COMMUNITY ECOLOGY – ORIGINAL RESEARCH

Predator population size structure alters consumption of prey from epigeic and grazing food webs

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Abstract

Numerous studies have found that predators can suppress prey densities and thereby impact important ecosystem processes such as plant productivity and decomposition. However, prey suppression by spiders can be highly variable. Unlike predators that feed on prey within a single energy channel, spiders often consume prey from asynchronous energy channels, such as grazing (live plant) and epigeic (soil surface) channels. Spiders undergo few life cycle changes and thus appear to be ideally suited to link energy channels, but ontogenetic diet shifts in spiders have received little attention. For example, spider use of different food channels may be highly specialized in different life stages and thus a species may be a multichannel omnivore only when we consider all life stages. Using stable isotopes, we investigated whether wolf spider (*Pardosa littoralis*, henceforth *Pardosa*) prey consumption is driven by changes in spider size. Small spiders obtained > 80% of their prey from the epigeic channel, whereas larger spiders used grazing and epigeic prey almost equally. Changes in prey consumption were not driven by changes in prey density, but by changes in prey use by different spider size classes. Thus, because the population size structure of *Pardosa* changes dramatically over the growing season, changes in spider size may have important implications for the strength of trophic cascades. Our research demonstrates that life history can be an important component of predator diet, which may in turn affect community- and ecosystem-level processes.

Keywords Diet shift · Food web · Multichannel omnivory · Predation · Stable isotopes

Introduction

Across a wide array of terrestrial and aquatic ecosystems, predators suppress prey densities, which can in turn affect important ecosystem services (Tscharntke et al. 2008). The ability of generalist predators to consume more than one prey resource and switch among prey can stabilize prey populations, and indirectly affect primary production and decomposition. In many food webs, predators link the plant-based, grazing energy channel with the detritus-based, soil-surface epigeic channel by consuming prey from both channels (Polis and Strong 1996; Ward et al. 2015; Wimp et al. 2013; Wolkovich et al. 2014). Here we use the term grazing channel to refer to herbivores that feed on live plants and the term epigeic channel to refer to consumers of plant detritus, its associated microbes, and algae found at the soil surface. Theoretical models show that such channel linkage can stabilize food webs when predators shift between channels in response to changes in relative prey abundance (Rooney et al. 2006; Ward et al. 2015; Wolkovich et al. 2014). However, the stabilizing effect may be considerably weaker if some predator size classes can shift between channels and respond to changes in prey availability, while other size classes cannot, potentially due to negative interactions among size classes of predators (Rudolf 2006). When predators can not only shift between different prey species, but also between prey from different food webs (multichannel omnivory), these different food webs can sustain predator populations at different times of the year, which can increase predator population density and stability (Settle et al. 1996).

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Multichannel omnivory by generalist predators can lead to prey suppression in both food webs, with cascading effects on primary producers (Oelbermann and Scheu 2002; Polis and Strong 1996; von Berg et al. 2010) and the detrital food web (Leroux and Loreau 2010; Wise et al. 1999). However, the ability of such multichannel omnivores to effectively suppress prey populations depends on their ability to switch to a new prey resource as it becomes abundant, and constraints such as age or size may hinder their ability to shift. Previous research has often treated related species or even members of the same broad trophic group (such as herbivores or predators) as functionally equivalent. However, enormous diversity exists in how predators respond to prey within a trophic group, among closely related species, and even within the same species (Wimp et al. 2019). Indeed, directly examining such variability may explain why predator initiation of top-down effects and trophic cascades is so variable from one system to the next and at different points in time.

Development-related diet shifts are common among consumers with complex life cycles, such as amphibians, marine invertebrates, and holometabolous insects. Fish and reptiles have simple life cycles, but are frequently gape limited, and their diets change as their mouths enlarge (e.g. Scharf et al. 2000). Spiders are important predators in many arthropod food webs, and external digestion frees them somewhat from gape limitation; spider prey can range from a small fraction of the spider's size to several times its size (e.g. Huseynov 2006). Spiders frequently eat prey from multiple food webs (Wise et al. 2006; Settle et al. 1996; Perkins et al. 2018), and would seem to be ideally suited to link energy channels as envisioned by theoretical models. However, little is known about the way in which diet changes with spider size (but see Wise 2006 (and references therein); Wise et al. 2006; Oelbermann et al. 2008; Bartos 2011). Life-history diet shifts have rarely been studied in spiders, and even fewer size-related shifts between energy channels have been reported (but see Shimazaki and Miyashita 2005).

A predator's diet can be affected by factors other than the ability to capture desired prey. A predator may evade its own predators, including conspecific cannibals, by modifying its activity schedule, foraging activity, or habitat use (Rudolf 2007). We previously showed that a wolf spider common in salt marshes, *Pardosa littoralis* (henceforth *Pardosa*), feeds from both grazing and epigeic energy channels (Wimp et al. 2013). However, whether *Pardosa* consumption from the two food webs remains constant throughout the season, or changes with spider size, remains unknown. *Pardosa* are univoltine, with reproduction beginning in early summer. As a result, size structure of the *Pardosa* population changes substantially over the course of the season (personal observations). While *Pardosa* are not gape limited, spider size may affect behavior and prey consumption. For example,

Pardosa is cannibalistic, with the smallest individuals most likely to become victims (Langellotto and Denno 2006). The layer of dead leaves at the base of marsh grass, known as thatch, offers some refuge from cannibalism (Langellotto and Denno 2006) and any small spiders spending time there would encounter epigeic prey almost exclusively, since grazing herbivores generally occur above the thatch layer (Denno et al. 2003). Small *Pardosa* might, therefore, be unlikely to increase consumption of herbivores in response to an herbivore outbreak and thus not suppress herbivore prey populations, but instead continue to consume epigeic prey even if those prey densities are declining. Here, we address the following research question: does the reliance of *Pardosa* on grazing and epigeic energy channels change as *Pardosa* grow? We used stable isotopes of carbon and nitrogen to examine shifts in *Pardosa* prey use with ontogenetic changes in body size. While we measured nitrogen isotopes to confirm trophic status, 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 remain relatively unchanged from food source to consumer (Fry 2006).

Materials and methods

Study site and organisms

We conducted this study at a salt marsh near Tuckerton, New Jersey, USA (39° 30.8′ N, 74° 19.0′ W) that is dominated by the cordgrass *Spartina alterniflora* (Denno et al. 2002, now reclassified as *Sporobolus alterniflorus*). We focused on the dominant species in the live plant and epigeic (algal and detrital) food webs; relationships among these dominant arthropods have been well characterized (Finke and Denno 2002, 2003, 2004, 2005; Wimp et al. 2013). *Pardosa* hatch and grow during the summer, overwinter as late-instar juveniles, mature to adults in the spring and begin reproduction in early summer (Dobel et al. 1990). The grazing herbivore assemblage in *S. alterniflora* is dominated by two congeneric planthopper species, *Prokelisia dolus* and *P. marginata*, which constitute upwards of 80% of herbivore biomass (Denno et al. 2000). The planthopper *Delphacodes penedetecta* and the mirid bug *Trigonotylus uhleri* rank as the next most abundant herbivores. The mirid bug *Tytthus vagus* consumes planthopper eggs exclusively, and frequently falls prey to *Pardosa*.

We focused on three species to represent the marsh epigeic food web because of their abundance at the study marsh, similar to the high relative abundances of the herbivore species listed above: *Orchestia grillus*, *Venezillo parvus*, and *Saldula interstitialis*. The amphipod *O. grillus* is abundant and feeds on surface epiphyton as well as *Spartina* detritus

(Agnew et al. 2003; Lopez et al. 1977); although amphipods may not be part of a typical terrestrial detrital food web, they are commonly found in systems with a terrestrial–aquatic interface, both freshwater and marine. The isopod *V. parvus* is less abundant than *O. grillus* at this marsh, but ingests substantial amounts of *Spartina* litter (Zimmer et al. 2004). Finally, the saldid bug *S. interstitialis* is saprophagous in early instars, while older nymphs and adults are active predators feeding on surface and subsurface arthropods, including amphipods (Griesinger and Bauer 1990).

Arthropod samples

Four times during the summer of 2009 we sampled marsh arthropods from six blocks, each composed of three 10-m^2 sample plots. Within each block, the three plots were located in different habitats. One plot was located near the upland border of *S. alterniflora* with *S. patens* (this border occurs at mean high water level), a second plot was located in the center of the *S. alterniflora* meadow, and the third in intermediate form *S. alterniflora* near a tidal creek. We sampled the entire arthropod community on 16 Jun 2009, 20 Jul 2009, 18 Aug 2009, and 15 Sept 2009 using a D-vac suction sampler that we placed in ten different locations within each plot for 3-s periods following the methods of Wimp et al. (2013) and Murphy et al. (2012). We immediately placed the collected arthropods into closed containers with ethyl acetate, then transported them to the laboratory in coolers with dry ice and stored in a −20 °C freezer until they were processed.

We sorted arthropod samples by species, counted the abundance of each species, cleaned them of foreign debris, and dried them at 60 °C for 3 days. *Pardosa* were then weighed and assigned to one of six size classes by dry weight (Appendix A). Size classes were chosen to divide the collected *Pardosa* into roughly equally represented groups.

Stable isotope analysis

We used stable isotopes of carbon to assess the level of multichannel omnivory by *Pardosa* over the course of the summer, by measuring $\delta^{13}C$ values of *Pardosa* and their grazing and epigeic prey. While $\delta^{15}N$ values are useful for determining the trophic level of an organism and we measured them in this study for this purpose, $\delta^{13}C$ values reflect changes in food web use. Carbon isotopes have proven useful in determining the relative importance of dual food webs in the diets of generalist predators (Newsome et al. 2007; Wimp et al. 2013; Wise et al. 2006), because carbon isotopic signatures, $\delta^{13}C$, remain relatively unchanged from food source to consumer (Fry 2006). Therefore, if the $\delta^{13}C$ values of the bases of two food webs are sufficiently distinct, a predator's $\delta^{13}C$ value reflects its relative consumption from the two webs even when intermediate feeding links are unclear (DeNiro

and Epstein 1981; Post 2002). In previous work, we found that $\delta^{13}C$ values in salt marsh grazing and epigeic webs differed substantially for at least part of the summer (Wimp et al. 2013). In the present study, we examined both $\delta^{13}C$ to examine whether *Pardosa* diet changes across different size classes, and $\delta^{15}N$ to confirm trophic position. We had to combine individuals of the smaller size classes to obtain sufficient tissue for stable isotope analysis, but only individuals collected in the same plot on the same day were combined. We then ground samples and obtained their isotopic values as described in Wimp et al. (2013).

Statistical analyses

We performed an ANOVA on *Pardosa* $\delta^{15}N$ values across the different collection months to confirm predator status and see how this status might change during the season or depending on the *S. alterniflora* habitat type (center, intermediate, edge; Appendix B). In all ANOVA and regressions involving *Pardosa* isotopes, we treated all *Pardosa* recovered from a plot as repeated measures from that plot. We also examined how *Pardosa* $\delta^{15}N$ changed with spider size using a correlation analysis (Appendix B).

To examine how multichannel omnivory was related to the size of *Pardosa*, we used carbon stable isotopes. Initially, we collected *Pardosa* from different habitats, but we wanted to determine whether carbon isotopes differed according to habitat or could be combined. Thus, we performed a repeated measures ANOVA by SAS proc mixed (SAS 2002), which showed that habitat within block had no effect on the $\delta^{13}C$ of grazing prey ($F_{2,17.1} = 0.03$, $P = 0.97$), epigeic prey ($F_{2,14.3} = 2.45$, $P = 0.12$), or *Pardosa* ($F_{2,12} = 1.32$, $P = 0.30$), and that habitat had no effect on *Pardosa* size ($F_{2,15.5} = 1.24$, $P = 0.32$). Thus, the different habitats in each of our transects did not affect $\delta^{13}C$ isotopic ratios and were combined for further analysis.

We were able to collect a large range of *Pardosa* sizes only in June and July (Appendix A), so we examined the relationship between $\delta^{13}C$ and size only during those months. Because we had to combine individuals of the smaller size classes (1–3) to obtain sufficient tissue for stable isotope analysis (explained above), we were not able to collect enough individuals of the smaller size classes to obtain even a single sample for the months of August and September, and we only had a single sample in size class 4 (Appendix A, Figs. A1, A2). We performed separate ANOVA analyses in June and July with size class as a discrete explanatory variable and $\delta^{13}C$ as the response. We included only size classes for which we had at least five measurements in a given month. Variances were not equal across size classes, so the ANOVA was performed using separate variance estimates for each size class with SAS proc mixed.

We used the IsoError mixing model (Phillips and Gregg 2001) to estimate percent consumption from the two food webs in each of the 4 months, based on $\delta^{13}C$ values of *Pardosa* and their grazing and epigeic prey. Separate estimates were made for small *Pardosa* (size classes 1, 2 and 3), and large *Pardosa* (size classes 5 and 6). We omitted size class 4 to maximize the contrast between the two size categories and also because this size class had the fewest samples (it was absent or had a single sample in June, August, and September). These models assumed that *Pardosa* $\delta^{13}C$ values were 0.5‰ higher than those of their prey, based on studies of congeneric *Pardosa* species by Oelbermann and Scheu (2002) and Mellbrand and Hamback (2010). IsoError takes into account the amount of data available and variation within those data to calculate confidence intervals for diet estimates.

To examine how prey density and the size of *Pardosa* might influence their reliance on the grazing and epigeic food webs, we first examined whether the densities of grazing and epigeic prey and the grazer/epigeic prey ratio changed according to month using a one-way ANOVA. To assess the effect of prey densities and *Pardosa* size on *Pardosa* diet ($\delta^{13}C$ value), we performed regressions separately on data from June and July, the 2 months in which a wide range of *Pardosa* size classes coexisted. Our response variable was *Pardosa* $\delta^{13}C$, and explanatory variables consisted of log-transformed *Pardosa* dry weight, grazer density, and epigeic feeder density, as well as all interactions. We removed non-significant terms from the model in a stepwise fashion until only significant terms remained.

Results

Trophic position of *Pardosa*

Pardosa $\delta^{15}N$ values changed according to month of study, but not in a consistent way ($F_{3,155=12.77}$, $P < 0.0001$, Appendix B1). We also found that the $\delta^{15}N$ values for *Pardosa* changed according to habitat and were greatest in the intermediate *S. alterniflora* along tidal creeks relative to *S. alterniflora* in the center of a patch or along the high-elevation habitat edge ($F_{2,10.3} = 17.93$, $P = 0.0004$, values for other taxa in Appendix B2). Finally, we found that *Pardosa* $\delta^{15}N$ values increased with an increase in spider weight ($\rho = 0.572$, $P < 0.0001$, Appendix B3).

Multichannel omnivory by *Pardosa* of different sizes

We found that large *Pardosa* consume substantial amounts of both grazing and epigeic prey, while small *Pardosa* primarily consume epigeic prey. The largest *Pardosa* individuals, those with dry weights greater than 4 mg, had carbon isotopic values generally intermediate between those of grazing and epigeic prey during all 4 months (Fig. 1) indicating that large *Pardosa* are consistent multichannel omnivores throughout the season. The $\delta^{13}C$ values for small *Pardosa* were lower than large *Pardosa* in both June ($F_{2,35} = 11.19$, $P = 0.0002$) and July ($F_{4,50} = 6.20$, $P = 0.0004$), the only months when large and small *Pardosa* coexisted (Fig. 2). During both June and July, some small *Pardosa* had $\delta^{13}C$ values in the same range as large *Pardosa*, but others had $\delta^{13}C$ values much lower than those of any large individual (Fig. 1), indicating a much heavier reliance on epigeic prey than grazing prey. Mixing models also confirmed that large and small *Pardosa* consumed very different diets. Using mixing models, we estimated that diets of large *Pardosa* (size classes 5 and 6) contained roughly twice as much grazing prey as small *Pardosa* (size classes 1, 2, and 3). Models estimated that in June, 41% of the carbon in tissues of large *Pardosa* came from the grazing food channel, while only 19% of carbon in small *Pardosa* came from that channel (Fig. 3). The 95% confidence intervals for those estimates overlapped by only two percent. Similarly, in July, we estimated that the diets of large *Pardosa* contained roughly three times as much grazing prey as small *Pardosa*. Models estimated that in July, 43% of the carbon in tissues of large *Pardosa* came from the grazing channel, while only 15% of carbon in small *Pardosa* came from this channel, and confidence intervals overlapped by less than one percent. In August and September, the fraction of grazing prey in the diets of large *Pardosa* increased to 60% (Fig. 3). There were too few small *Pardosa* in those later months to estimate diets.

These changes in *Pardosa* diet happened even though prey carbon isotopic values were relatively consistent throughout the season. Mean $\delta^{13}C$ of prey in the grazing channel varied less than 0.33‰ throughout the study. Prey values in the epigeic channel were also very similar in June, August, and September, differing by at most 0.43‰, but $\delta^{13}C$ in July was 0.73‰ higher than in any other month (Fig. 1). These results contrast with our earlier study (Wimp et al. 2013) in which $\delta^{13}C$ values for epigeic feeders changed by 3.07‰ over the course of the season and changed in a consistent way; epigeic prey fed primarily on algae early in the season and then switched to the *Spartina* web later in the season. However, in the present study, epigeic prey continued to use algal resources throughout the growing season (Fig. 1). Such variation in the use of algal detrital webs (e.g. between our last study and this current study) may be driven by the enormous annual variation in benthic microalgal abundance (Van Raalte et al. 1976). Within each sample date, $\delta^{13}C$ of epigeic prey varied much more than $\delta^{13}C$ of grazing prey (Fig. 1), possibly reflecting the greater variety of resources at the base of the epigeic web, but did not become more enriched as the season progressed.
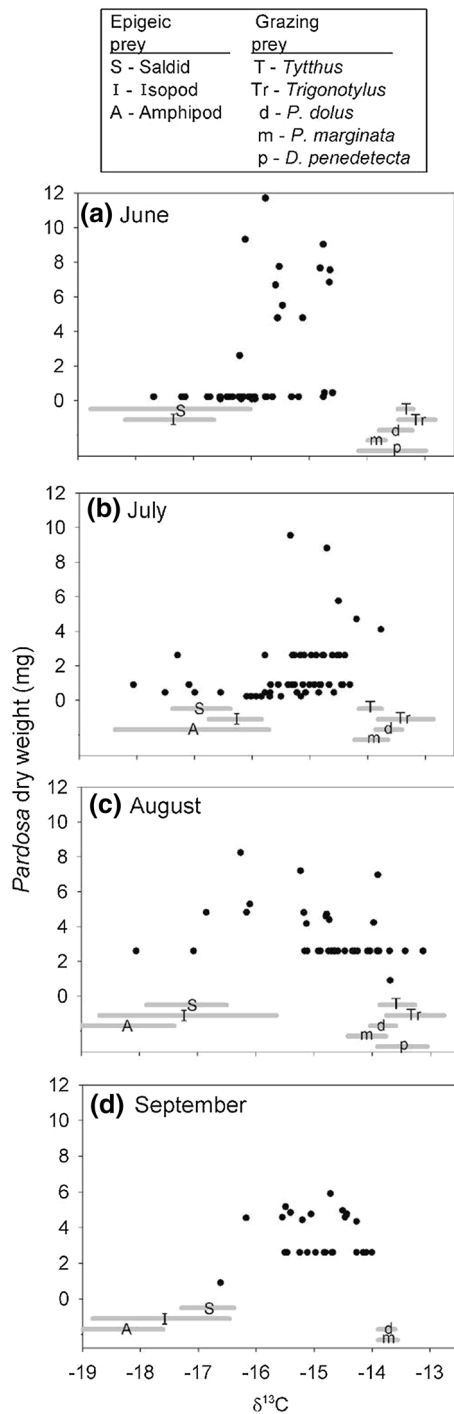
Fig. 1 Carbon isotopic values, δ^{13}C, of *Pardosa* (black circles) during each of the 4 months **a** June, **b** July, **c** August, and **d** September. Gray bands show mean ± standard deviation of δ^{13}C for prey taxa, with letters identifying taxa described in the figure legend. *Pardosa* dry weights represent median values for size classes (described in Appendix A) except for individuals > 4.0 mg (size class 6), in which actual dry weights are used because each data point represents a single *Pardosa* individual
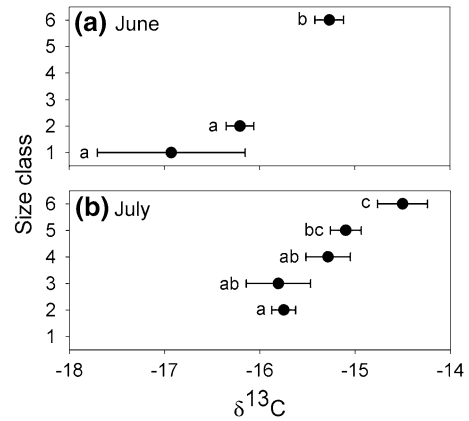

Fig. 2 Mean δ^{13}C ± standard error for *Pardosa* of different size classes in **a** June and **b** July. Letters indicate significant differences between means, $\alpha = 0.05$. Means are shown only for size classes for which there were at least five observations
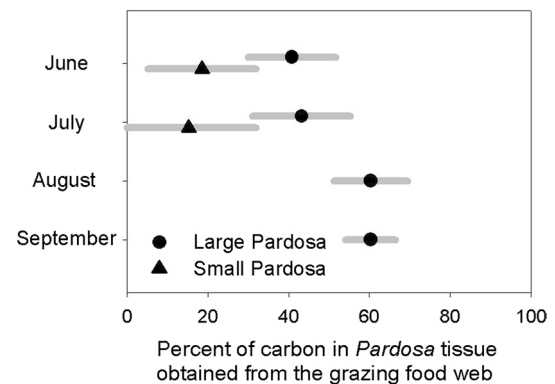

Fig. 3 IsoError mixing model estimates and 95% confidence intervals for percent of carbon in *Pardosa* tissue obtained from prey in the grazing food web by small (≤ 0.6 mg, size classes 1–3, black triangles) and large (> 1.3 mg, size classes 5–6, black circles) *Pardosa* during each of the four sample months. Small *Pardosa* were numerous only in June and July

Impact of prey density and *Pardosa* size on multichannel omnivory

Densities of grazers, epigeic feeders, and their log ratio differed significantly among months (grazers $F_{3, 35.3} = 4.02$, $P = 0.015$; epigeic feeders $F_{3, 34.9} = 3.03$, $P = 0.042$; ratio $F_{3, 35.2} = 7.18$, $P = 0.0007$, Appendix C). When grazing and epigeic prey were examined separately in June, *Pardosa* δ^{13}C was significantly correlated with both *Pardosa* weight ($F_{1,36.6} = 18.04$, $P = 0.0001$) and grazer density ($F_{1,12.4} = 17.62$, $P = 0.0012$), but not epigeic feeder density. When examined as a ratio, we found that the ratio of grazing to epigeic prey did not affect *Pardosa* δ^{13}C in June ($F_{1,11.9} = 2.76$, $P = 0.12$). When grazing and epigeic prey were examined separately in July,

Pardosa δ^{13}C was significantly correlated with *Pardosa* weight ($F_{1,40.1} = 32.71$, $P < 0.0001$), epigeic density ($F_{1,7.3} = 13.05$, $P = 0.008$), and their interaction ($F_{1,40.4} = 27.02$, $P < 0.0001$), but not with grazer density. When examined as a ratio in July, we found that *Pardosa* δ^{13}C was significantly correlated with the grazer-to-epigeic ratio ($F_{1,10.2} = 10.19$, $P = 0.0093$), log *Pardosa* weight ($F_{1,44.9} = 6.07$, $P = 0.018$), and their interaction ($F_{1,43.7} = 13.65$, $P = 0.0006$; Fig. 4). This interaction in July occurred because small *Pardosa* were relatively unaffected by the grazer/epigeic prey ratio, but the δ^{13}C value for larger *Pardosa* increased with an increase in grazing prey density (Fig. 4; for each *Pardosa* individual collected in July, the figure shows an individual's weight (mg), δ^{13}C value, and the grazer/epigeic ratio for prey found in the plot where that *Pardosa* individual was collected). Thus, the larger *Pardosa* were better able to track changes in prey density than small *Pardosa*.

Discussion

Spiders are abundant predators that have been shown to link grazing and epigeic webs in natural and managed ecosystems (Wise et al. 2006; Settle et al. 1996; Perkins et al. 2018), and early season feeding from the epigeic web can
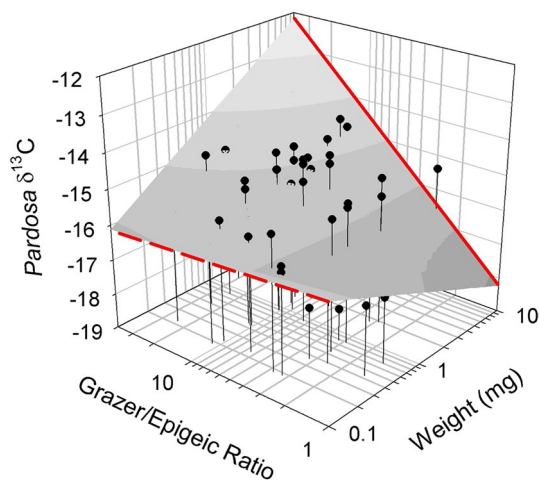

Fig. 4 *Pardosa* diet changes as a result of grazing/epigeic prey density and *Pardosa* size. For each *Pardosa* individual collected in July, the figure shows that individual's weight (mg), δ^{13}C value, and the grazer/epigeic ratio for prey found in the plot where that *Pardosa* individual was collected. Using the smallest and largest *Pardosa* as examples, for the smallest *Pardosa* individuals (red dashed line in figure), their δ^{13}C did not change in response to changes in the grazer/epigeic ratio. For the largest *Pardosa* individuals (red solid line in figure), their δ^{13}C decreased with a decrease in the grazer/epigeic ratio. Thus, diets of small *Pardosa* were relatively unaffected by the ratio of grazers and epigeic feeders (red dashed line), whereas larger *Pardosa* adjusted their consumption as the ratio changed (red solid line) (color figure online)

increase prey suppression on the grazing food web later in the season (Rypstra et al. 1999; Rypstra and Marshall 2005; Sunderland 1999; Wise et al. 1999). However, the impacts of spiders on top-down control of the grazing food web can be temporally variable (DeBach and Rosen 1991). We found that *Pardosa* diet changes as individuals grow larger during the season, and that these changes in diet are not due solely to variability in prey population densities.

We found that multichannel omnivory is influenced by spider size; small spiders rely more heavily on the epigeic food web, whereas large spiders remain multichannel omnivores throughout the season yet increase their use of grazing prey. Importantly, these results were not driven by changes in δ^{13}C values for grazing or epigeic prey, which remained relatively consistent across months. Additionally, the ratio of grazing to epigeic prey did not change in a consistent way across the season (e.g., more grazing prey as the season progressed), yet large *Pardosa* obtained more of their carbon from the grazing food web as the season progressed. Our findings here may help to explain why spider initiation of trophic cascades can be temporally variable, since spider size affects their ability to consume grazing prey. During June and July, months when large and small *Pardosa* coexisted, small *Pardosa* had lower δ^{13}C values than did large *Pardosa*, indicating heavier dependence on epigeic prey. Mixing models estimated that 40% to 60% of the carbon in tissues of large *Pardosa* came from the grazing channel, whereas small *Pardosa* obtained less than 20% of their carbon from that channel. Thus, size structure of the *Pardosa* population may affect suppression of grazing prey in June and July.

The reliance of small *Pardosa* on epigeic prey means that the density of epigeic prey early in the growing season could impact the strength of trophic cascades later in the season via changes in *Pardosa* density. For example, abundant epigeic prey in June and July could lead to especially high densities of small *Pardosa*, which could exert strong predation pressure on grazing prey as *Pardosa* grow, thereby increasing chances for trophic cascades later in the season as envisioned by Polis and Strong (1996) and shown in other systems (e.g. Settle et al. 1996). However, a shortage of epigeic prey early in the growing season could depress *Pardosa* density later in the growing season, which could dampen a late-season trophic cascade even if grazing prey is abundant. Numerous other studies have found variation in the top-down effects of spiders (consumptive or non-consumptive) on herbivores that indirectly affect primary producers across different studies (spiders affect herbivory with subsequent impacts on primary producers Hlivko and Rypstra 2003; Rypstra et al. 1999; Rypstra and Marshall 2005; Sunderland 1999; Wise et al. 1999) (spiders dampen trophic cascades Birkhofer et al. 2008; Finke and Denno 2004; Halaj and Wise 2002; Hogg and

Daane 2015; Sanders et al. 2011), and also within the same study (e.g. Gratton and Denno 2003; Murphy et al. 2012; Snyder and Wise 2001). Size structure of the spider population and the abundance of early season epigeic prey may thus help us to understand the variable ability of spiders to initiate trophic cascades in the grazing food web.

Why small *Pardosa* rely more heavily on the epigeic food web is unknown, but there are several possible mechanisms. First, small *Pardosa* may be physically unable to capture grazing prey, but the wide range of $\delta^{13}C$ values exhibited by small *Pardosa* suggests that this is unlikely. Second, there may be a nutritional advantage in epigeic prey for small *Pardosa*. Other *Pardosa* species are capable of selecting prey based on nutritional needs (Mayntz et al. 2005) and those needs can change over time (Bressendorff and Toft 2011). However, a nutritional need for epigeic prey would not likely produce the wide range of diets that we observed in small *Pardosa*. Third, and we believe the most likely explanation, is that the ecology of fear explains why small *Pardosa* avoid habitats with grazing prey. Grazing prey and epigeic prey are vertically stratified in the *Spartina* marsh with epigeic prey found near the soil beneath the thatch layer and grazing prey found above the thatch (Denno 1977). Thatch is known to protect small *Pardosa* not only from cannibalism by larger *Pardosa*, but also cannibalism by small *Pardosa* (Langellotto and Denno 2006). Our results show that large *Pardosa* feed on grazing prey more than small *Pardosa* and thus we suggest that small *Pardosa* may avoid the habitat where grazing prey and large *Pardosa* are found due to the risk of cannibalism. However, behaviors of small *Pardosa* may be variable, with some bold individuals venturing above the thatch layer, while others remain hidden in the thatch.

Intimidation of potential prey is known to have as great an effect on trophic cascades as direct consumption of prey in many predator–prey systems (Preisser et al. 2005). A number of studies have examined the impacts of non-consumptive effects on herbivores (reviewed by Finke and Snyder 2010) and detritivores (reviewed by Sitvarin et al. 2016); while we did not investigate non-consumptive effects directly, our results suggest that they may lead to changes in resource use by conspecific predators and that this should be investigated. In both June and July, some small *Pardosa* had very low $\delta^{13}C$, but others had $\delta^{13}C$ in the same range as large individuals, indicating the same mixture of grazing and epigeic prey. This overlap with large *Pardosa* could not occur if small individuals were unable to capture grazing prey, but would occur if some especially bold small individuals ventured into the more dangerous habitat above the thatch, or if grazing prey were driven into the thatch to avoid predators. However, small *Pardosa* may pay a price for increased herbivore consumption in the form of increased cannibalism, as has been shown for other *Pardosa* species (Buddle et al. 2003; Rickers and Scheu 2005). For example, Samu et al.

(1999) found that cannibalism between individuals could be explained by differences in body size for *Pardosa agretis*; large spiders could cannibalize smaller spiders if they were 2× larger, and if large spiders were 4× larger, then cannibalism was almost always the outcome. In June, our largest spiders (size class 6) were more than 30× larger than the smallest spiders (size class 1), so behavioral modifications to avoid cannibalism seem likely. More importantly, previous studies have found that larger spiders (conspecific or different species) can impact the spatial distribution of smaller spiders, because smaller spiders respond to cues from larger spiders by avoiding those areas (Persons and Rypstra 2001; Folz et al. 2006; Rypstra et al. 2007). If we consider only data from July when we have adequate representation of both large and small spiders from the same plots, we found that the $\delta^{13}C$ values of large spiders reflected increased use of the more abundant grazing food channel, whereas small spiders were unaffected by this change in prey densities. Thus, unlike the larger spiders, smaller spiders are less capable of shifting to the most abundant prey and we suggest that this may be related to the ecology of fear, specifically fear of becoming prey for larger spiders.

Studies of predator diversity and its effects on prey suppression have largely focused on species richness (Finke and Snyder 2010), but intraspecific interactions, including cannibalism, can alter prey suppression (Takizawa and Snyder 2011, and references therein; Toscano and Griffen 2012). Cannibalism is common among spiders (Wise 2006), thus dietary shifts to avoid cannibalism similar to that of *Pardosa* may be widespread and have important implications for both food web theory and biological control of pest herbivores. The importance of size structure on diet has been frequently studied in aquatic systems, especially fish, where morphological constraints such as gape limitation alter prey usage (e.g. Scharf et al. 2000). But there is a need to understand how intraspecific interactions may affect the diet choice of predators more broadly to understand when and how predators initiate trophic cascades (Miller and Rudolf 2011). Here we show that size structure can affect diet even when morphological constraints are not present; thus, the ability of multichannel omnivores to fully use different prey resources may be constrained by the size of the predator and not simply the abundance of prey.

Author contribution statement All authors conceived the ideas, designed methodology, and collected the data. DL performed the statistical analyses. SM and GW led the writing of the manuscript; all authors contributed critically to the drafts and gave final approval for publication.

Compliance with ethical standards

Conflict of interest The authors declare no conflicts of interest.

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