective was to test whether the very different abiotic conditions in the thatch layers of the two grasses were accompanied by a change in the prey consumed by *Pardosa* from the two food webs.

Materials and methods

Study site and organisms

We conducted this study at an expansive salt marsh near Tuckerton, New Jersey (39°30.8′N, 74°19.0′W) that is dominated by large, natural monocultures of cordgrass *Spartina alterniflora* (Denno et al. 2002) with abutting monocultures of marsh hay *Spartina patens*. The herbivore assemblage in both grasses is dominated numerically by a small number of planthopper species. In *S. alterniflora*, two congeneric planthoppers, *Prokelisia dolus* and *P. marginata*, constitute upwards of 80 % of herbivore biomass (Denno et al. 2000), with the planthopper *Delphacodes penedetecta* ranking as the third most abundant herbivore

species. In *S. patens*, the planthoppers *Tumidagena minuta* and *Delphacodes detecta* are an order of magnitude more abundant than any other herbivore species (Denno 1980; Raupp and Denno 1979). All five planthopper species specialize on one of the two *Spartina* species (Raupp and Denno 1979). The grazing food web in both grasses also includes specialized predators of planthopper eggs. The mirid bug *Tytthus vagus* attacks planthopper eggs only in *S. alterniflora*, whereas its congener *T. alboornatus* is restricted to planthopper eggs in *S. patens*. Because both species of *Tytthus* are specialists on planthoppers in their respective habitats, they provide a means of comparison with generalist spiders that may feed on prey from both the grazing and epigeic food webs.

We focused on three abundant taxa to represent the marsh epigeic food web. The most abundant epigeic feeder was the amphipod *Orchestia grillus* which feeds on surface epiphyton as well as detritus in both *Spartina* grasses (Agnew et al. 2003; Lopez et al. 1977). The isopod *Venezillo parvus* is less abundant than *O. grillus*, but ingests substantial amounts of *Spartina* litter (Zimmer et al. 2004). Oribatid mites of the genus *Diapterobates*, which feed on both detritus and living microbes (Walter and Proctor 1999), are patchily distributed on this marsh, but are sometimes quite abundant. In general, organisms on the marsh surface are likely to consume a mixture of detritus and algae (hence our use of the term "epigeic feeders"); previous studies have found epiphytic diatoms, brown algae, green algae, red algae, and cyanobacteria growing on the culms and thatch of *S. alterniflora* and *S. patens* (Blum 1968; Quinones-Rivera and Fleeger 2005). Epigeic microalgae living on the marsh surface under the grass canopy could make a substantial contribution to salt marsh food webs, as they produce biomass equivalent to approximately 25–35 % of the biomass produced by *S. alterniflora* (Sullivan and Currin 2000). However, while such algal resources are abundant early in the growing season, they decline as the season progresses and the *Spartina* canopy limits algal growth (Pickney and Zingmark 1993; Sullivan and Moncreiff 1988). We combined arthropods that feed on detritus, its associated fauna, and epigeic microalgae into a single category (sensu Settle et al. 1996). This group is referred to as epigeic feeders, and the food web to which they belong as the epigeic food web. Alternately, the food web based on live vascular plant biomass and its herbivores are referred to as the grazing food web.

The web-building spider *Grammonota* is the most abundant spider in *S. alterniflora*, where it reaches densities of 500–1,500 individuals/m^2 (Denno et al. 2004), but is rarely found in *S. patens*. The hunting spider *Pardosa* is common in both grasses, and reaches average densities of 300 individuals/m^2 (Döbel and Denno 1994). Both *Pardosa* and *Grammonota* are known to consume planthoppers

(Denno et al. 2004), and *Pardosa* are known to also consume both species of *Tytthus* (Döbel and Denno 1994), as well as *Grammonota* (Denno et al. 2004). However, very little is known about consumption of epigeic prey by either spider species. The three representatives of the epigeic web were therefore chosen not because they are known to be attacked by these spiders but because they are generally abundant on this marsh. If the carbon isotopic signatures of these taxa remained similar to one another throughout the summer, we reasoned that they would be representative of the epigeic food web as a whole (sensu Post 2002).

Arthropod and plant samples

We established four blocks in June 2005, each composed of four 10-m^2 sample plots. Within each block, one plot was located in *S. patens* and three in *S. alterniflora*, to capture the greater amount of variation in *S. alterniflora* vegetation structure. One of the *S. alterniflora* plots was located in a high-marsh meadow, one in intermediate-form *Spartina* near a tidal creek, and one in tall-form *Spartina* along the tidal creek bank. In July 2005, we added two additional blocks to the survey, for a total of six blocks that were sampled in July and August. All blocks were at least 100 m from the nearest neighboring block.

We sampled plants and arthropods from the plots three times during the summer of 2005: June 9, July 16, and August 17. Within each plot, we collected arthropods using a D-vac suction sampler with a 21-cm aperture, which was placed in ten different locations within the plot for 3-s periods. We collected arthropods during low tides so that we could place the D-vac head on the ground to effectively capture the epigeic community. Previous studies have demonstrated that the D-vac suction sampler can effectively sample ground-dwelling arthropods in *S. alterniflora*, where it can remove 97 % of the spiders in a collection area (Döbel et al. 1990). We immediately placed collected arthropods into closed containers with ethyl acetate. On each sample date, we also collected 15–20 live *Spartina* culms from each plot, and on July 19, we collected live and dead plant biomass (or thatch) in 0.047-m^2 quadrats (Denno et al. 2002). We transported arthropods, live *Spartina* culms, and quadrats back to the laboratory in coolers either with ice (*Spartina*) or dry ice (arthropods) and stored them in a −20 °C freezer until they were processed. We counted arthropods in each sample and converted them to number per square meter for each focal species.

Stable isotope analyses

We used stable isotopes of carbon to assess the level of multichannel omnivory over the course of the summer by the two most abundant generalist predators (spiders) in the salt marsh. Carbon isotopes have proven useful in determining the relative importance of dual food webs in the diets of generalist predators (e.g., Wise et al. 2006) because carbon isotopic signatures, $\delta^{13}C$, remain relatively unchanged from food source to consumer (Fry 2006). As a result, if the $\delta^{13}C$ values of the prey resource bases are sufficiently distinct, a predator's $\delta^{13}C$ value reflects its relative consumption from the two webs even when intermediate feeding links are unknown (DeNiro and Epstein 1981; Peterson and Fry 1987; Post 2002). To confirm trophic relationships among species, we examined $\delta^{15}N$ for the same producers and consumers that have been previously described.

We processed plant samples by cleaning *Spartina* culms of foreign debris, drying them at 60 °C for 3 days, and grinding them in a Wiley Mill (Thomas Scientific). We separated live plant material in quadrats from thatch, and live and dead biomass was processed as described for culms. We sorted arthropod samples by species, cleaned them of foreign debris, dried them at 60 °C for 3 days, and ground them in 1.5-mL Eppendorf tubes with a pellet pestle. We then packed all plant and arthropod samples in tin capsules (Elementar Americas) and sent them to the Cornell University Stable Isotope Laboratory where they were analyzed using an elemental analyzer-stable isotope ratio mass spectrometer system (Thermo Delta V Advantage IRMS and Carlo Erba NC2500 EA systems). Samples are reported relative to the standards, atmospheric N_2 and Vienna Pee Dee Belemnite (VPDB) carbon. Stable isotope values are reported in δ notation with $\delta^{13}C$ or $\delta^{15}N = [(R_{sample}/R_{standard}) - 1] \times 10^3$, where R is either $^{13}C/^{12}C$ or $^{15}N/^{14}N$.

Statistical analyses

Objective 1: Occurrence of multichannel omnivory

Our data showed that the $\delta^{13}C$ of epigeic feeders increased consistently over the course of the summer while $\delta^{13}C$ of herbivores remained fixed. This difference allowed us to examine whether a spider's $\delta^{13}C$ paralleled that of either web, as it would if the spider consumed only prey from that web. If, on the other hand, the slope of spider $\delta^{13}C$ as a function of time was intermediate between the slopes of the herbivore and epigeic consumer webs, this would provide evidence that spiders used resources from both webs. We implemented a repeated measures mixed model with three fixed effects: functional group (with three levels: herbivore, epigeic feeder, and either *Pardosa* or *Grammonota*), sample month (treated as a continuous variable), and their interaction (SAS proc mixed; SAS Institute, 2002). The dependent variable was $\delta^{13}C$ and sample locations were the multiply-sampled experimental units. Sample-site block

was treated as a random effect. These regressions were carried out separately for each spider and in each grass, and planned contrasts compared the spider's slope with that of each of the channels. To partially check the validity of this test for multichannel omnivory, the same regressions were performed using *Tytthus* instead of spiders. The *Tytthus* species in both grasses are known to prey only on planthopper eggs and thus do not engage in multichannel omnivory; their δ^{13}C slope should therefore differ significantly from that of epigeic feeders but closely parallel that of herbivores.

We used a more traditional mixing model approach as a second test for multichannel omnivory. The mixing model IsoError v.1_04 (Phillips and Gregg 2001) was used to estimate the relative contributions of grazing and epigeic prey to spider tissues. A single-isotope (carbon) mixing model calculated the proportions from the two webs that would be required to produce the carbon isotopic signature (δ^{13}C) observed in each spider species. IsoError also calculates 95 % confidence intervals around estimated food-web contributions by taking into account the amount of data and its variation. When there are many potential diet items, it is common to combine logically related taxa for analysis (Phillips et al. 2005): we combined all planthoppers to represent the grazing food web, and the amphipod *O. grillus* was combined with the isopod *V. parvus* to represent the epigeic food web. Very few individuals of the mite *Diapterobates* sp. were collected in August for analysis, so they were not included in mixing models. Because of the temporal change in δ^{13}C of epigeic feeders, we were forced to run separate models for each of the three collection months.

Objective 2: Differences in resource use between spider species

To test for differences in resource use between the two spider species, we used a repeated measures mixed ANOVA. Fixed effects included spider species (*Pardosa* or *Grammonota*), sample month (treated as three discrete levels), and their interaction. The dependent variable was spider δ^{13}C, and sample locations were the multiply-sampled experimental units. Sample-site block was treated as a random effect. Because *Grammonota* are found only in *S. alterniflora*, we restricted our comparison of spider species to this habitat. A significant spider species effect or a significant interaction would indicate different resource use by the two spider species over the course of the season.

Objective 3: Temporal changes in prey abundance

To examine the effect of herbivore-to-epigeic feeder ratio on spider diet, we examined shifts in spider consumption identified by the IsoError mixing model with shifts in relative prey density identified by a repeated measures model with fixed effects of food web (epigeic or grazing), sample month (treated as a continuous variable), and their interaction. The model was run separately in the two grass habitats. The dependent variable consisted of log-transformed prey densities. Log-transformation resulted in a multiplicative model in which a significant interaction would indicate that the ratio of herbivorous to epigeic prey changed over time.

### Objective 4: Spatial differences in prey between grass species

To test whether the relative abundance of prey in the two food webs differed between the two grass species, and whether *Pardosa* consumption reflected the difference, we compared IsoError estimates of *Pardosa* consumption with a mixed model of log-transformed prey densities in the two grasses. Fixed effects in the model were food web (epigeic or grazing), grass species (*S. alterniflora* or *S. patens*), and their interaction. Log-transformation resulted in a multiplicative model in which a significant interaction would indicate that the ratio of herbivorous to epigeic prey differed between grasses. A significant effect of grass species would indicate that total prey density differed between the grasses. Sample locations were the multiply-sampled experimental units and sample month was treated as a discrete random factor.

Results

When we examined overall patterns in carbon and nitrogen isotopes among producers and consumers, we found that carbon isotopic values did not differ among the three *S. alterniflora* sub-habitats for any arthropod (Appendix S1 in Electronic Supplementary Material). Therefore, data from tall, intermediate, and meadow *S. alterniflora* sub-habitats were combined in all analyses, leaving two grass habitats: *S. alterniflora* and *S. patens*. Furthermore, nitrogen isotopic values reflected the expected trophic relationships (Fig. 1): *Spartina* and thatch had the lowest δ^{15}N values, planthopper δ^{15}N was somewhat higher, and δ^{15}N for *Tytthus* egg predators was still higher. The δ^{15}N values for epigeic feeders were equal to or slightly higher than that of planthoppers. The highest δ^{15}N values were shared by the two spider species, which suggests that, at least in this study, *Grammonota* did not represent a large component of the *Pardosa* diet.

Mean δ^{13}C of *Spartina*, its herbivores, and their specialist *Tytthus* predators remained virtually unchanged over the course of the season at approximately −13.6 ‰ in

Fig. 1 Stable isotope values (mean ± SD) for arthropods and grass in *S. alterniflora* (*left column*) and *S. patens* (*right column*) during June, July, and August 2005. *Pardosa* and *Grammonota* are collectively referred to as *Spiders*. (No *Grammonota* were collected in *S. patens*.) The *Spartina food web* includes: live *Spartina*, *Spartina* thatch (July only), planthoppers and the egg predator *Tytthus*. *Epigeic feeders* includes representatives of the epigeic food web, the amphipod *O. grillus*, and the isopod *V. parvus*
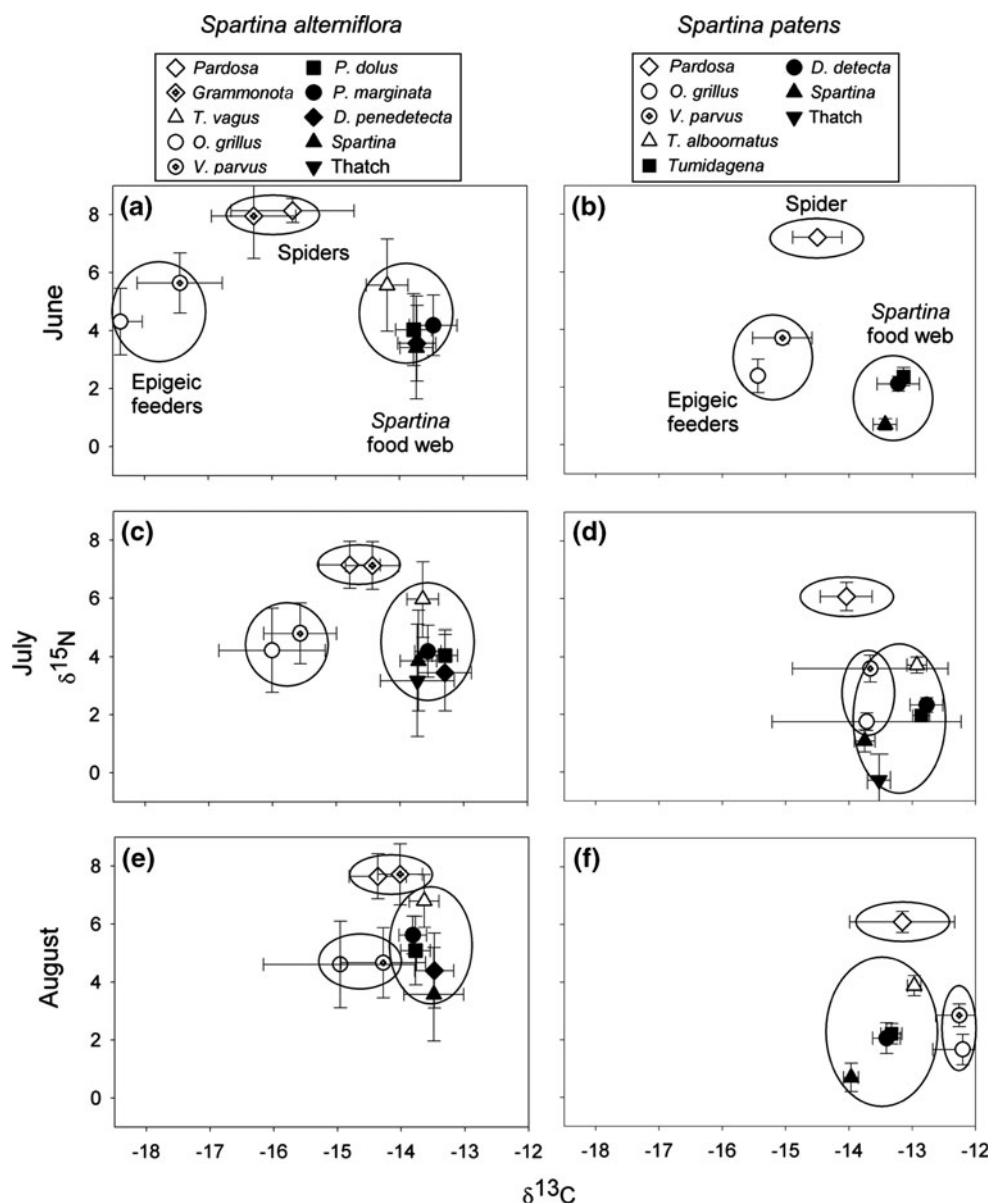

S. alterniflora (Fig. 1a, c, e) and −13.4 ‰ in *S. patens* (Fig. 1b, d, f). The highest and lowest monthly means differed by only 0.28 ‰ in *S. alterniflora* and 0.39 ‰ in *S. patens*. These $\delta^{13}C$ values for *S. alterniflora* fall within the range found by earlier studies, as does a constant value throughout the season (Currin et al. 1995). In sharp contrast, mean $\delta^{13}C$ of epigeic feeders became consistently more enriched from June to August in both *S. alterniflora* (by 3.07 ‰) and *S. patens* (by 2.97 ‰). In June, the $\delta^{13}C$ values for epigeic feeders in *S. alterniflora* was 4.05 ‰ more depleted than herbivore $\delta^{13}C$ (Fig. 1a), but by August, the difference had diminished to 1.02 ‰ (Fig. 1e). In *S. patens*, the $\delta^{13}C$ values for epigeic feeders was 1.40 ‰ more depleted than herbivore $\delta^{13}C$ in June (Fig. 1b), but by August, the $\delta^{13}C$ values for epigeic

feeders was more enriched than herbivore $\delta^{13}C$ by 1.00 ‰ (Fig. 1f). The depleted $\delta^{13}C$ values for epigeic feeders early in the season suggest that algae are an important component of the diet, as previous studies have found that filamentous and epiphytic algae growing in salt marshes can be 4 ‰ more depleted than *S. alterniflora* and *S. patens* (Galvan et al. 2008). Differences in the temporal trajectories of prey $\delta^{13}C$ from the two food webs were significant, as indicated by interactions between food web and sample date in *S. alterniflora* ($F_{1,209} = 188.40$, $P < 0.0001$) and in *S. patens* ($F_{1,55} = 53.95$, $P < 0.0001$). Since no *Diapterobates* mites were collected in August, they were not included in these analyses, but from June to July their $\delta^{13}C$ became enriched by 2.63 ‰ in both grasses, similar to patterns of enrichment by amphipods and isopods.

Objective 1: Occurrence of multichannel omnivory

Spider $\delta^{13}C$ did not parallel the $\delta^{13}C$ of either food web over the course of the summer (Fig. 2), indicating consumption of prey from both webs. The slope of $\delta^{13}C$ versus time for *Pardosa* in *S. alterniflora* differed from the slope for herbivores ($t_{256} = 3.62$, $P = 0.0004$) and for epigeic feeders ($t_{257} = 5.62$, $P < 0.0001$; Fig. 2a), and the slope for *Grammonota* in *S. alterniflora* also differed from prey in both food webs (herbivores $t_{247} = 8.47$, $P < 0.0001$; epigeic feeders $t_{247} = 2.80$; $P = 0.0056$; Fig. 2a). Similarly,
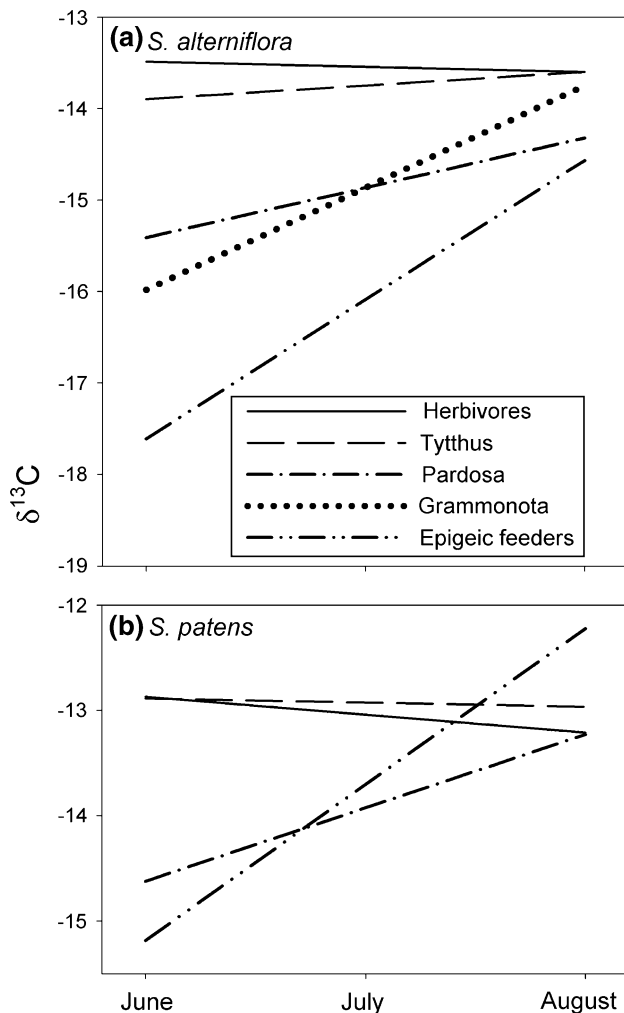
Fig. 2 Linear regressions of $\delta^{13}C$ against time for herbivores, epigeic feeders; and three predators in *S. alterniflora* (**a**), and *S. patens* (**b**). The slope of the herbivore specialist *Tytthus* did not differ from the herbivore slope in either grass ($P = 0.24$ in *S. alterniflora*, and $P = 0.22$ in *S. patens*), but did differ from epigeic feeders in both grasses ($P < 0.0001$ in *S. alterniflora*, and $P = 0.037$ in *S. patens*). The slope of the spider *Pardosa* differed from slopes of herbivores ($P = 0.0004$ in *S. alterniflora*, and $P = 0.0009$ in *S. patens*), and also from the slopes of epigeic feeders ($P < 0.0001$ in *S. alterniflora*, and $P = 0.0013$ in *S. patens*). The slope of the spider *Grammonota* also differed from both herbivores ($P < 0.0001$) and epigeic feeders ($P = 0.0013$) in its *S. alterniflora* habitat

the slope for *Pardosa* in *S. patens* differed from that of prey from both food webs (herbivores $t_{72.5} = 3.46$, $P = 0.0009$; epigeic feeders $t_{72} = 3.36$, $P = 0.0013$; Fig. 2b). As expected, the slope for the herbivore specialist *Tytthus* did not differ from the slope for herbivores in either *S. alterniflora* ($t_{243} = 1.17$, $P = 0.24$; Fig. 2a) or *S. patens* ($t_{13.5} = 1.30$, $P = 0.22$; Fig. 2b), but it did differ from the slope for epigeic feeders in both habitats (*S. alterniflora* $t_{243} = 6.94$, $P < 0.0001$; *S. patens* $t_{13.5} = 2.31$, $P = 0.037$; Fig. 2).

Mixing model estimates for *Pardosa* diet composition in both grass habitats generally had such wide confidence intervals that no conclusions could be drawn (Fig. S1 in ESM). The exception was July in *S. alterniflora*, when the 95 % confidence interval for fraction of grazing carbon in *Pardosa* tissues extended only from 32 to 54 %, providing good evidence for substantial use of prey from both food webs. The wide confidence intervals in June were caused by small sample sizes, and the wide intervals in August were caused by the similarity in prey $\delta^{13}C$ between the two food webs. Because of larger sample sizes and smaller variance for *Grammonota*, mixing model estimates were more precise than for *Pardosa*. *Grammonota* made substantial use of prey from both food webs during all 3 months (Fig. S1 in ESM). Data from separate months could not be combined in mixing models because of the change in the $\delta^{13}C$ of prey from the epigeic food web.

Objective 2: Differences in resource use between spider species

We found a significant month-by-species interaction when comparing $\delta^{13}C$ of the two spiders in *S. alterniflora* ($F_{2,69.3} = 4.95$, $P = 0.01$), caused by the fact that *Grammonota* $\delta^{13}C$ became much more enriched over the course of the summer relative to *Pardosa*. In June, *Grammonota* $\delta^{13}C$ was more depleted than *Pardosa* ($t_{2.20} = 74.1$, $P = 0.03$), but in both July and August, *Grammonota* $\delta^{13}C$ was more enriched than *Pardosa* (July: $t_{2.39} = 64.9$, $P = 0.03$; August: $t_{2.07} = 59.5$, $P = 0.04$). Over the course of the summer, $\delta^{13}C$ of *Grammonota* increased by 2.18 ‰ compared to 1.19 ‰ for *Pardosa*, indicating that *Pardosa* did not shift toward the grazing food web to the extent that *Grammonota* did.

Objective 3: Temporal changes in prey abundance

The herbivore-to-epigeic feeder ratio increased from June to August in both habitats (Fig. 3). The increase was significant in *S. alterniflora* (food web × date interaction $F_{1,24.4} = 18.99$; $P = 0.0002$), but not in *S. patens* ($F_{1,27} = 3.11$; $P = 0.09$). *Grammonota* exhibited a parallel
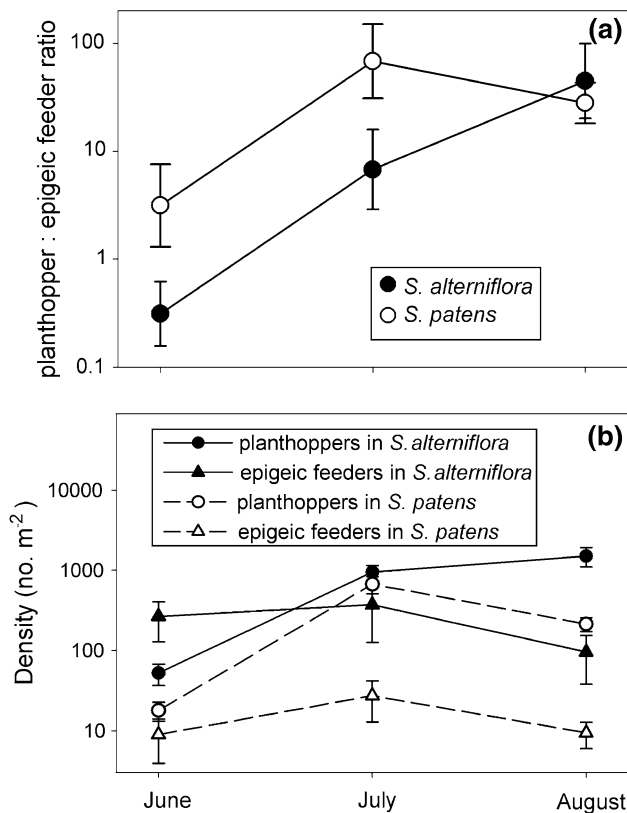
Fig. 3 **a** Herbivore-to-epigeic feeder ratio (mean ± SE), and **b** densities of representatives of the epigeic and grazing food webs (mean ± SE) throughout the summer. The herbivore-to-epigeic feeder ratio increased significantly over time in *S. alterniflora*, *P* = 0.0002, but not in *S. patens*, *P* = 0.09. Averaged over the course of the summer, total prey density in *S. alterniflora* was significantly greater than in *S. patens*, *P* < 0.0001. Relative abundance of grazing and epigeic prey differed only marginally between grasses, *P* = 0.064.

increase in herbivore consumption, as indicated by mixing model results: there is virtually no overlap between its 95 % confidence interval for herbivore consumption in June and those for July and August (Fig. S1 in ESM). Unfortunately, uncertainty in mixing model results for *Pardosa* prevented an assessment of temporal changes in that spider's diet (Fig. S1 in ESM).

Objective 4: Spatial differences in prey between grass species

Averaged over the course of the summer, total prey density in *S. alterniflora* was more than three times prey density in *S. patens* ($F_{1,64}$ = 24.78; *P* < 0.0001). Epigeic feeders constituted 22 % of total prey in *S. alterniflora*, and only 5 % in *S. patens*, but due to high spatial variation within both grasses, the relative abundance of prey from the two food webs differed only marginally between grasses (habitat by food web interaction $F_{1,64}$ = 3.55; *P* = 0.064).

Discussion

In two different grass habitats, the carbon isotopic signature of the epigeic food web became dramatically more enriched over the course of the summer, while the isotopic values of the grazing web remained unchanged. Isotopic values of *Pardosa* and *Grammonota* also became more enriched, and remained intermediate between the signatures of the two webs. This suggestion of multichannel omnivory by spiders was strengthened by the fact that neither spider species' δ^{13}C changed in parallel with prey from either food web, as it would if a spider species consumed prey from only one web. The extent of multichannel omnivory by the spider *Grammonota* appeared to be influenced by the relative abundance of prey. As expected, the herbivore-to-epigeic feeder ratio increased as the summer progressed, and the fraction of grazing carbon in *Grammonota* tissues increased simultaneously.

The extent to which the spiders fed on prey from the grazing and epigeic food webs also differed according to hunting mode. We predicted that *Grammonota* would rely more heavily on the epigeic food web relative to *Pardosa* because *Grammonota* builds horizontal webs in the lower canopy that might increase encounters with epigeic prey. However, the magnitude of the δ^{13}C shift by *Grammonota* towards the grazing web was more than twice that of *Pardosa*, suggesting that microhabitat domain was not the only factor driving spider use of the epigeic and grazing food webs. While previous studies on linyphiid spiders found that species occupying the lower canopy fed on epigeic prey to a larger extent than species that inhabit the upper canopy (Harwood et al. 2003), other factors may determine spider diets. For example, even when different spider species occupy the same microhabitat, smaller spiders are often unable to capture larger grazing prey, which can lead to greater dependence on epigeic prey (Shimazaki and Miyashita 2005). Additionally, spider hunting strategies could impact their ability to respond to seasonal fluctuations in the abundance of grazing and epigeic prey. The webs of linyphiid spiders are a relatively passive form of prey capture and could therefore represent a random sample of prey abundance in a given area. Linyphiid spider webs are often found in areas with high prey densities (Harwood et al. 2003), and other families of web-building spiders are known to relocate their webs if they are not capturing enough prey (Olive 1982). While lycosid spiders are also able to track prey densities, this response is mediated by sensory stimuli (Persons and Uetz 1998). If lycosid spiders are only presented with vibratory cues, they will not respond to differences in prey density among patches, but if they are presented with visual cues or a combination of visual and vibratory cues, they will aggregate in patches with higher prey densities (Persons

and Uetz 1998). Thus, differences in prey activity levels among epigeic and grazing prey could expose them to different levels of predation risk by hunting spiders.

Previous studies have similarly found that other *Pardosa* species consistently feed on prey from the epigeic food web, regardless of the relative abundance of these prey (Kuusk and Ekbom 2010). The use of the epigeic food web by *Pardosa* could result from differences in the visual and vibratory cues presented by epigeic and grazing prey, or could be driven by nutritional requirements. For example, prey species commonly consumed by lycosid spiders differ in amino acid composition, and by feeding on a mixture of prey species, spiders are able to optimize the proportions of essential amino acids in their diet (Greenstone 1979). Future research should therefore work to disentangle the impact of predator functional characteristics and nutritional demands on the use of epigeic and grazing prey.

Multichannel omnivory may stabilize spider population dynamics by increasing their minimum densities (McCann et al. 2005), but differences in hunting strategy may alter spider effects on food web stability. Because *Grammonota* is more responsive to changes in prey abundance, multichannel omnivory by this spider would be expected to have a stabilizing effect on both the epigeic and grazing food webs (e.g., McCann et al. 2005). In contrast, the much weaker tendency of *Pardosa* to respond to changes in relative densities of prey in the two webs could result in over-exploitation of epigeic feeders, which may lead to unstable prey population dynamics (e.g., Wise et al. 1999). However, more research into the effect of *Pardosa* on the population dynamics of epigeic feeders will be required before this possibility can be evaluated.

It is striking that the $\delta^{13}C$ values of epigeic taxa as diverse as amphipods, isopods, and mites exhibited similar temporal shifts and that patterns were similar in the two *Spartina* habitats. Carbon isotopic values of epigeic feeders in *S. patens* were enriched by an average of 2.4 ‰ relative to those in *S. alterniflora*, yet the increase among epigeic feeders from June to August was virtually identical in the two habitats: 2.97 ‰ in *S. patens* and 3.07 ‰ in *S. alterniflora*. Wise et al. (2006) found similar enrichment in the $\delta^{13}C$ values of epigeic feeders from spring to late summer in garden plots. Such shifts could be caused by simultaneous diet changes by many epigeic-feeding species, or by changes at a lower trophic level in the epigeic food web. For example, Currin et al. (1995) found that the $\delta^{13}C$ of benthic microalgae in a North Carolina marsh became enriched by 4.5 ‰ from April to September. This pattern may also be explained by a decline in the fraction of detritus composed of algae. The abundance of filamentous green algae is greatest during the winter months and early spring (Sullivan and Currin 2000), but declines throughout the summer as the development of the *Spartina* canopy

limits algal growth (Pickney and Zingmark 1993; Sullivan and Moncreiff 1988).

Although live *Spartina* may be the most visually apparent basal resource in the intertidal salt marsh, less conspicuous resources such as algae and detritus may also significantly impact species interactions. The demonstrated ability of marsh spiders to suppress planthopper densities and even to initiate trophic cascades (Finke and Denno 2006) may be based in part on their use of prey from the epigeic food web (Gratton and Denno 2003). Such multichannel omnivory has been shown to increase spider densities on forest floors (Chen and Wise 1999) and vegetable gardens (Halaj and Wise 2002), and to suppress herbivore densities in rice (Settle et al. 1996) as well as on desert islands (Polis and Hurd 1996), and may contribute to planthopper suppression in salt marshes. Prey subsidies from the epigeic food web may also explain spatial (Denno et al. 2005) and seasonal (Gratton and Denno 2003) variation in the magnitude and occurrence of trophic cascades previously found in the salt marsh system. If the epigeic food web sustains salt marsh spiders at times when grazing prey are scarce, this could increase spider mean population densities, which could in turn exert a stronger top–down impact on planthopper populations later in the season. Moreover, mesocosm and field studies that examine the impact of spiders on trophic cascades in the grazing food web should also incorporate epigeic prey, as this often overlooked component of food webs may be essential for understanding the roles of generalist spiders in natural and managed systems.

Conclusions

We found evidence of multichannel omnivory in two generalist spider predators with different hunting styles. Based on previous research, we predicted that the web-building spider *Grammonota* would use prey from the epigeic food web to a greater extent than the hunting spider *Pardosa* due to a narrow habitat domain in the lower canopy. However, *Grammonota* fed upon a higher fraction of prey from the grazing food web relative to the diet of *Pardosa* in both July and August. The web-building spider *Grammonota* was also influenced to a larger extent by the relative abundance of prey in the epigeic and grazing food webs during the course of the season compared to the hunting spider *Pardosa*, possibly due to a more passive hunting strategy. Therefore, while both spiders engaged in multichannel omnivory, the importance of epigeic prey diminished through time for the web-building spider yet remained important to the hunting spider. Although prey abundance has previously been linked to the use of grazing and epigeic food webs by generalist predators, here we

demonstrate that hunting mode also influences the extent to which predators feed upon grazing and epigeic prey. Although generalist predators such as spiders are often abundant in natural and managed systems, their top–down influence on pest suppression, primary productivity, and nutrient dynamics will not only be affected by the temporal and spatial abundance of epigeic and grazing prey resources but also by predator foraging behaviors.

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