



Contents lists available at ScienceDirect

## Current Research in Insect Science

journal homepage: [www.elsevier.com/locate/cris](http://www.elsevier.com/locate/cris)

## Prey identity but not prey quality affects spider performance

Gina M. Wimp<sup>a,\*</sup>, Danny Lewis<sup>a</sup>, Shannon M. Murphy<sup>b</sup><sup>a</sup> Department of Biology, Georgetown University, Washington, DC, USA<sup>b</sup> Department of Biological Sciences, University of Denver, Denver, CO, USA

## ARTICLE INFO

## Keywords:

Diet  
 Intraguild predation  
 Fertilization  
 Intertidal salt marsh  
 Generalist predator

## ABSTRACT

Increasing host plant quality affects higher trophic level predators, but whether such changes are simply a result of prey density or are also affected by changes in prey quality remain uncertain. Moreover, whether changes in prey quality affect measures of predator performance is understudied. Using a combination of field and greenhouse mesocosm experiments, we demonstrate that the survival and body size of a hunting spider (*Pardosa littoralis* Araneae: Lycosidae) is affected more by prey species identity than the trophic level of the prey. Furthermore, increasing host plant quality does not necessarily propagate through the food web by altering prey quality. While changes in plant quality affected spider body mass, they did so in opposite ways for spiders feeding on *Prokelisia* (Hemiptera: Delphacodes) herbivores relative to *Tythus* (Hemiptera: Miridae) egg predators, and had no impact on spider body mass for two additional species of intraguild prey. These changes in body mass were important because greater body mass increased spider egg production. To examine the generality of this pattern, we reviewed the literature and found a consistent positive relationship between female body size and egg production for *Pardosa* species, indicating that body size is a reliable proxy for fitness. While many studies emphasize the importance of nitrogen to arthropod diets, this focus may be driven largely by our understanding of herbivore diets rather than predator diets. Thus, the positive impact of host plant quality on higher trophic level predators appears to be driven more by altering prey composition, density, and availability rather than simply providing predators with more nutritious prey.

## Introduction

An increase in primary producer quality, such as an increase in percent nitrogen or phosphorus, supports greater herbivore biomass, which in turn affects the abundance, diversity and biomass of higher trophic level predators and parasitoids (Siemann 1998; Haddad et al., 2000; Cebrian et al., 2009). Herbivores, particularly in terrestrial habitats, are strongly limited by producer quality and an increase in nitrogen and phosphorus content increases herbivore metabolism and growth (Cebrian et al., 2009). An increase in primary producer productivity may also expand the number of feeding niches available to herbivores by altering plant architecture (Lawton 1983), thus increasing herbivore diversity. Predators may respond positively to nutrient addition via an increase in herbivore prey density (Abrams 1995; Siemann 1998), altered prey composition that leads to more diversified prey species (Kneitel and Miller 2002; Bumpers et al., 2017), or an increase in prey quality (Mayntz and Toft 2001; Mayntz et al., 2003, reviewed by Wilder 2011). However, few studies have disentangled whether shifts in prey species composition or prey quality *per se* impact predator performance.

While herbivore nutrition has received far more attention, spiders are also affected by prey quality (reviewed by Wilder 2011). For example, the nutritional quality of the prey can affect spider growth and fecundity (Denno et al., 2002, Mayntz and Toft 2000, 2001, Wilder et al., 2010), and different prey species differentially affect spider performance (reviewed by Wilder et al., 2010). Moreover, the factors that have long been known to affect the nutrition of herbivores also affect their spider predators (Schmitz et al., 2010). Notably, similar to the majority of predators, spiders are generalists with a wide diet breadth (Pekár and Toft 2015) and are therefore model organisms for understanding the factors that impact predator nutrition. While spiders may share some aspects of their feeding ecology with herbivores, extraoral digestion also distinguishes spiders from many herbivores. For example, herbivores frequently feed on plant tissues that are mechanically or chemically difficult to process (Price et al., 2011). However, spiders liquify their prey by injecting enzymes, so they are able to largely separate edible from inedible prey tissues (Cohen 1995; Wilder 2011). While extraoral digestion still comes with an energetic cost, spider predators reduce the amount of inedible prey tissues they have to process internally as an insect herbivore would and can even selectively liquify different prey parts based-on digestibility (reviewed by Wilder et al., 2010).

\* Corresponding author.

E-mail address: [gmw22@georgetown.edu](mailto:gmw22@georgetown.edu) (G.M. Wimp).<https://doi.org/10.1016/j.cris.2021.100013>

Received 28 December 2020; Received in revised form 11 March 2021; Accepted 15 March 2021

2666-5158/© 2021 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license

<http://creativecommons.org/licenses/by-nc-nd/4.0/>

Differences in prey quality may also help to explain the benefits of eating other carnivores via intraguild predation or cannibalism (Wise 2006). For example, carnivores typically have higher nitrogen content than herbivores (Denno and Fagan 2003; Fagan and Denno 2004; Fagan et al., 2002; Matsumura et al., 2004; Wilder and Eubanks, 2010), and spider fitness can be strongly affected by nitrogen limitation (Uetz et al. 1992; Toft 1999). One strategy for omnivorous predators to overcome nitrogen limitation from herbivorous prey is to feed on intraguild prey with higher nitrogen content, and high protein diets often increase predator growth rates (Strohmeyer et al., 1998).

Consistent with the observation that higher prey quality positively impacts carnivores, plant fertilization has been shown to have strong, consistent impacts on higher trophic levels predators in a salt marsh system. In previous studies, we have manipulated nutrient inputs into a salt marsh ecosystem and have found that arthropod predators as a group were more consistently and positively impacted by increased plant quality relative to herbivores (Wimp et al., 2010; Murphy et al., 2012; Wimp et al., 2019). Notably, predators often had a sustained, positive response to nutrient additions, whereas herbivore responses to nutrient additions varied greatly through time and often did not differ from controls. Moreover, some of the most abundant predators in the salt marsh are spiders that are multichannel omnivores that feed on prey from both the live plant (grazing) and epigeic (algal and detrital) food webs (Wimp et al., 2013; Murphy et al., 2020). However, epigeic prey do not demonstrate a response to nutrient addition (Wimp et al., 2019). Thus, the strong predator response to nutrient addition seems puzzling; predators are positively and consistently affected by nutrient additions even though their prey are only intermittently (grazing) or not affected (epigeic) by nutrient additions (Wimp et al., 2010; Murphy et al., 2012; Wimp et al., 2019). While prey abundance is one way that predators may be indirectly affected by nutrient addition, other mechanisms may be at play.

Fertilization could impact predators by increasing prey quality; however, this mechanism cannot be uncoupled from differences in prey behavior that make them more or less susceptible to predation. Previous work in the salt marsh system has found that predators do not necessarily always do best on high nitrogen diets and that the behaviors of intraguild prey are also important (Matsumura et al., 2004). For instance, *Pardosa littoralis* fed on a mirid egg predator (*Tytthus vagus*) perform well, but they perform poorly and have low survivorship when fed a diet of sheet web-building spiders (*Grammonota trivittata*, Matsumura et al., 2004). Matsumura et al. (2004) suggested that these results depended greatly on intraguild prey behavior; while *Tytthus* was lower in %N than most other marsh predators, this mirid egg predator is easy for *Pardosa littoralis* to catch, whereas *Grammonota* web-building spiders have high %N but are challenging to catch. Indeed, previous studies have shown that while nitrogen content is important, prey behavior and toxicity affect prey choice by spiders (Toft et al. 1999; Toft and Wise 1999; Theodoratus and Bowers 1999). Thus, comparing how predators perform when fed different prey species is less of a test of prey quality and more of a test of differences in prey behavior and toxicity that may impact predator prey selection. In order to control for these differences in prey behavior and prey toxicity, it becomes important to increase the quality of individual prey species and examine the impact of increased prey quality on intraguild predator performance. Lastly, researchers often assume that increased body size is a proxy for performance and fitness, but this relationship is actually rarely tested specifically and has never been studied for *Pardosa littoralis*.

One of the major goals in studying spider ecology is to examine how prey nutrient content, not simply prey species composition, affects spider performance (Wilder 2011). We had three research objectives. First, to determine the effect of *Spartina alterniflora* (smooth cordgrass) fertilization on *Pardosa littoralis* survival and nutritive quality. Such research is especially needed because arachnids can respond very differently to nitrogen limitation in their prey relative to other predatory arthropods (Fagan and Denno 2004). Second, to test if there was an interaction

between different prey species and fertilization on *Pardosa littoralis* survival, body size, and nutritive quality. Third, to determine whether female body size predicts potential fecundity for *Pardosa* species and thus could be used as a proxy for lifetime fitness. We therefore conducted an experiment where we reared *Pardosa littoralis* on five different prey species for which we attempted to increase the quality of prey food via fertilization. This study design allows us to test how increasing prey quality affects predator fitness without confounding changes in prey quality with changes in prey behavior or toxicity as is the case if we only compare different prey species that vary in quality. Additionally, because we reared *Pardosa* to adulthood, we were able to examine how bottom-up changes in host plant quality could impact spider body size, nutritive quality, survival and fecundity. Finally, we conducted a literature search to examine the extent to which changes in body size within the genus *Pardosa* translated into measurable impacts on fecundity.

## Methods

### Study system

We conducted the field component of our research at a salt marsh located in Sheepshead Meadows, which is part of the New Jersey Department of Environmental Protection's Great Bay Wildlife Management Area and the Jacques Cousteau National Estuarine Research Reserve (39°33'09.5"N 74°20'09.1"W), USA. This salt marsh is composed of large swaths of the cordgrass *Spartina alterniflora* (Family: Poaceae; hereafter *Spartina*), which is the only host plant for the dominant herbivores in the system, both of which are *Prokelisia* planthoppers (*Prokelisia dolus* and *P. marginata*; Hemiptera: Delphacodes). *Prokelisia* planthoppers are fed upon by the specialist predator *Tytthus vagus* (Hemiptera: Miridae), which feeds only on planthopper eggs, and *Grammonota trivittata* (Araneae: Linyphiidae), which is a generalist web-building spider. The saldid *Saldula interstitialis* (Hemiptera: Saldidae) is a predator of epigeic prey. All of these species are prey for the top intraguild predator in the system *Pardosa littoralis* (hereafter *Pardosa*; Araneae: Lycosidae), which is a hunting spider. Previous studies in this system have identified the primary components of *Pardosa* diet, both through stable isotope (Wimp et al., 2013; Murphy et al. 2019), as well as field and lab mesocosm experiments (Denno et al. 2003, Gratton et al. 2003, Finke and Denno 2004, 2005, 2006).

### Mesocosm establishment and field manipulation

In the greenhouse at Georgetown University (Washington, D.C.) we established 120 mesocosms (30 cm in height and 7.5 cm in diameter) that each housed an individual *Pardosa* spider. Mesocosms were made of cellulose butyrate plastic and we created four gauze-covered ports (6.5 cm diameter) and also covered the top of the mesocosm with gauze to ensure proper ventilation. We pressed each mesocosm into a sand-filled flower pot that was embedded in a large plastic bin filled with water. We collected *Spartina* plants to be the basal resource in the mesocosms from our field site on May 10, 2012 and transplanted the plants into greenhouse mesocosms the following day. Each mesocosm plot initially contained 4–5 *Spartina* culms. For the next 51 days we continually removed any arthropods that we found in the mesocosms, which consisted mostly of planthopper nymphs that likely hatched from eggs that were laid in culms before we collected the plants. We fertilized half of the mesocosms ( $n=60$ ) that would later house prey from our fertilization treatment and our fertilization treatment in the greenhouse was at the same level as the field plots.

In the field, we established 5 plots that were each 10m<sup>2</sup> and fertilized them with a total of 180 g/m<sup>2</sup> of ammonium nitrate and 60 g/m<sup>2</sup> triple phosphate over a 4-week period in May of 2012 (plots were fertilized once per week). These fertilized plots are where we collected arthropod prey and *Pardosa* for the fertilized, high-nutrient mesocosms.

We collected control arthropod prey and *Pardosa* for the control mesocosms from areas at least 5 m away from the fertilized plots. We did this to maximize differences in prey quality: high quality prey were collected from fertilized plots and transferred to mesocosms with fertilized *Spartina*, and low quality prey were collected from a control plot and reared in mesocosms with *Spartina* that was not fertilized. We collected *Pardosa* and prey from the field on June 28, 2012 from both control and fertilized plots and transferred them to mesocosms in the Georgetown University greenhouse the following day. We collected additional prey from control and fertilized field plots weekly on July 3, 11, 18 and 25, 2012. In the greenhouse, *Pardosa* in the control mesocosms were fed prey from the control plots and *Pardosa* in the fertilization treatment mesocosms were fed prey from the fertilization plots.

### Experimental design

In addition to the fertilization treatment (control vs. fertilized), we also had 5 *Pardosa* diet treatments to form a 2×5 factorial study design that was replicated 12 times (2 fertilization treatments × 5 diet treatments × 12 replicates = 120 mesocosms). *Pardosa* were fed a single prey species or starved during the duration of the experiment. The 5 diet treatments were a starvation treatment, 3 treatments in which *Pardosa* was fed a single predator species (the generalist web-building spider *Grammonota trivittata*, the generalist salpid *Salidula interstitialis*, or the planthopper egg specialist *Tythus vagus*), and 1 herbivore treatment (*Prokelisia* planthoppers that were a mixture of *Prokelisia dolus* and *P. marginata* found in the field for each collection time). For the predator prey we only used adult life stages, but the planthopper diet consisted of the seasonally available life stages found in the field.

The *Pardosa* we used to stock the mesocosms were all mid-stage juveniles. We used *Pardosa* in this life stage because it is the predominant stage found during most of the *Spartina* growing season when all prey types are active. Additionally, small spiderlings travel on the back of their mother, and are at high risk of cannibalism once they become independent, both of which can affect their behavior and feeding. Differences in feeding behavior between males and females are also not as pronounced during the juvenile stage but will become very pronounced once the female begins carrying an egg sac or spiderlings on her back. While we collected *Pardosa* as juveniles, we reared them all the way to the adult stage to examine the impacts of prey type and quality on fitness.

We restocked mesocosms with prey every 3–5 days whenever prey in mesocosms became scarce; we monitored the mesocosms to ensure that prey in the mesocosms remained alive (*Pardosa* will not eat dead prey) and also that the prey items were disappearing as *Pardosa* ate them. We removed most *Pardosa* from mesocosms on July 30, after 32 days of feeding. Some prey were very scarce in the marsh on July 18, so we were forced to remove *Pardosa* from 3 treatments early; *Pardosa* were removed on July 23 (after 25 days of feeding) from: control *Salidula* mesocosms and from both control and fertilized *Tythus* mesocosms. After removing *Pardosa* from mesocosms in the greenhouse, we immediately froze them and then later dried them at 60 °C for 3 days and then weighed each individual; when we found *Pardosa* females with egg sacs, we counted all of the eggs in her egg sac as well. To assess the effects of the greenhouse environment on the *Spartina* plants and the effectiveness of our fertilization treatment in the greenhouse, we harvested the *Spartina* in the 12 starvation mesocosms ( $n=6$  control,  $n=6$  fertilization) on July 31 and dried them at 60 °C for 3 days. We then ground the arthropod and plant samples and obtained their percent element values of nitrogen and carbon as described in Wimp et al. (2013).

We examined whether or not our data met normality and equality of variance assumptions using p-p and residual plots. Only, C/N data did not meet assumptions initially, but met assumptions after a log transformation. Differences in percent survival for *Pardosa* across prey species were analyzed using a Chi-square. To examine the impacts of fertilization and prey species identity on *Pardosa* body mass and C:N ratio, we

used a two-factor ANOVA. Similarly, we used a two-factor ANOVA to examine differences in C:N ratio across different prey species under control and fertilized treatments. Post-hoc comparisons were made using Tukey's HSD. To examine the effects of *Pardosa* body mass on egg production, we used a linear regression analysis. We conducted all statistical analyses in JMP pro 14 (SAS Institute, 2019). All of our data is available in the online Supplement.

### *Pardosa* fecundity and literature review

To quantify fecundity for *Pardosa* in our study, at the end of our greenhouse experiment when we found female *Pardosa* with egg sacs, we weighed the females after drying (to the nearest 0.01 mg) and also counted all of the eggs in each egg sac. We did not use females from the "starvation" treatment for this analysis because none produced egg sacs. We then reviewed the literature to determine the relationship between female body size and egg production for *Pardosa* species to test if body size is generally a reliable proxy for fitness.

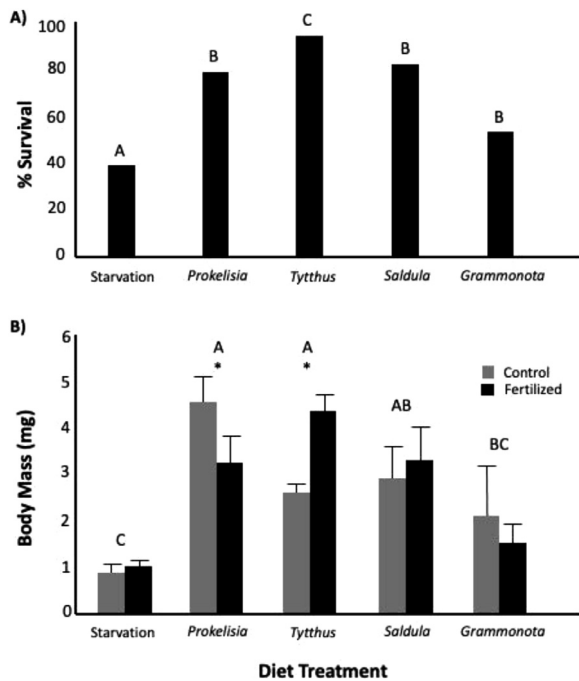
We reviewed the literature for other studies that have investigated the relationship between female body size and fecundity for spiders in the genus *Pardosa* on October 27, 2020. We performed keyword searches on Web of Science and Google Scholar using various combinations of the following terms: egg\*, fecundity, fitness, lifetime fitness, *Pardosa*, and realized fitness. In our initial search we found 122 papers plus an additional 14 papers that we found cited within those papers, for a total of 136 papers. We then read all of the papers and removed any papers that were not in English, did not include empirical data, and/or did not focus on a species of *Pardosa*. We then limited the results to studies that ran a regression of female body size by potential fecundity. Following Awmack and Leather (2002), potential fecundity is a measure of the number of eggs an individual produces, while realized fecundity refers to the number of offspring produced. This review narrowed the pool of 136 papers to 16 papers. However, some studies reported results for more than *Pardosa* species or for more than one measure of female body size, leading to multiple cases per paper. Thus, we collected data for 42 cases on 19 *Pardosa* species. Female body size was measured in several different ways including body mass, prosoma/carapace width, cephalothorax length, etc.; we recorded the terms as the authors used them, but for simplicity report the data using a consistent terminology.

### Results

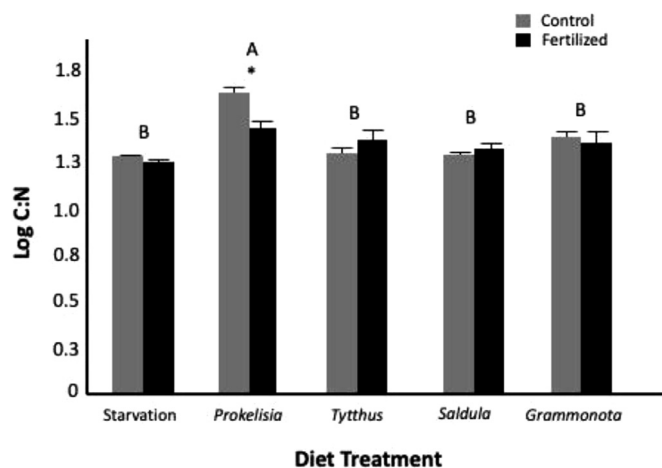
Our mesocosms successfully mimicked field conditions for *Spartina* percent nitrogen as the percent nitrogen of *Spartina* was 1.5% for plants in the control and 3.0% for plants in the fertilization treatment, which is similar to results we have found in our field plots for July in previous years (Wimp et al., 2010; Murphy et al., 2012).

Percent survival of *Pardosa* differed significantly across diet treatments ( $n=120$ ,  $df=4$ ,  $\chi^2=24.66$ ,  $P<0.0001$ , Fig. 1A) with higher survival when fed *Tythus* than when fed the other diets ( $P<0.05$ ) and lowest survival in the starvation treatment ( $P<0.05$ ). *Pardosa* survival did not vary with fertilization treatment ( $n=120$ ,  $df=1$ ,  $\chi^2=1.01$ ,  $P=0.31$ ). *Pardosa* body mass followed a similar pattern as percent survival with differences across diet treatments ( $F_{4,84}=6.05$ ,  $P=0.0003$ ), but notably there was also an interaction between diet and fertilization treatment ( $F_{4,84}=2.72$ ,  $P=0.0358$ , Fig. 1B). Starvation again had the strongest negative effect on *Pardosa* body mass and the *Salidula* and *Grammonota* diets resulted in intermediate values for *Pardosa* body mass independent of fertilization treatment. Fertilization treatment interacted with diet treatment for *Prokelisia* and *Tythus*; for *Pardosa* reared on *Prokelisia*, body mass was greater in the control treatment compared to the fertilization treatment whereas for *Pardosa* reared on *Tythus*, body mass was greater for individuals reared in the fertilization treatment compared to the control.

We found an effect of prey diet ( $F_{4,72}=10.23$ ,  $P<0.001$ ) and an interaction between prey diet and fertilization treatment ( $F_{4,72}=3.4$ ,

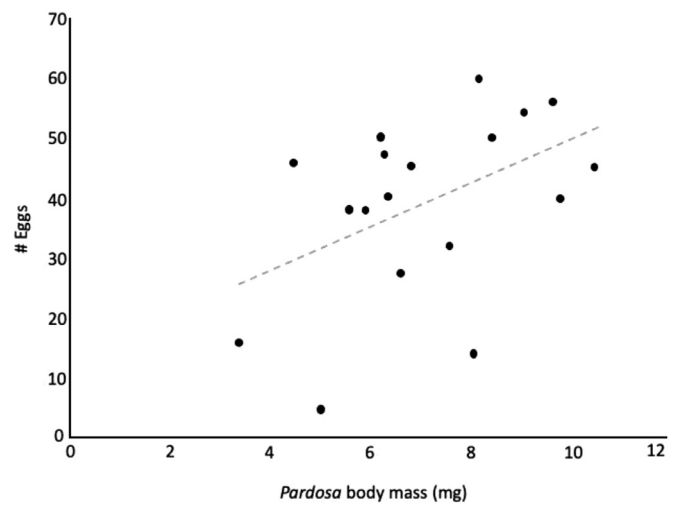


**Fig. 1.** *Pardosa littoralis* performance when reared in two fertilization treatments (control and fertilized) and in the five diet treatments: starvation, *Prokelisia* (herbivore), *Tytthus* (specialist predator), *Saldula* (generalist predator), *Grammonota* (multichannel omnivore). Performance of *Pardosa* as measured by A) percent survival (fertilized and control combined because not significantly different) and B) body mass. Bars represent mean  $\pm$  SE. Diet treatments with the same letters are not significantly different and \* indicate significant differences between control and fertilized treatments within a diet treatment.



**Fig. 2.** C:N ratio for *Pardosa littoralis* when reared in two fertilization treatments (control and fertilized) in the five diet treatments: starvation, *Prokelisia* (herbivore), *Tytthus* (specialist predator), *Saldula* (generalist predator), *Grammonota* (multichannel omnivore). Bars represent mean  $\pm$  SE. Diet treatments with the same letters are not significantly different and \* indicate significant differences between control and fertilized treatments within a diet treatment.

$P=0.0139$ , Fig. 2) on the C:N ratio of *Pardosa*. *Pardosa* reared on the herbivore *Prokelisia* had the highest C:N ( $P<0.05$ ) but there was an interaction with fertilization in that only *Pardosa* fed *Prokelisia* from the control treatment had an extremely elevated C:N ratio compared to the other diet and fertilization treatments. We found a difference in C:N ratio across prey species ( $F_{3,51} = 10.67$ ,  $P<0.001$ , Appendix 1), but neither fertilization ( $F_{1,51} = 0.108$ ,  $P=0.74$ ) nor the interaction between fertilization and prey species ( $F_{3,51} = 1.44$ ,  $P=0.24$ ) affected C:N ratio.



**Fig. 3.** The relationship between female *Pardosa littoralis* body mass and the number of eggs in her egg sac. *Pardosa littoralis* females that had more mass tended to lay more eggs ( $R^2 = 0.22$ ,  $n = 18$ , slope = 3.6,  $p = 0.05$ ) indicating that female mass is a predictor of fitness.

Finally, we found a positive relationship between the body mass of female *Pardosa* and the number of eggs in her egg sac ( $R^2 = 0.22$ ,  $F_{1,16} = 4.4$ ,  $P = 0.05$ ). For every additional mg of body mass, a female laid an additional 3.6 eggs (Fig. 3). Our literature review demonstrated that there is a significant, positive relationship between female body size and potential fecundity for all *Pardosa* species for which this relationship has been investigated (Table 1) and we were the first to measure this relationship for *P. littoralis* (Fig. 3).

## Discussion

We found that *Pardosa* survival was affected by prey species identity, but fertilization did not reliably increase prey quality. *Pardosa* survival was highest when fed a diet of *Tytthus* egg predators, lowest under starvation conditions, and intermediate on *Prokelisia* herbivores, *Saldula* predators, and *Grammonota* web-building spiders. Thus, similar to the findings of Matsumura et al. (2004), we found that prey type was more important than trophic level of the prey; *Pardosa* survival was highest when fed one type of intraguild prey (*Tytthus*) but did not differ from an herbivore diet when fed two additional types of intraguild prey (*Saldula* and *Grammonota*). While web-building may effectively prevent *Pardosa* predation on *Grammonota* and thus decrease survival on this diet, *Pardosa* can easily catch *Saldula* (personal observation), so other differences such as handling time might help explain our findings.

*Pardosa* body mass also varied across prey diets, but we found an interaction between prey diet and fertilization treatment. *Pardosa* body mass was greatest when fed a diet of *Prokelisia* herbivores, *Tytthus* egg predators, and *Saldula* predators, and lowest in the starvation and *Grammonota* web-building spider treatment. We also found an interaction between prey type and fertilization level because while *Pardosa* body size increased when fed *Tytthus* egg predators from fertilized plots compared to control plots, their body size decreased when fed *Prokelisia* herbivores from fertilized plots. Notably, these results are not well explained by prey quality as we found no significant differences in the C/N ratio for prey collected from the control versus the fertilized plots, but differences existed across prey species. Furthermore, the C/N ratio of *Pardosa* fed on *Prokelisia* herbivores was higher on control than fertilized diets, as we would expect from unfertilized plants with low nitrogen content, but *Pardosa* body mass was also higher when fed *Prokelisia* herbivores from control plots, which is challenging to understand. Yet, while protein is often considered most important to spiders and other carnivores, car-

**Table 1**

Compilation of data that examined the relationship between female *Pardosa* body size (how size was measured is listed as body measure) and potential fecundity from studies of 19 *Pardosa* species gathered from the literature. The slope represents the increase in the number of eggs per mm/mg/g of additional body size of the female; not all studies reported the slope of this relationship, so we simply noted if the relationship was positive (+) or negative (-) if slope was not available. All relationships were reported as significant unless noted 'ns' for not significant. Other values given in the table are the correlation coefficient (r) and the number of individuals in the study (n). If a variable was not reported by the authors then it was left blank in the table. Authors used a variety of terms to refer to the kind of body size that they measured, but for simplicity we report the data using a consistent terminology (\* indicates when the term we use here was not the term that the author used, e.g. prosoma width used in place of carapace width).

<i>Pardosa</i> sp.	Body measure	Slope	r	n	Authors
<i>agricola</i>	prosoma width (mm)	63.2	0.46	68	Ameline et al. (2017)
<i>amentata</i>	prosoma mass (mg)*	11.4		126	Bayram (2000)
	prosoma width (mm)	63.2	0.46	65	Ameline et al. (2017)
	prosoma width (mm)	+		218	Hein et al. (2015)
<i>astrigera</i>	body mass (mg)	+			Jiao et al. (2011)
	prosoma area (mm <sup>2</sup> )	15.8	0.36	25	Drapela et al. (2011)
	prosoma width (mm)*	+			Yang et al. (2018)
<i>furcifera</i>	prosoma width (mm)	81.9	0.34	59	Ameline et al. (2017)
	prosoma width (mm)	81.0	0.34	59	Ameline et al. (2018)
<i>glacialis</i>	prosoma width (mm)*	67.6	0.43	38	Simpson (1993)
	prosoma width (mm)*	44.1	0.44	55	Simpson (1993)
	prosoma width (mm)	82.9	0.47	151	Ameline et al. (2018)
	prosoma width (mm)*	68.5	0.34	238	Hoye et al. (2020)
	prosoma width (mm)*	3.1(ns)	0.01	42	Hoye et al. (2020)
<i>hyperborea</i>	prosoma width (mm)	36.6	0.48	60	Ameline et al. (2017)
	prosoma width (mm)	33.0	0.32	465	Ameline et al. (2018)
	prosoma width (mm)	+		121	Hein et al. (2015)
<i>lapponica</i>	Log prosoma width (cm)*	3.8	0.21	184	Bowden and Buddle (2012)
	Log prosoma width (cm)*	3.7	0.21	89	Bowden and Buddle (2012)
	Log prosoma width (cm)*	3.2	0.17	178	Bowden and Buddle (2012)
<i>littoralis</i>	body mass (mg)	3.6	0.22	18	Wimp et al. (this study)
<i>lugubris</i>	prosoma width (mm)	+		204	Hein et al. (2015)
<i>mackenziana</i>	prosoma width (mm)*	20.9	0.06	73	Buddle (2000)
<i>moesta</i>	Log prosoma width (cm)*	4.0	0.25	78	Bowden and Buddle (2012)
	Log prosoma width (cm)*	4.7	0.38	39	Bowden and Buddle (2012)
	prosoma width (mm)*	45.3	0.26	66	Buddle (2000)
<i>palustris</i>	body mass (mg)	42.2	0.71	94	Peterson (1950)
	prosoma length (mm)*	42.1	0.61	98	Peterson (1950)
	prosoma mass (mg)*	13.9		58	Bayram (2000)
	prosoma width (mm)	47.5	0.32	90	Ameline et al. (2018)
	prosoma width (mm)	+		712	Hein et al. (2015)
	prosoma width (mm)	29.4	0.56	241	Hein et al. (2018)
<i>prativaga</i>	prosoma length (mm)*	35.7	0.61	21	Peterson (1950)
<i>pullata</i>	body mass (mg)	26.9	0.82	23	Peterson (1950)
	prosoma mass (mg)*	13.4		250	Bayram (2000)
<i>purbeckensis</i>	body mass (mg)	5.0		60	Puzin et al. (2011)
<i>riparia</i>	prosoma width (mm)	+		120	Hein et al. (2015)
<i>saltans</i>	prosoma width (mm)*	+		205	Eraly et al. (2011)
<i>sierra</i>	prosoma width (mm)*	+	0.08	117	Punzo and Farmer (2006)
<i>sodalis</i>	Log prosoma width (cm)*	6.7	0.38	51	Bowden and Buddle (2012)
	Log prosoma width (cm)*	2.6(ns)	0.09	16	Bowden and Buddle (2012)
	Log prosoma width (cm)*	3.4	0.20	109	Bowden and Buddle (2012)

bohydrates are also critical. Predators need carbohydrates for energy, and carbohydrates can also be important for venom production in spiders (Bednaski et al., 2015). Indeed, spiders have been shown to have faster growth and higher survival rates when supplemented with carbohydrates (Vogelei and Greissl 1989; Taylor and Pfannenstiel 2009; Wilder 2011). Thus, nitrogen limitation may be more of an issue for herbivores that feed on carbohydrate-rich plants than for predators that are feeding on a more well-balanced C:N.

There are several possible reasons why plant fertilization did not translate into higher quality prey that would lead to higher performance by spiders. First, the planthopper herbivores were primarily *P. dolus*, which was the most abundant on the salt marsh during our study; however, *P. dolus* demonstrates a muted response to nitrogen addition relative to *P. marginata* (Huberty and Denno 2006). Second, while

Huberty and Denno (2006) found an increase in *P. dolus* density, survival, and development with fertilization, they did not examine how nitrogen addition affected *P. dolus* quality. Here, we show that fertilization does not affect *P. dolus* nitrogen content, so it is not surprising that *Pardosa* was unaffected by plant fertilization. Indeed, while the impacts of fertilization on planthopper life history traits are clear (Huberty and Denno 2006), one of the only studies to examine fertilizer effects on planthopper nitrogen content showed only a slight increase (Rashid et al., 2016). In part, this relationship may be driven by a feedback loop; feeding by *P. dolus* reduces host plant quality, and these effects are only partly offset by nitrogen addition (Olmstead et al., 1997). Thus, positive responses by *Pardosa* to increased plant quality via fertilization in field experiments may not be due to increases in prey quality but rather changes in prey density and life history traits.

Extraoral digestion allows spiders to mediate their intake of proteins and lipids from a single prey item (Wilder 2011). While some spiders can selectively feed on different prey parts, wolf spiders such as *Pardosa* masticate their prey (Wilder 2011). This does not mean, however, that they do not regulate their ingestion of nutrients, they simply feed on overall quantities of prey that allow them to balance their lipid and protein intake (Mayntz et al., 2005; Jensen et al., 2011; Wilder 2011). Indeed, we have found that *Pardosa* spiders in the field balance prey intake from the epigeic and grazing food webs, even when epigeic prey become less abundant than grazing prey or when prey densities do not differ (Wimp et al., 2013; Murphy et al., 2020). Because proteins and carbohydrates support different essential functions for spiders (e.g., proteins for silk production and carbohydrates for venom production, Wilder 2011), it is unlikely that a single prey resource will meet their essential needs, but a mixture of different prey resources may be needed to sustain dietary demands.

Differences in *Pardosa* body size are important because larger spiders produce more eggs, which affects fitness. Thus, differences in prey diet may ultimately affect *Pardosa* population dynamics. We found a positive relationship between female *Pardosa* body mass and the number of eggs in her egg sac. The results from our study and also from our literature review demonstrate that body size may be used as a predictor of potential female fecundity and thus is a reliable proxy for fitness for *Pardosa* species.

## Conclusion

We demonstrate that spider nutrition is affected more by prey species identity than the trophic level of the prey, and an increase in plant quality does not necessarily propagate through the food web. While changes in plant quality affected spider body mass, they did so in opposite ways for *Prokelisia* herbivores relative to *Tytthus* egg predators and had no impact on spider body mass for two additional species of intraguild prey. Changes in body mass were important because they actually drove differences in spider egg production and thus fitness. While many studies emphasize the importance of nitrogen to arthropod diets, this focus may be driven largely by our understanding of herbivore diets rather than predator diets. For predators such as spiders, nitrogen limitation in many habitats may not be as much of an issue but gaining access to carbohydrates for energy and to support essential functions such as venom production may be equally important. Thus, for predators it may be more important to understand how they combine different essential nutrients via diet mixing (Greenstone 1979).

## Author statement

**Gina Wimp:** Conceptualization, Methodology, Investigation, Data Curation, Writing – Original Draft, Writing – Review and Editing, Supervision, Funding acquisition **Danny Lewis:** Conceptualization, Methodology, Investigation, Data Curation, Supervision, Funding acquisition **Shannon Murphy:** Conceptualization, Methodology, Formal Analysis, Investigation, Data Curation, Writing – Original Draft, Writing – Review and Editing, Visualization, Supervision, Funding acquisition

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Acknowledgments

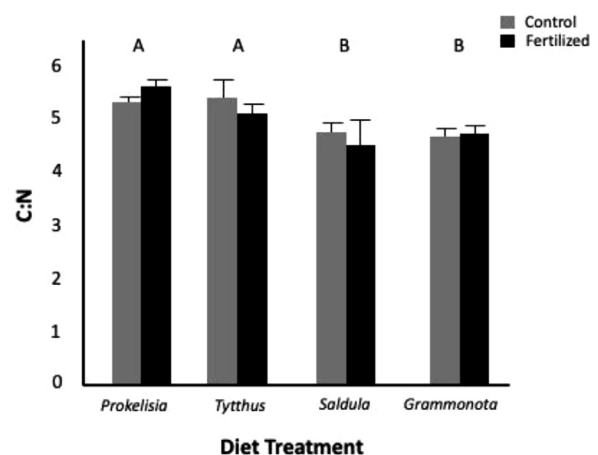
Ken Able at the Rutgers University Marine Station facilitated our research at the Tuckerton field site. We thank A. Ayotte, E. Barnes, K. Beins, M. Brabson, G. Connor, E. Gates, K. Grenis, C. Hallagan, M. Hayes, B. Herb, E. Kuras, K. Loewy, M. Lynch, V. Lynch, K. Hale, J. McCarty, E.

Powell, B. Rojewski, A. Styer, and R. Whalen for their help in the field or lab. This research was supported by the National Science Foundation (NSF-DEB 1026067 to GMW; NSF-DEB 1026000 to SMM).

## Supplementary materials

Supplementary material associated with this article can be found in the online version, at doi:10.1016/j.cris.2021.100013.

**Appendix 1. C:N ratio for four prey species (*Prokelisia* (herbivore), *Tytthus* (specialist predator), *Saldula* (generalist predator), *Grammonota* (multichannel omnivore)) that we fed to *Pardosa* in our diet experiment. The prey were collected from two fertilization treatments (control and fertilized). Bars represent mean  $\pm$  SE. Prey species with the same letters are not significantly different; there were no significant differences between fertilization treatments within a prey species**



## References

- Ameline, C., Hoye, T.T., Bowden, J.J., Hansen, R.R., Hansen, O.L.P., Puzin, C., Vernon, P.P., Pétilion, J., 2018. Elevational variation of body size and reproductive traits in high-latitude wolf spiders (Araneae: Lycosidae). *Polar Biol.* 41 (12), 2561–2574.
- Ameline, C., Puzin, C., Bowden, J.J., Lambeets, K., Vernon, P., Pétilion, J., 2017. Habitat specialization and climate affect arthropod fitness: a comparison of generalist vs. specialist spider species in Arctic and temperate biomes. *Biol. J. Linnean Soc.* 121 (3), 592–599.
- Abrams, P.A., 1995. Monotonic or unimodal diversity-productivity gradients: what does competition theory predict? *Ecology* 76, 2019–2027.
- Awmack, C.S., Leather, S.R., 2002. Host plant quality and fecundity in herbivorous insects. *Annu. Rev. Entomol.* 47, 817–844.
- Bayram, A., 2000. A study of egg production in three species of wolf spiders (Araneae, Lycosidae), *Pardosa amentata*, *P. palustris*, and *P. pullata* in the field. *Isr. J. Zool.* 46 (4), 297–303.
- Bednaski, A.V., Trevisan-Silva, D., Matsubara, F.H., Boia-Ferreira, M., Oliverio, M.M., Gremski, L.H., Cavalheiro, R.P., De Paula, D.M.B., Paredes-Gamero, E.J., Takahashi, H.K., Toledo, M.S., Nader, H.B., Veiga, S.S., Chaim, O.M., Senff-Ribeiro, A., 2015. Characterization of Brown spider (*Loxosceles intermedia*) hemolymph: cellular and biochemical analyses. *Toxicon* 98, 62–74.
- Bowden, J.J., Buddle, C.M., 2012. Life history of tundra-dwelling wolf spiders (Araneae: Lycosidae) from the Yukon Territory, Canada. *Can. J. Zool.* 90 (6), 714–721.
- Buddle, C.M., 2000. Life history of *Pardosa moesta* and *Pardosa mackenziana* (Araneae, Lycosidae) in central Alberta, Canada. *J. Arachnol.* 28 (3), 319–328.
- Bumpers, P.M., Rosemond, A.D., Maerz, J.C., Benstead, J.P., 2017. Experimental nutrient enrichment of forest streams increases energy flow to predators along greener food-web pathways. *Freshw. Biol.* 62, 1794–1805.
- Cebrian, J., Shurin, J.B., Borer, E.T., Cardinale, B.J., Ngai, J.T., Smith, M.D., Fagan, W.F., 2009. Producer nutritional quality controls ecosystem trophic structure. *PLoS ONE* 4 (3), e4929.
- Cohen, A.C., 1995. Extra-oral digestion in predaceous terrestrial arthropoda. *Annu. Rev. Entomol.* 40, 85–103.
- Denno, R.F., Fagan, W.F., 2003. Might nitrogen limitation promote omnivory among carnivorous arthropods? *Ecology* 84, 2522–2541.
- Denno, R.F., Gratton, C., Peterson, M.A., Langellotto, G.A., Finke, D.L., Huberty, A., 2002. Bottom-up forces mediate natural-enemy impact in a phytophagous insect community. *Ecology* 83 (5), 1443–1458.

- Drapela, T., Frank, T., Heer, X., Moser, D., Zaller, J.G., 2011. Landscape structure affects activity density, body size and fecundity of *Pardosa* wolf spiders (Araneae: Lycosidae) in winter oilseed rape. *Eur. J. Entomol.* 108 (4), 609–614.
- Eraly, D., Hendricks, F., Backeljau, T., Bervoets, L., Lens, L., 2011. Direct and indirect effects of metal stress on physiology and life history variation in field populations of a lycosid spider. *Ecotoxicol. Environ. Saf.* 74 (6), 1489–1497.
- Fagan, W.F., Denno, R.F., 2004. Stoichiometry of actual vs. potential predator-prey interactions: insights into nitrogen limitation for arthropod predators. *Ecol. Lett.* 7, 876–883.
- Fagan, W.F., Siemann, E., Mitter, C., Denno, R.F., Huberty, A.F., Woods, H.A., Elser, J.J., 2002. Nitrogen in insects: implications for trophic complexity and species diversification. *Am. Naturalist* 160, 784–802.
- Greenstone, M.H., 1979. Spider feeding behaviour optimises dietary essential amino acid composition. *Nature* 282, 501–503.
- Haddad, N.M., Haarstad, J., Tilman, D., 2000. The effects of long-term nitrogen loading on grassland insect communities. *Oecologia* 124, 73–84.
- Hein, N., Brendel, M.R., Feilhauer, H., Finch, O.D., Löffler, J., 2018. Egg size versus egg number trade-off in the alpine-tundra wolf spider, *Pardosa palustris* (Araneae: Lycosidae). *Polar Biol.* 41 (8), 1607–1617.
- Hein, N., Feilhauer, H., Löffler, J., Finch, O.D., 2015. Elevational variation of reproductive traits in five *Pardosa* (Lycosidae) species. *Arct. Antarct. Alp. Res.* 47 (3), 473–479.
- Huberty, A.F., Denno, R.F., 2006. Consequences of nitrogen and phosphorus limitation for the performance of two planthoppers with divergent life-history strategies. *Oecologia* 149, 444–455.
- Kneitel, J.M., Miller, T.E., 2002. Resource and top-predator regulation in the pitcher plant (*Sarracenia purpurea*) inquilin community. *Ecology* 83, 680–688.
- Jensen, K., Mayntz, D., Toft, S., Raubenheimer, D., Simpson, S.J., 2011. Nutrient regulation in a predator, the wolf spider *Pardosa prativaga*. *Anim Behav* 81, 993–999.
- Jiao, X.G., Guo, L., Chen, Z.Q., Wu, J., Chen, J., Liu, F.X., Li, D.Q., 2011. Experimental evidence for female-driven monandry in the wolf spider, *Pardosa astrigera*. *Behav. Ecol. Sociobiol.* (Print) 65 (11), 2117–2123.
- Lawton, J.H., 1983. Plant architecture and the diversity of phytophagous insects. *Annu. Rev. Entomol.* 28, 23–39.
- Matsumura, M., Trafelet-Smith, G.M., Gratton, C., Finke, D.L., Fagan, W.F., Denno, R.F., 2004. Does intraguild predation enhance predator performance? A stoichiometric perspective. *Ecology* 85, 2601–2615.
- Mayntz, D., Raubenheimer, D., Salomon, M., Toft, S., Simpson, S.J., 2005. Nutrient-specific foraging in invertebrate predators. *Science* 307, 111–113.
- Mayntz, D., Toft, S., 2001. Nutrient composition of the prey's diet affects growth and survivorship of a generalist predator. *Oecologia* 127, 207–213.
- Mayntz, D., Toft, S., Vollrath, F., 2003. Effects of prey quality and availability on the life history of a trap-building predator. *Oikos* 101, 631–638.
- Murphy, S.M., Lewis, D., Wimp, G.M., 2020. Predator population size structure alters consumption of prey from epigeic and grazing food webs. *Oecologia* 192, 791–799.
- Murphy, S.M., Wimp, G.M., Lewis, D., Denno, R.F., 2012. Nutrient presses and pulses differentially impact plants, herbivores, detritivores and their natural enemies. *PLoS ONE* 7 (8), e43929.
- Olmstead, K.L., Denno, R.F., Morton, T.C., Romeo, J.T., 1997. Influence of *Prokelisia* planthoppers on amino acid composition and growth of *Spartina alterniflora*. *J. Chem. Ecol.* 23, 303–321.
- Pekár, S., Toft, S., 2015. Trophic specialisation in a predatory group: the case of prey-specialised spiders (Araneae). *Biological Rev.* 90, 744–761.
- Peterson, B., 1950. The relation between size of mother and number of eggs and young in some spiders and its significance for the evolution of size. *Experientia* 3, 96–98.
- Price, P.W., Denno, R.F., Eubanks, M.D., Finke, D.L., Kaplan, I., 2011. *Insect Ecology: Behavior, Populations and Communities*. Cambridge University Press, Cambridge, UK. 816 pages.
- Punzo, F., Farmer, C., 2006. Life history and ecology of the wolf spider *Pardosa sierra* Banks (Araneae: Lycosidae) in Southeastern Arizona. *Southwestern Naturalist* 51 (3), 310–319.
- Puzin, C., Acou, A., Bonte, D., Pétilion, J., 2011. Comparison of reproductive traits between two salt-marsh wolf spiders (Araneae, Lycosidae) under different habitat suitability conditions. *Animal Biol.* 61 (2), 127–138.
- Rashid, M.M., Jahan, M., Islam, K.S., 2016. Impact of nitrogen, phosphorus and potassium on brown planthopper and tolerance of its host rice plants. *Rice Sci.* 23, 119–131.
- Schmitz, O.J., Hawlena, D., Trussell, G.C., 2010. Predator control of ecosystem nutrient dynamics. *Ecol. Lett.* 13, 1199–1209.
- Siemann, E., 1998. Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. *Ecology* 79, 2057–2070.
- Simpson, M.R., 1993. Reproduction in 2 species of arctic arachnids, *Pardosa glacialis* and *Alopecosa hirtipes*. *Can. J. Zool.* 71 (3), 451–457.
- Strohmeier, H.H., Stamp, N.E., Jarzomski, C.M., Bowers, M.D., 1998. Prey species and prey diet affect growth of invertebrate predators. *Ecol Entomol* 23, 68–79.
- Taylor, R.M., Pfannenstiel, R.S., 2009. How dietary plant nectar affects the survival, growth, and fecundity of a cursorial spider *Cheiracanthium inclusum* (Araneae: miturgidae). *Environ. Entomol.* 38, 1379–1386.
- Theodoratus, D.H., Bowers, M.D., 1999. Effects of sequestered iridoid glycosides on prey choice of the prairie wolf spider, *Lycosa carolinensis*. *J. Chem. Ecol.* 25, 283–295.
- Toft, S., 1999. Prey choice and spider fitness. *J. Arachnol.* 27, 301–307.
- Toft, S., Wise, D.H., 1999. Growth, development, and survival of a generalist predator fed single- and mixed-species diets of different quality. *Oecologia* 119, 191–197.
- Uetz, G.W., 1992. Foraging strategies of spiders. *Trends Ecol. Evol.* 7, 155–159.
- Vogelei, A., Greissel, R., 1989. Survival strategies of the crab spider *Thomisus onustus* Walckenaer 1806 (Chelicerata, Arachnida, Thomisidae). *Oecologia* 80, 513–515.
- Wilder, S.M., 2011. Spider nutrition: an integrative perspective. *Adv. In. Insect. Phys.* 40, 87–136.
- Wilder, S.M., Eubanks, M.D., 2010. Might nitrogen limitation promote omnivory among carnivorous arthropods? *Comment. Ecol.* 91, 3114–3117.
- Wilder, S.M., Mayntz, D., Toft, S., Rypstra, A.L., Pilati, A., Vanni, M.J., 2010. Intraspecific variation in the quality of prey: a comparison of nutrient presence in prey and nutrient extraction by spiders. *Oikos* 119, 350–358.
- Wimp, G.M., Murphy, S.M., Finke, D.L., Huberty, A.F., Denno, R.F., 2010. Increased primary production shifts the structure and composition of a terrestrial arthropod community. *Ecology* 91, 3303–3311.
- Wimp, G.M., Murphy, S.M., Douglas, M.R., Lewis, D., Gratton, C., Ambikapathi, R., Van-Tull, L., Denno, R.F., 2013. Predator hunting mode influences patterns of prey use from grazing and epigeic food webs. *Oecologia* 171, 505–517.
- Wimp, G.M., Lewis, D., Murphy, S.M., 2019. Impacts of nutrient subsidies on salt marsh arthropod food webs: a latitudinal survey. *Front. Ecol. Evol.* 7, 350.
- Wise, D.H., 2006. Cannibalism, food limitation, intraspecific competition and the regulation of spider population. *Ann. Rev. Entomol.* 51, 441–465.
- Yang, J.J., Wu, Q.J., Xiao, R., Zhao, J.P., Chen, J., Jiao, X.G., 2018. Seasonal variations in body melanism and size of the wolf spider *Pardosa astrigera* (Araneae: Lycosidae). *Ecol. Evol.* 8, 4352–4359.