Dietary supplementation with pollen enhances survival and Collembola boosts fitness of a web-building spider

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Abstract

Uncertainties exist about the value of non-prey food for predators that are commonly food-limited, and the dietary conditions where non-prey foods are beneficial for carnivorous species. Prior studies show that large quantities of pollen grains are intercepted in the webs of web-building spiders. We examined the nutritional benefits of pollen as a non-prey food for a common ground-dwelling, sheet web-building spider, *Mermessus fradeorum* (Berland) (Araneae: Linyphiidae). These predators were provided diets of prey or no prey in the presence and absence of pollen. Treatment effects were quantified by measuring predator body nutrient composition, survival, body size, and offspring production. Per unit dry weight, pollen had less nitrogen and lipids than prey, although relative quantities of these nutrients per meal were not measured. Dietary treatments altered the body tissue composition of the spiders, leading to the highest N content and lipid reserves in spiders provided with Collembola. Supplementing diets with pollen increased both juvenile and adult survival, and the greatest survivorship and offspring production was observed when spiders were provided diets of Collembola supplemented with pollen. Our results show that Collembola are high-quality prey for spiders and pollen has positive effects on nutritional status and survival of a carnivorous species. Foraging on plant material potentially promotes population growth at early and late developmental stages by supplementing diets of poor-quality prey, and preventing starvation when prey are scarce.

Introduction

Foraging flexibility may allow consumers to switch between food sources to promote survival and reproduction. Of particular importance in terrestrial food webs are predatory arthropods; feeding on plant resources by this group affects (functional and numerical) response to prey and therefore subsequent trophic interactions (Lundgren, 2009b; Wilder & Eubanks, 2010). It is becoming increasingly evident that the omnivorous tendencies displayed by many natural enemies can affect their feeding behavior and role in biological control (Hunter, 2009). Dietary diversification via consumption of both prey and plant material by predatory arthropods can be beneficial in multiple ways; dietary diversity provides essential or limiting nutrients, sustains predators during periods of prey scarcity, and reduces interspecific competition (Coll & Guershon, 2002).

Plant-provided food can act as a nutritional supplement to predators (Wäckers, 2005; Lundgren, 2009b). Review and meta-analysis of recent studies show that a variety of plant-provided foods (i.e., nectar, pollen, and seeds) improves survivorship and fecundity of a wide range of arthropod predators during periods of prey scarcity (Lundgren, 2009a,b). For instance, in some predatory Heteroptera, feeding on plant juices and phloem not only sustains these predators when prey is unavailable, but can also increase their fitness when supplementing a prey-based diet (Coll, 1998). The addition of non-prey foods to the diets of ladybird beetles aids in their biological control efficacy by encouraging immigration into crop systems, increasing survival during periods of low prey availability

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and diapause, and increasing their reproductive ability (Agrawal et al., 1999; Lundgren, 2009a). Some predators, historically considered strict carnivores, are even capable of completing their entire life cycle on a diet of non-prey food (McMurtry & Rodriguez, 1987; Pilcher et al., 1997; Lundgren & Wiedenmann, 2005). Thus, omnivorous predators can benefit from both plant and animal resources, which contribute unique components of a balanced diet.

Spiders in the family Linyphiidae are some of the most abundant predators in many temperate agroecosystems (Nyffeler & Sunderland, 2003). Studies show that there is a potential for these spiders to control pests such as aphids (Chiverton, 1986; Sunderland et al., 1987; Nyffeler, 1999), whereas alternative prey, such as Collembola, have the potential to sustain their populations early in the season prior to aphid population increase (Harwood et al., 2004). Recent molecular work has documented that these spiders consume a diversity of prey (Lundgren & Fergen, 2011; Chapman et al., 2013), yet are commonly food-limited in the field (Romero & Harwood, 2010). Additional studies provide evidence that increased dietary diversification influences life-history traits of linyphiid spiders and other common spiders (Marcussen et al., 1999; Toft & Wise, 1999b; Oelbermann & Scheu, 2002; Pfannenstiel, 2008; Harwood et al., 2009; Pfannenstiel & Patt, 2012). Dietary mixing has the potential to accelerate growth and development of spiders by balancing the set of nutrients consumed by these important predators (Greenstone, 1979; Mayntz et al., 2005).

Pollen grains contain a diversity of nutrients such as nitrogen and lipids (Roulston & Cane, 2000). Availability of pollen fluctuates seasonally, and at times represents a significant resource pulse. For instance, during anthesis, maize pollen is highly abundant within crop fields (Pleasants et al., 2001) and up to 30 m from its source (Raynor et al., 1972). Pollen is a component of the diets of some generalist predators, including ladybird beetles, lacewings, ground beetles, hoverflies, predatory mites, and spiders (Lundgren, 2009b). A pollen-based diet can increase spiderling survival for the crab spider *Thomisus onustus* Walckenaer (Vogelei & Greissl, 1989), the orb-web spider *Araneus diadematus* Clerck (Smith & Mommsen, 1984), and the cursorial spider *Cheiracanthium inclusum* Hentz (Pfannenstiel, 2012). With the exception of pine pollen (Carrel et al., 2000), linyphiid spiders have been found to readily consume pollen intercepted in their webs (Sunderland et al., 1987; Peterson et al., 2010). During anthesis in maize fields, Peterson et al. (2010) observed that the combination of high pollen deposition (upwards of 4 000 pollen grains per web during peak pollen shed), and low prey interception rates at ground-based linyphiid webs, may increase pollen consumption within this group of predators.

In this study, we explore the suitability of pollen as an alternative nutritional resource for a linyphiid spider. We examine pollen consumption driven by food limitation, as well as the effects of dietary supplementation on predator growth, survival, and reproductive fitness. We also link these results to changes in body nutrient composition as a result of feeding on pollen, prey, or combined diets. We focus this study on two common prey items of varying quality for linyphiid spiders. Aphids are considered to be a poor-quality food source (Bilde & Toft, 2001), but may be better than non-prey foods for supporting spider growth and development (Smith & Mommsen, 1984). Conversely, many Collembola are cited as being high quality (Bilde et al., 2000) and may promote spider populations early in the season prior to pest arrival (Harwood et al., 2004). Using this system of prey and non-prey food, we test the hypothesis that pollen feeding complements nutrient-poor prey diets and improves survival of spiders under food-limited conditions.

Materials and methods

The experimental system consisted of the linyphiid spider *Mermessus fradeorum* (Berland) (Araneae: Linyphiidae) as the predator, the cowpea aphid, *Aphis craccivora* Koch (Hemiptera: Aphididae) and the springtail *Sinella curviseta* Brook (Collembola: Entomobryidae) as two prey sources, and maize pollen, *Zea mays* L. (Poaceae), as an alternative non-prey food source. Adult *M. fradeorum* were collected by aspirator from agricultural fields at University of Kentucky Spindletop Research Farm, Lexington, KY, USA (GPS coordinates: 38°07.555′N, 84°30.901′W). Male–female pairs were established in small plastic containers (6 cm diameter, 4 cm high) containing a 1.5-cm layer of moist soil and an active Collembola culture. *Aphis craccivora* (hereafter 'aphids') cultures were laboratory-reared on *Vicia faba* L. (Fabaceae). *Sinella curviseta* (hereafter 'Collembola') cultures were reared in small plastic containers on a substrate of peat moss and soil mixture, and were provided potato dusted with baker's yeast as food, a modified version of Waldorf (1971). Maize pollen (hereafter 'pollen') was obtained from Novartis hybrid NK 4640, non-transgenic plants grown under greenhouse conditions and stored at −80 °C until use [see Pilorget et al. (2010) for details]. During experiments, spiders were provided standardized environmental conditions with a temperature of 25 °C and L16:D8 photoperiod.

Experiment 1: Nutrient levels in pollen vs. prey food sources and effects on spider tissue

The percentage dry mass of nitrogen, carbon, and lipids of each food source (n = 10 per source) was determined

using chloroform lipid extraction and carbon–hydrogen–nitrogen analysis (CHN analysis) following standard protocols (Wilder et al., 2010). To assess how dietary treatments affect the nutrient levels in spider tissues, adult female spiders (n = 10 per food source) were fed each food source for 2 weeks before CHN and chloroform lipid analyses. Food sources and spiders were frozen and held at −80 °C until nutrient extraction. All samples were dried at 60 °C for 48 h and weighed. Chloroform lipid extraction was performed using three applications of 2 ml of chloroform once per day for three successive days to extract lipids. Following the three applications, the excess chloroform was removed and the samples were dried for 6 h then the mass was again measured. CHN analysis was conducted using an organic elemental analyzer (Flash EA 1112 Series; Thermo Electron, Delft, The Netherlands) to determine the percentage of nitrogen and carbon present.

Experiment 2: Demonstrating propensity to feed on pollen

To test the effects of food limitation on the likelihood of pollen feeding, female *M. fradeorum* spiders were either food-limited (n = 11) or fed ad libitum Collembola (n = 11) for 8 days (Peterson et al., 2010). Following this period, ca. 2.7 mg of maize pollen was lightly dusted onto the web of each spider using a paint brush, and feeding was observed under a stereomicroscope. Spiders were monitored constantly for the first 15 min following introduction of pollen and checked for 1 min at 15-min intervals, thereafter for a total of 120 min. At each observation, spiders were scored for whether they were actively feeding or not.

Experiment 3: Spiderling growth, body condition, and survival

Diet-specific spiderling survival was assessed by producing 12 broods through randomly pairing field-collected adults. Eggsacs produced were separated into Petri dishes (60 mm diameter, 15 mm high) prepared with a moistened plaster of Paris and charcoal base. Following spiderling emergence, individuals were transferred to separate Petri dishes containing Collembola eggs and small collembolans. After completing two molts, the spiderlings were randomly assigned to one of six dietary treatments (n = 15 per treatment). The dietary treatments were: food-limited, pollen, aphid, Collembola, aphid + pollen, and Collembola + pollen. Spiderlings were examined every 4 days for 30 days, at which time feces and unconsumed food were cleaned from the Petri dish and food and water were replenished. The mass (accuracy: ± 0.001 mg; MX5 microbalance; Mettler Toledo, Columbus, OH, USA), and two morphometrics (cephalothorax width and abdomen width at the widest point) were measured prior to the start and at the end of the experiment. These

measurements are frequently used in spiders to determine body condition and feeding history (Jakob et al., 1996; Uetz et al., 2002). The cephalotharox width is fixed at adulthood and represents a size measure and the abdomen varies with recent feeding history. Body condition was then analyzed using a size-corrected index (i.e., ANCOVA; see Garcia-Berthou, 2001). Images used for morphometric data were captured using a Wild M5A Heerbrugg Stereomicroscope equipped with a Sony DXC-390 DSP 3CCD Color Video Camera ExwaveHAD (Sony, Park Ridge, NJ, USA) to capture the image data as tif-files in Scion Image 4.0 software (Scion, Frederick, MD, USA). For the morphometric measurements, the image pixel data were imported into Image J64 (http://rsb.info.nih.gov/ij/index.html). A calibration micrometer was included for every image taken and was used to calculate the conversion factor of pixels to mm (accuracy: ± 0.012 mm). Each individual spider was photographed with a micrometer in view, and to ensure repeatability, each spider body region was measured four times, and the mean of these measurements was used as the response variable (Swaddle et al., 1994). There was only one food-limited spider measured for the final measurement, which was taken directly before it died. The poor quality of other food-limited spiders prevented reliable measurements being taken.

Experiment 4: Adult survival and reproductive output

Diet-specific adult female survival and eggsac production was conducted using the basic experimental conditions as described above. Morphometric measurements were likewise recorded at the beginning of the experiment to compare size and body condition between females prior to assigning them to dietary treatments. We fed adult females for 2 weeks on the dietary treatments prior to mating, each with randomly selected males from the laboratory population. No two females were mated with the same male. Males and females were allowed to interact until we observed copulation. Once copulation had concluded, each female was placed in a clean Petri dish and returned to its respective dietary treatment. The number of eggsacs produced by each female was monitored daily, Petri dishes cleaned, and food and water replenished until all adult female spiders died. Eggsacs were removed and the number of spiderlings that emerged from each eggsac was recorded.

Statistical analysis

Separate univariate analysis of variance (ANOVA) tests were used to compare mean nutrient content between food sources and the effects of food sources on spider nutrient composition. ANOVA was used to compare initial spider sizes among treatments. Significant main effects

were compared using Tukey HSD multiple comparisons. Change in size was analyzed using a linear mixed effects model (Pinheiro & Bates, 2000) with 'individual' as the random variable and 'size' (cephalothorax width) as the response variable to dietary treatments. Change in body condition (abdomen width) was analyzed using a linear mixed model with 'size' (cephalothorax width) as a covariate to scale the response variable for size of individual spiders for body condition effects of dietary treatments (Garcia-Berthou, 2001), and 'individual' as a random effect. Kaplan–Meier survival analysis (Kaplan & Meier, 1958) was used to estimate survival rates and log-linear analysis was used to assess treatment-specific survival rates. The effect of dietary treatments on eggsac and spiderling production (ln-transformed, which improved variance structure and residuals of model fit) was analyzed using univariate ANOVA. All analyses were conducted using R version 2.15 (R Core Team, 2012).

Results

Experiment 1: Nutrient levels in pollen vs. prey food sources and effects on spider tissue

Food sources were composed of unique combinations of nutrients (i.e., C, N, C:N; Table 1). These corresponded with changes in spider tissue levels of nutrients following feeding on dietary treatments (Table 2). Pollen contained the lowest percent dry mass of N and lipids as compared to aphids or Collembola. Correspondingly, spiders fed a diet of only pollen had the lowest N content in their tissues as compared to other dietary treatments (Table 2). Similarly, aphid-only diets resulted in lower levels of N and lipids in spider body tissues than diets containing Collembola. However, supplementing aphid diets with pollen slightly increased N levels and this combined diet provided higher N than a diet composed of only pollen (Table 2). Collembola represented the food resource with the highest percentage of N relative to carbon (C:N ratio), but similar lipid content to aphids (Table 1). The highest levels of these nutrients were observed in spiders supplied Collembola or a diet of Collembola and pollen (Table 2).

Experiment 2: Demonstrating propensity to feed on pollen

Food-limited spiders had a significantly higher probability of consuming pollen (n = 9 of 11 sampled; 82%) than spiders that were fed ad libitum Collembola prior to exposure to pollen (n = 4 of 11 sampled; 36%) (logistic regression; odds ratio = 7.88, χ^2 = 4.92, d.f. = 1, P = 0.03). Furthermore, pollen consumption did not commence immediately upon dusting the webs with pollen (range: 1–80 min). For spiders in the food-limited group that fed on pollen, the mean $\pm$ SEM time to initiate feeding was marginally shorter than the mean time for the ad libitum group (14 $\pm$ 7.79 vs. 36 $\pm$ 14.74 min; t = 4.56, d.f. = 21, P = 0.06). Although the pattern is the same, the mean duration of pollen feeding was highly variable in both

Table 1 Analysis of the nutritional composition of pollen and dried prey (aphids and Collembola) food sources. Mean ($\pm$ SEM) percentage nutrient content and results from univariate ANOVAs comparing the nutrient content among dietary treatments

Variable	Pollen	Aphid	Collembola	$F_{2,28}$	P
C (%)	45.35 $\pm$ 0.18a	46.71 $\pm$ 0.12a	36.99 $\pm$ 1.43b	47.96	<0.0001
N (%)	4.17 $\pm$ 0.03a	8.99 $\pm$ 0.09b	9.81 $\pm$ 0.51b	143.85	<0.0001
C:N	10.87 $\pm$ 0.04a	5.20 $\pm$ 0.04b	3.80 $\pm$ 0.07c	486.50	<0.0001
Lipids (%)	11.73 $\pm$ 1.36a	26.36 $\pm$ 0.95b	28.41 $\pm$ 2.30b	95.94	<0.0001

Means within a row followed by different letters are significantly different (Tukey HSD: P<0.05).

Table 2 Analysis of the *Mermessus fradeorum* tissue nutrient levels in response to feeding on pollen and dried prey (aphids and Collembola) food sources examined in Experiment 1. Mean ($\pm$ SEM) percentage nutrient content and results from univariate ANOVAs comparing the nutrient content among dietary treatments

Variable	Pollen	Aphids	Collembola	Pollen + aphids	Pollen + Collembola	$F_{4,49}$	P
C (%)	47.22 $\pm$ 1.28	46.04 $\pm$ 0.62	46.12 $\pm$ 0.34	47.17 $\pm$ 0.21	46.59 $\pm$ 0.16	0.94	0.45
N (%)	8.07 $\pm$ 0.52a	9.97 $\pm$ 0.59b	11.14 $\pm$ 0.38c	10.02 $\pm$ 0.31bc	11.18 $\pm$ 0.30c	9.06	0.0001
C:N	5.93 $\pm$ 0.32a	4.70 $\pm$ 0.36b	4.16 $\pm$ 0.15b	4.73 $\pm$ 0.15b	4.18 $\pm$ 0.11b	10.07	<0.0001
Lipids (%)	10.43 $\pm$ 1.67a	6.81 $\pm$ 1.56a	35.39 $\pm$ 2.21b	7.95 $\pm$ 0.86a	39.14 $\pm$ 2.67b	91.25	<0.0001

Means within a row followed by different letters are significantly different (Tukey HSD: P<0.05).

groups and not significantly different between groups (t = 1.81, d.f. = 21, P = 0.20). Food-limited spiders were observed feeding for a mean duration of 82.22 ± 8.65 min, and ad libitum spiders for 61.50 ± 20.09 min.

Experiment 3: Spiderling growth, body condition, and survival

Dietary treatments had significant effects on survival of spiderlings (log-rank χ^2 = 78.2, d.f. = 5, P<0.0001; Figure 1). Pollen feeding significantly improved survival of immature spiders compared to starved individuals (χ^2 = 5.10, d.f. = 1, P = 0.023). Spiders fed a diet of either aphids or Collembola survived at equivalent rates indicated by survival curves (χ^2 = 0.41, d.f. = 1, P = 0.54), and although the addition of pollen to either of these diets increased survivorship to 100% over the 30-day period of the experiment (Figure 1), the number of spiderlings surviving was not statistically different from diets of aphids (χ^2 = 1.00, d.f. = 1, P = 0.32) or of Collembola (χ^2 = 2.6, d.f. = 1, P = 0.11). In addition, increase in size was highest when spiders were provided diets of Collembola (Figure 2A; χ^2 = 24.9, d.f. = 1, P<0.0001). Body condition (change in abdomen corrected for size) was greatest when spiderlings were fed nutrient-rich Collembola, and addition of pollen to aphid diets significantly improved body condition (Figure 2B; χ^2 = 31.19, d.f. = 1, P<0.0001). Differences in initial size, initial body condition, or mass between treatments cannot account for these results as they did not differ significantly before the experiment (initial size, ANOVA: $F_{5,72}$ = 0.42, P = 0.83;
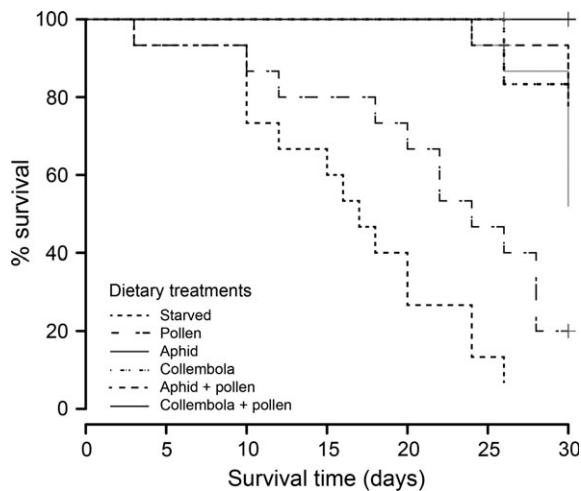
initial body condition, ANCOVA: $F_{5,70}$ = 0.16, P = 0.97; mass between treatments, ANOVA: $F_{5,72}$ = 0.29, P = 0.91; Table 3).

Experiment 4: Adult survival and reproductive output

Dietary treatments had significant effects on adult survivorship (log-rank χ^2 = 24.0, d.f. = 5, P = 0.0002; Figure 3). Pollen feeding by adult female spiders improved survivorship over starved individuals (χ^2 = 8.4, d.f. = 1, P = 0.003), and a diet of Collembola supplemented with pollen increased survival time to the greatest extent
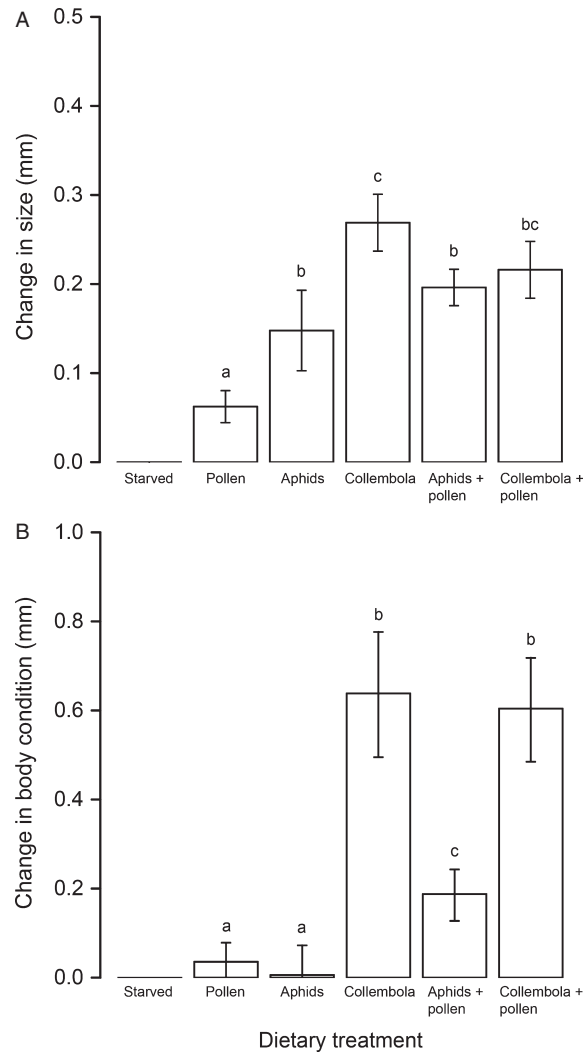

Figure 2 Mean (± SEM) morphometric data on *Mermessus fradeorum* (A) growth, as measured by change in cephalothorax width (mm), and (B) body condition, analyzed as change in abdomen width (mm) relative to size at the end of the 30-day period. Bars within a panel capped with different letters are significantly different (Tukey HSD: P<0.05).

Figure 1 Kaplan–Meijer survival analysis of juvenile *Mermessus fradeorum* spiders reared on different diets. Crosses on the survival lines indicate spiders where the final day of death is unknown.

Table 3 Mean morphometrics ($\pm$ SEM) measured using Image J64 for juvenile spiderlings fed on different diets (pollen, aphids, or Collembola) in Experiment 3

Variable	Starved	Pollen	Aphids	Collembola	Aphids + pollen	Collembola + pollen
Initial cephalothorax width (mm)	0.62 $\pm$ 0.03	0.63 $\pm$ 0.03	0.66 $\pm$ 0.03	0.60 $\pm$ 0.03	0.62 $\pm$ 0.03	0.62 $\pm$ 0.03
Final cephalothorax width (mm)	0.63	0.69 $\pm$ 0.05	0.81 $\pm$ 0.02	0.86 $\pm$ 0.01	0.82 $\pm$ 0.02	0.83 $\pm$ 0.01
Initial abdomen width (mm)	0.61 $\pm$ 0.05	0.72 $\pm$ 0.07	0.74 $\pm$ 0.03	0.72 $\pm$ 0.05	0.72 $\pm$ 0.07	0.73 $\pm$ 0.05
Final abdomen width (mm)	0.63	0.79 $\pm$ 0.05	0.78 $\pm$ 0.08	1.34 $\pm$ 0.12	0.91 $\pm$ 0.07	1.33 $\pm$ 0.09
Initial mass (mg)	0.68 $\pm$ 0.10	0.79 $\pm$ 0.19	0.76 $\pm$ 0.04	0.67 $\pm$ 0.09	0.69 $\pm$ 0.07	0.69 $\pm$ 0.10
Final mass (mg)	0.69	0.97 $\pm$ 0.24	1.22 $\pm$ 0.22	3.12 $\pm$ 0.53	1.51 $\pm$ 0.21	2.89 $\pm$ 0.36
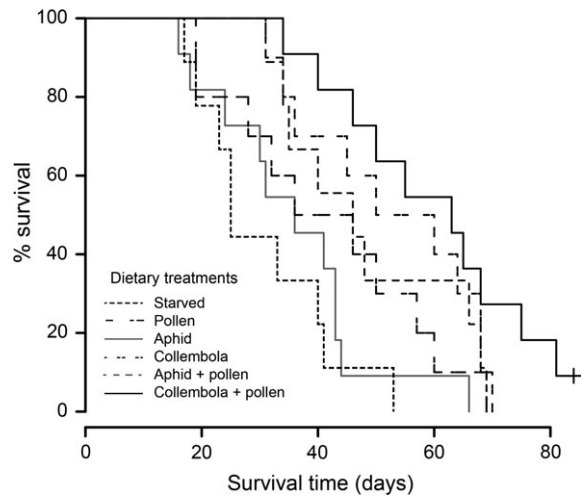
Figure 3 Kaplan–Meijer survival analysis of adult *Mermessus fradeorum* spiders fed on different diets.

($\chi^2 = 6.1$, d.f. = 1, P = 0.014; Figure 2A). Aphids were a poor prey source for adult female spiders as survivorship was not significantly different from starved spiders ($\chi^2 = 0.8$, d.f. = 1, P = 0.36), and the addition of pollen to an aphid diet had no effect on survival as compared to aphid-only diet ($\chi^2 = 1.3$, d.f. = 1, P = 0.26; Figure 3). Offspring production was also influenced by diet with a significantly greater number of eggsacs produced in treatments in which spiders were fed diets containing Collembola ($F_{5,36} = 9.67$, P<0.0001; Figure 4A). Pollen fed spiders produced an average of one eggsac over their lifetime, which was similar to the number of eggsacs produced when spiders were fed a diet of aphids or aphids + pollen (Figure 4B). Spiders that produced more eggsacs correspondingly had higher rates of successful offspring emergence ($F_{5,36} = 5.34$, P = 0.0009; Figure 4B and C). Although spiders fed a diet of only pollen produced eggsacs, only one spiderling emerged from these eggsacs (Figure 4B and C). Initial size differences or body condition of spiders assigned to treatments cannot account for these results because the average size of the
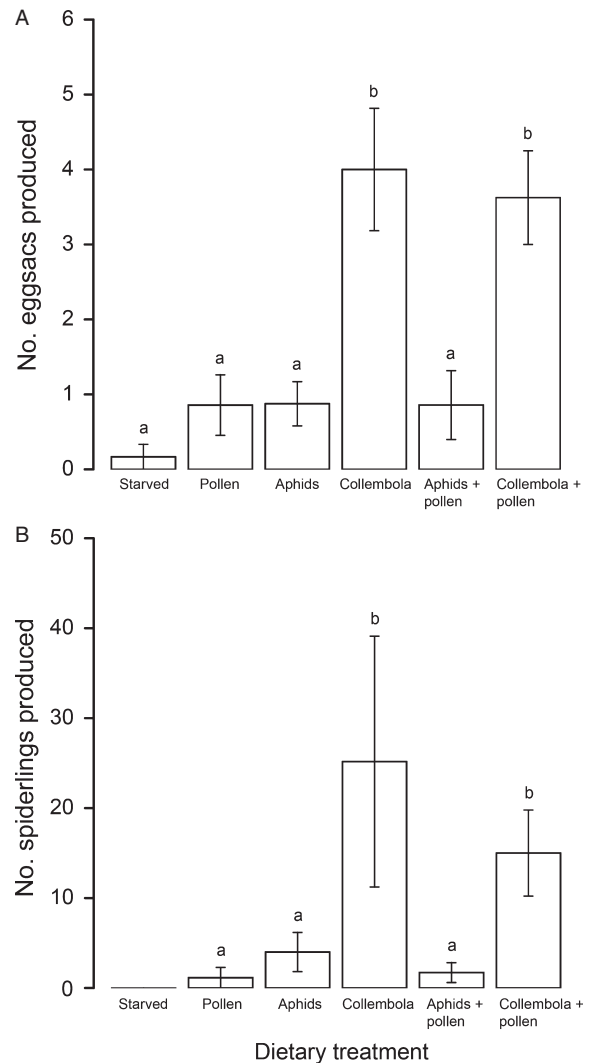
Figure 4 Mean ($\pm$ SEM) (A) life-time eggsac production, and (B) number of emerging spiderlings from eggsacs produced by *Mermessus fradeorum* females assigned to different dietary treatments. Females were mated with randomly selected males following 14 days of feeding on the various diets. Bars within a panel capped with different letters are significantly different (Tukey HSD: P<0.05).

spiders (0.91 ± 0.01 mm) and condition (1.27 ± 0.02 mm) was similar directly before the experiment ($F_{5,48} = 1.16$, P = 0.34; $F_{5,42} = 1.07$, P = 0.39).

Discussion

Our data have shown that multiple aspects of the life history of small web-building spiders are positively enhanced by pollen feeding. In particular, pollen consumption improved survivorship rates in spiderlings and adult females, and promoted growth of spiderlings (as measured by change in cephalothorax width). In addition, food limitation enhanced the tendency to consume pollen; under field conditions, this tendency is predicted to be affected by changes in availability and quality of prey and non-prey sources. Despite increasing survival, ingestion of pollen corresponded with lower levels of lipids and protein in spider tissues as compared to prey or mixed diets. Although Collembola were the highest-quality food resource in this study, supplemental feeding on pollen in addition to these prey significantly enhanced survivorship. These results indicate that spiders are capable of extracting nutrients from pollen, which temporarily releases them from nutrient limitation.

Pollen is a rich source of nutrients (Roulston & Cane, 2000) and is, therefore, implicated as an alternative food source for entomophagous arthropods (Lundgren et al., 2005). However, still little is known about the effects of feeding on pollen on the nutritional status of spiders (Pfannenstiel & Patt, 2012). Our data show that nutrient levels in the food resources provided influenced spider tissue composition (Table 2). Pollen provided the nutrients necessary to increase survival rates above food-limited spiders (Figure 1), but did not provide adequate essential nutrients required to complete development (Figure 2A). There are multiple nutrients that a diet of only pollen could lack, including essential amino acids necessary for ecdysis, and micronutrients (Smith & Mommsen, 1984) or sterols (Pilorget et al., 2010). Studies on nutrition in predators currently focus on the effects of lipid and nitrogen content in the prey (Mayntz & Toft, 2006; Wilder et al., 2010; Jensen et al., 2012), but the effects of essential micro-nutritional components on spiders and other predators require further study (Wilder, 2011). The mass of lipid and nitrogen present in dry pollen was significantly lower than in dry prey (Table 1), which does not necessarily correspond to the amount of nitrogen consumed by the spiders, because pollen is dry and prey is mostly water which affects nutrient content per meal and the ultimate nutrition eaten by an animal (Lundgren, 2009b). Therefore, we speculate that the correspondingly lower lipid and nitrogen found in tissues from spiders that were provided

a diet of only pollen may have arisen from a different form of these nutrients in the pollen relative to prey that was less easily utilized by the spiders in our experiment (Table 2). A competing explanation for the spiders becoming nutrient-limited relates to the long-term effects of digestive inefficiency. Pollen grains are not always easily digested by animals (Roulston & Cane, 2000), so this indicates a nutrient quantity vs. accessibility issue for spiders that lack specialized digestive machinery to extract nutrients from pollen. Although some carnivorous arthropods can complete their life cycle on a diet of pollen alone (Lundgren & Wiedenmann, 2005), the nutrition provided or extracted by *M. fradeorum* from pollen alone is not sufficient for these spiders to complete their life cycle.

Observational and molecular data show that spiders consume aphids in the field (Nyffeler, 1999) and potentially contribute to biological control (Harwood et al., 2004); however, aphids tend to be poor-quality food sources for spiders (Bilde & Toft, 2001). Alternative prey such as Collembola are commonly found in spider diets (Agusti et al., 2003) and potentially help sustain spider populations to further aid in biological control. Our data provide nutritional and life-history evidence that corroborates these past studies by showing that Collembola consumption has significant positive effects on tissue nutrient levels, as well as survival, growth, and reproduction. Nutrient levels present in the dry mass of aphids and Collembola differed in C and N concentrations, and ratio of C:N, and spiders appeared to gain more lipid and protein from treatments containing Collembola (Table 1), which emphasizes the importance of prey nutrient levels in determining predator performance. Furthermore, although we provided the same biomass of aphids or Collembola in our treatments, growth and body condition of spiders fed on aphids was significantly reduced as compared to spiders fed Collembola diets (Figure 2). That there was always prey of either type remaining after feeding indicates that adequate amounts of food were provided. These combined results on single prey diets provide further support of nutritional ecology as an important consideration in promoting spider populations early in the season to fuel-enhanced biological control of aphids. For spiders, it has been frequently posited that dietary diversification is advantageous because mixed diets contain a greater number of essential nutrients (Riechert & Luczak, 1982; Riechert & Lawrence, 1997), and at times this may be true (Greenstone, 1979). However, some research shows that mixed diets or greater diversity of material consumed in the laboratory does not always correlate with increased performance (Toft & Wise, 1999a). That spiders were able to incorporate pollen nutrients into their bodies, which increased survivorship, provides evidence that pollen is a

viable alternative non-prey resource. When spiders were provided mixed diets containing aphids or Collembola combined with pollen, this improved survivorship of spiderlings and of adult spiders (Figures 1 and 3). In addition, the spiderlings were in better condition as compared to spiderlings fed on pollen or aphids alone, providing evidence that addition of non-prey food to a low-quality prey diet (aphids) can improve nutritional status of these spiders. Conversely, addition of pollen to a diet of Collembola improved survivorship, but final size was lower and body condition was similar to when spiderlings were fed only Collembola. In addition, spiders fed a diet of Collembola only or Collembola paired with pollen had the greatest reproductive output. This indicates that Collembola are high-quality prey that enhance fitness of these spiders. These results combined suggest that the nutritional benefits of supplementing a prey diet with pollen are prey- and pollen-specific and may provide benefits only at times when mixed with low-quality prey or when prey are scarce.

In conclusion, studies have shown that interception of pollen in webs potentially represents a substantial resource available to spiders (Sunderland et al., 1987; Ludy & Lang, 2006; Peterson et al., 2010). Recent studies also show that pollen and other non-prey foods such as sugars and nutrient-rich powders enhance the growth of spider populations (Patt et al., 2012; Pfannenstiel & Patt, 2012). However, additional research is clearly required to understand the consequences of these pulses of non-prey resources on predator population dynamics. Here we show that a common Linyphiidae spider readily consumes maize pollen, which enhances survival of immatures and adults and can alter nutritional status. The nutritional status of predators has been shown to influence feeding rates on prey (Bressendorff & Toft, 2011; Schmidt et al., 2012), and here we show that nutritional status is altered by pollen consumption. The current findings provide evidence that pollen is a beneficial nutritional resource to these predators that are often food-limited in the field. Non-prey foods for generalist predators, therefore, may provide the added nutrition necessary to reduce intraguild or cannibalistic interactions, a tendency that has been linked to starvation (Mayntz & Toft, 2006). The ability to consume non-prey foods could indirectly enhance their top-down effects on prey or biological control efficacy in managed systems. The fact that maize pollen was readily consumed is especially interesting, given that maize is wind pollinated. Thus, no selection will have acted on the plant for producing this resource for spiders that would favor pollenivory (as might occur, for example, with bee-pollinated plants). Our results contribute to the discussion of the importance of dietary balancing in generalist predators by documenting nutritional changes in spider tissues driven by availability of non-prey food sources.

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