

Effects of nectar feeding on cannibalism in striped lynx spiderlings *Oxyopes salticus* (Araneae: Oxyopidae)

Laurel B. Lietzenmayer^{1,2} and James D. Wagner¹: ¹Department of Biology, Transylvania University, Brown Science Building, 300 North Broadway, Lexington, Kentucky 40508-1797 USA; ²Present address: Department of Entomology and Nematology, University of Florida, Steinmetz Hall, 1881 Natural Area Drive, Gainesville, FL 32608-1902 USA; E-mail: lblietzenmayer@gmail.com

Abstract. The timing and nutritional value of a first meal is important for spiderlings, but little is known about what spiderlings specifically consume. For wandering spiders, nectar feeding is a common occurrence thought to be directly beneficial in providing nutrients and serving to fuel energy costly for foraging. Cannibalism is also prevalent among many spiders. We suspect in spiderlings of the cursorial species, *Oxyopes salticus* Hentz, 1845, nectar feeding could decrease cannibalism by causing satiation, or increase cannibalism by enhancing energy levels and rates of interaction. We conducted laboratory experiments to test the longevity of newly hatched *O. salticus* in the presence of different nutrient resources and the effect these resources had on cannibalism rates. Spiderlings were housed solitarily or in pairs and given access to different nutrient resources that reflect those available in the wild, including nectar and insect prey items (fructose, protein, and water). In a 14-day period, we recorded the number of days each spiderling was alive to determine survivorship. By the end of the experiment, 60% of spiderlings housed with fructose were still alive and 10% survived when housed with protein or water. Based on survivorship models, the predicted mean age at death differed between treatments (15.9 days for fructose, 11.2 days for protein, and 9.5 days for water). Spiderlings housed in pairs declined more rapidly in survivorship compared to solitary spiderlings, suggesting cannibalism occurred across all treatments. Fructose significantly increased longevity of spiderlings regardless of their housing and reduced cannibalism.

Keywords: Lynx spider, nectivory, predation, survivorship

For spiderlings, finding nutrient resources in the early life stages is critical to their survival. Body size positively correlates with the supply of nutrient reserves in the body (Hvam et al. 2005), and newly hatched wolf spiderlings cannot survive more than a few weeks without a meal before their nutrient reserves fully depreciate (Toft & Wise 1999). Early stages molt more frequently than later instars (Foelix 2011), making the timing and nutritional value of that first meal essential. Highly nutritional meals that are quick and easy to obtain will result in more frequent molts earlier in life, allowing spiderlings to surpass competitors in size and expand the range of potential prey items (Oelbermann & Scheu 2002; Mayntz et al. 2003). However, it may be difficult for spiders like the striped lynx spider, *Oxyopes salticus* Hentz, 1845, to find appropriate sized prey compared to spiderlings of other species. Striped lynx spiderlings are relatively small; by carapace width, *O. salticus* spiderlings are 0.58 ± 0.04 mm (mean \pm SE) (Young & Lockley 1986) whereas wolf spiderlings, like *Tigrosa helluo* (Walckenaer, 1837) (given as *Hogna helluo* in Walker et al. 2003), are 0.88 ± 0.05 mm (Walker et al. 2003). Considering their smaller body size, amount of nutrient reserves, and range of potential prey items, striped lynx spider hatchlings may be attaining their first meal in alternative ways, including cannibalism or nectar feeding.

Nectar feeding has been observed in many wandering spiders (Taylor & Foster 1996; Jackson et al. 2001; Nyffeler et al. 2016). It is thought that wandering spiders are likely to nectar feed due to low success rates of hunting and the direct benefit they receive from feeding on the plant's extrafloral nectaries and flowers which are predictable and sessile food resources that could help fuel their cursorial lifestyle (Taylor & Bradley 2009). For two wandering spiders, *Hibana velox*

(Becker, 1879) (Anyphaenidae) and *Cheiracanthium mildei* L. Koch, 1864 (Eutichuridae), nectar has been shown to increase molting, foraging activity, and survival in spiderlings (Taylor & Bradley 2009). A ghost spider, *Hibana futilis* (Banks, 1898), can respond to and track chemical cues associated with nectar, allowing it to forage for nectar as it moves among particular plants (Patt & Pfannenstiel 2008). Overall, the high metabolic costs of the foraging strategy of wandering spiders can be supplemented by nectar as an energy rich food source.

Cannibalism provides another readily available nutrient source for spiderlings and is prevalent in many spider species during early life stages (Hvam et al. 2005; Wise 2006). However, the nutritional benefits of cannibalism are contested. Cannibalism has been argued to provide more optimal nutrients for conspecifics than heterospecific diets (Mayntz & Toft 2006), but it has also been shown that conspecifics provide a low-quality diet resulting in slow growth (Oelbermann & Scheu 2002; Mayntz & Toft 2006).

There are several costs to cannibalism that may reduce its prevalence among spiderlings, including the risk of injury from prey with similar predatory abilities, the possible reduction of inclusive fitness, and the potential of contracting pathogens from conspecifics (Pfennig et al. 1998; Jackson et al. 2001; Hvam et al. 2005; Mayntz & Toft 2006; Petersen et al. 2010). In two species of wolf spider, *Pardosa prativaga* (L. Koch, 1870) and *P. amentata* (Clerck, 1757), individuals were usually reluctant to cannibalize and only did so as a last resort to avoid starvation, suggesting that hunger level was the main motivator for cannibalistic behavior (Hvam et al. 2005; Petersen et al. 2010). For spiderlings, if an alternative food source like nectar is available and readily consumed, cannibalism may be less likely to occur. However, it is also

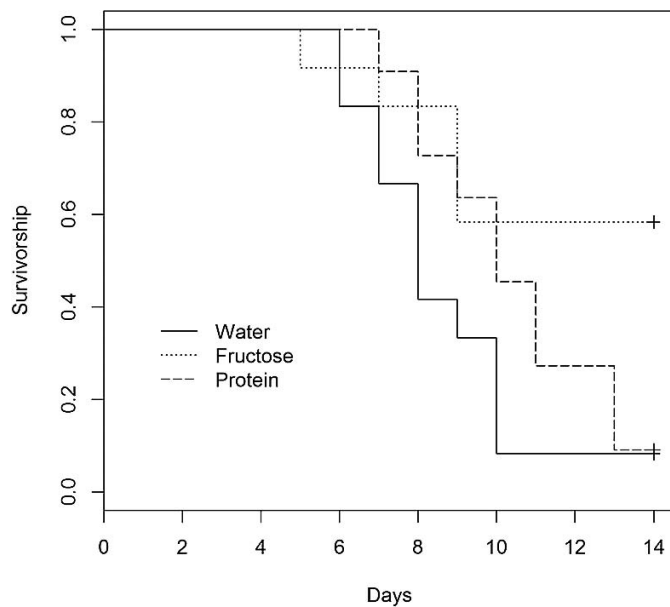


Figure 1.—Survivorship curves of solitary *O. salticus* spiderlings when housed with different food resources (Water, Fructose, Protein). Survivorship refers to the percentage of spiderlings alive each day for a 14-day period.

possible that higher energy levels associated with sugar intake from nectar could increase cannibalism rates, as spiderlings are more active and more likely to interact with conspecifics and partake in risky behaviors (Jackson et al. 2001; Taylor & Pfannenstiel 2009). For the wolf spider *T. helluo*, early instars were more cannibalistic when alternative food was available and exhibit high levels of aggression that can be directed toward conspecifics when contained in high densities (Roberts et al. 2003). Spiderlings may be using nectar as a preliminary energy source to fuel future hunting. Therefore, nectar feeding may be used by striped lynx spiderlings in different ways; nectar may satiate spiders and reduce their tendency to cannibalize or nectar may increase energy levels that drive cannibalistic events.

In this experiment, we tested cannibalism rates within pairs of unrelated lynx spider hatchlings in the presence of different nutrient sources: water, protein, or nectar. Through this laboratory study, we expected to gain information regarding (1) how different resources affect the longevity of newly hatched spiderlings and (2) how cannibalistic behavior varies in the presence of different resources. Our main goal was to detect the presence of nectar feeding in spiderlings and determine how this behavior ultimately affects the tendency to cannibalize.

METHODS

Mature female striped lynx spiders, *Oxyopes salticus*, were collected in grassy fields at the University of Kentucky Agricultural Farm (GPS: 38° 06' 30.7"N, 84° 29' 53.2"W). In the lab, females were kept in separate containers (8.5 cm x 8.5 cm x 16 cm) and were fed daily with field captured insects until they laid egg cases (6.33 ± 0.92 days [mean \pm SE]). This allowed for standardization of age and hunger level of new

hatchlings. Adult females tended to their egg cases until they hatched (19.67 ± 0.92 days [mean \pm SE]), and testing began after spiderlings dispersed throughout the container (24 hours). Three broods from three individual females were included in each treatment, with spiderling age varying only by one day.

Control survival treatments had a solitary housed spiderling while the cannibalism treatments housed a pair of unrelated spiderlings. Spiderlings were placed in plastic cylindrical vials (7×2.5 cm) with two 0.5 mL microcentrifuge tubes opened to the inside and secured in holes drilled into the lids. For both solitary and paired spiderlings, one microcentrifuge tube always contained water while the other tube was stocked with either water, artificial nectar, or protein solution. Artificial nectar was created using a 20% fructose solution (Nicolson & Thornburg 2007). Protein solution was created using EAS Soy Protein powder diluted to a 12.6% solution. Using the 20% fructose solution as a reference, both nectar and protein solutions were created with sterilized water at concentrations that yielded the same caloric value (1.8 cal/mL). Each treatment had 12 replicates and all broods were equally represented in each treatment.

To reduce mold and bacteria, tubes and vials were rinsed in ethanol prior to set up and sterile gauze was used to plug the microcentrifuge tubes. The duration of the experiment was 14 days and vials were checked daily for deaths. We could distinguish natural deaths from cannibalism when cannibalism was observed directly. Water, fructose, and protein solutions were replenished every three days.

Statistical analysis.—Statistical analyses were conducted using R (build version 3.2.3 (2015-12-10)) and R Studio (version 0.99.491) installed with the Survival (2.39-5) and Survminer (0.2.1) libraries (Crawley 2013). The best fit model for the survivorship curve utilized an underlying Weibull distribution where hazards were non-constant with age (can increase or decrease) typified by Type I and Type III survivorship curves. This model fit the data significantly better than the alternative model where hazards remained constant over age which is typified by the Type II survivorship curve. Because some treatments resulted in spiders surviving the entire length of the experiment, we used a survivorship model with censored data. Censored data biases the estimates of lifespan since those individuals did not die within the time frame of the experiment so our response variable is not lifespan per se. To acknowledge this, we use the term longevity instead because the data only represents how long the spiders endured within the time frame of the experiment. In Fig. 2 a post-hoc pairwise comparison of the survivorship curves was made using the Benjamini & Hochberg (1995) method to adjust p-values for multiple comparisons.

RESULTS

Survivorship curves.—Daily census data allowed us to generate survivorship curves for each of the food treatments. To examine how food influenced the shape of the survivorship curve, we restricted our analysis to solitary spiderlings to avoid any confounding influence a cannibalism event can have on survivorship. The type of food resources available significantly influenced the shape of the mortality curves and mean age at death for the solitary spiderlings (Fig. 1). By the end of the 14-day experiment, 60% of the spiderlings housed

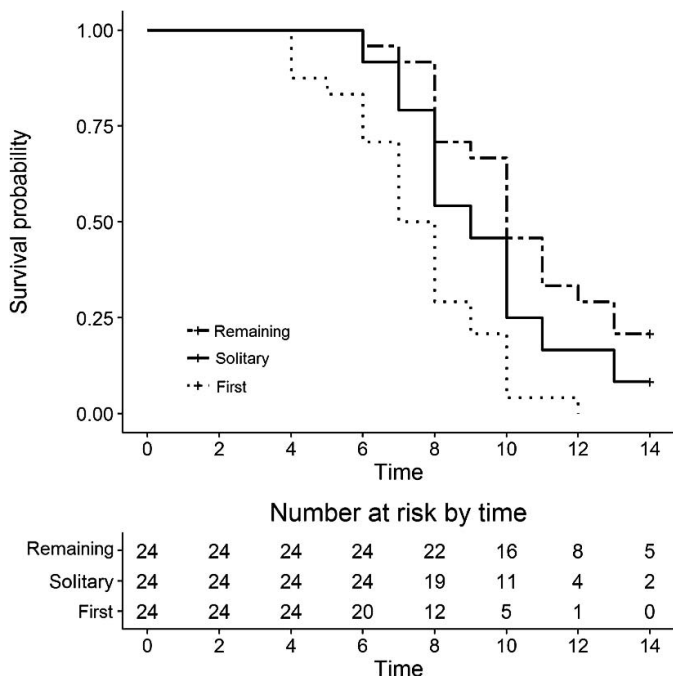


Figure 2.—Survivorship curves of solitary *O. salticus* spiderlings compared to both the first dead and remaining *O. salticus* spiderlings in pairs across water and protein treatments over the 14-day period. Fructose treatments are excluded. The table below the graph includes a summary of number of surviving individuals (at risk) at each time point.

with fructose were still alive, which was in sharp contrast to the protein and water treatment where only 10% survived. Analysis of the survivorship curves revealed that the fructose treatment was significantly different from the water treatment (Fig. 1; Survreg, Fructose: Water $z = 3.22$, $n = 36$, $P = 0.0013$). The protein treatment was intermediate between the water and fructose treatment but not significantly different from the water treatment (Survreg, Protein: Water $z = 1.20$, $n = 36$, $P = 0.229$). Based on the survivorship model for each treatment the predicted mean age at death for water was 9.5 days, fructose 15.9 days, and protein was 11.2 days. The predicted mean age of death for the fructose model exceeded that length of the experiment (14 days) because many of the spiderlings lived to the end of the experiment which increased the amount of censored data in the model.

Did cannibalism occur?—During the daily inspections of the paired vials, we observed five instances of spiderlings actively feeding on another individual although no direct attacks or captures were observed. To evaluate if housing with another spider increased rate of mortality, we compared the survivorship curves of the solitary spiders with that of the spider that died first and the remaining spider in the paired vial for the water and protein treatments. We excluded the fructose treatments in this analysis because fructose increased survival above expected and nearly eliminated cannibalism with 16 of the 24 spiderlings in paired treatment surviving the entire 14-day experiment. Spiderlings who died first in paired vials showed a more rapid decline in survivorship compared to solitary spiderlings (Fig. 2; $P = 0.011$) and the remaining paired spiderlings (Fig. 2; $P = 0.0001$). Solitary spiderlings

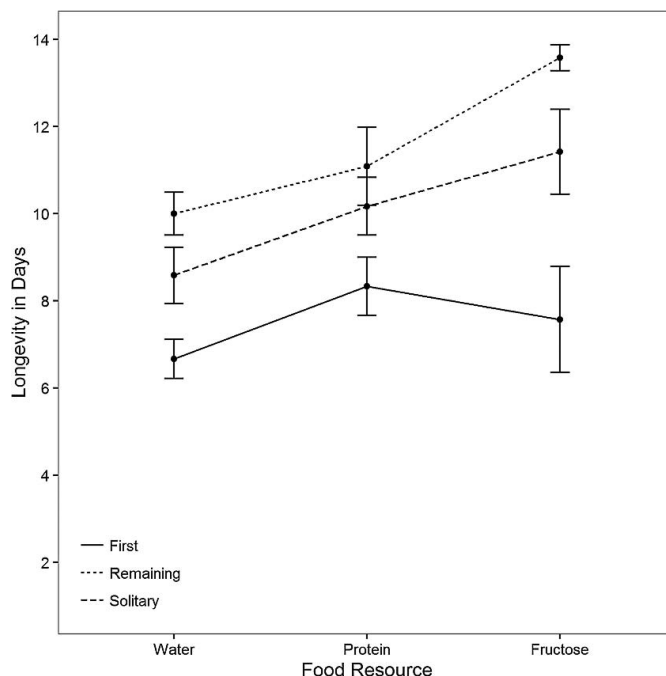


Figure 3.—Interactions between food resource and status (solitary, 1st dead spiderling, 2nd remaining spiderling) on *O. salticus* longevity. Spiderlings in a pair that survived to the end of the experiment were excluded. Points represent mean longevity for spiderlings in each treatment (mean \pm SE).

showed no difference in survival compared to the remaining paired spiderlings (Fig. 2; $P = 0.103$).

Cannibalism and longevity.—To examine how food resource may interact with cannibalism to influence longevity, we ran an ANOVA to see how status (solitary, 1st dead spiderling, 2nd remaining spiderling) and food resource (fructose, protein, water) influenced longevity. We excluded from the analysis pairs where both spiders survived to the end of the experiment since this analysis is designed to examine factors influencing cannibalism and cannibalism did not occur in those vials. A Bartlett's test for the homogeneity of variances determined that our data is normally distributed (status: $\chi^2(2) = 0.177$; food: $\chi^2(2) = 0.046$). The ANOVA indicated both main effects significantly predicted longevity (status: $F_{2,87} = 20.94$, $P < 0.001$; food: $F_{2,87} = 7.47$, $P < 0.0001$) with no significant interaction between status and the food available (Fig. 3; $F_{4,87} = 1.995$, $P = 0.102$).

DISCUSSION

Our data shows that different resources affect the longevity of newly hatched spiderlings (Fig. 1). Spiderlings readily fed on the fructose resource and it significantly increased their survival. In all the treatments, spiders were given access to two vials – all food types were paired with a vial of water. We interpret that spiders recognized the fructose as a food source different from water and took advantage of that resource to improve their survival. However, further studies are necessary to confirm spiderling recognition of artificial nectar over water. It is not clear that the spiders recognized the protein vials as readily. The protein food source was derived from a

vanilla flavored powder, which may have affected how the spiderlings reacted to it. This may explain why the survivorship of spiderlings from the protein treatment was not significantly different from the water treatment, as the spiderlings may have not recognized the protein solution as a resource superior to water alone. In future studies, soybean liquid may be a more beneficial alternative to protein powder as it has been shown as a successful protein source in artificial spider diets (Amalin et al. 1999, 2001). It is also important to note that in nature, nectar could also be providing spiderlings with some proteins (Nicolson & Thornburg 2007). Using mixtures that are more reflective of the protein compositions found in natural nectar that lynx spiderlings have access to in the wild may further reduce cannibalistic behavior, including various nectarins and phosphatases that are common in many plant nectars (Nicolson & Thornburg 2007).

This study has provided new insight on the nutritional ecology of *O. salticus*, a species of considerable interest from an agroecological point of view. As one of the most abundant spiders in field crops in the United States, *O. salticus* has been known to consume a number of common crop pests, including the tarnished plant bug, *Lygus lineolaris*, and the bollworm, *Helicoverpa zea* (Young & Lockley 1985; Young & Edwards 1990). Striped lynx spiders are also more tolerant of hot and dry crop situations than other common predators, making them an important species to consider for biocontrol efforts (Young & Edwards 1990; Nyffeler & Sunderland 2003). Our findings may be useful for supporting and rearing *O. salticus* populations for use in agroecosystems.

Creating artificial nectar of nectar proteins and accurate sugar compositions could help to more accurately reflect spiderling behavior after its consumption. Most plant nectar consists primarily of sucrose, but high variability among species requires more knowledge on the particular plant species within lynx spider habitats (Handel et al. 1972). If spiderlings do recognize and respond to fructose solutions in the lab, this may connect to the presence of nectar feeding in the wild by *O. salticus* spiderlings due to their small size and cursorial lifestyle among the vertical space of plants. Spending most of their juvenile life in close proximity to nectar resources, we suspect that these spiderlings are taking advantage of nectar as an energy source to increase their longevity. Nectar feeding has already been observed in wandering spiders (Taylor & Foster 1996; Jackson et al. 2001; Taylor & Bradley 2009), including two individual lynx spiders (Taylor & Pfannenstiel 2008).

The results of this experiment suggest that *O. salticus* spiderlings do exhibit cannibalistic behavior. Although we cannot explicitly conclude that all first deaths in paired spiderlings were a result of cannibalism, our data and direct observations provide strong evidence that cannibalism was occurring. In addition to directly observing five instances of spiderlings feeding on a conspecific, we explain cannibalism in terms of paired spiderling longevity compared to solitary spiderling longevity. Spiderlings that died first among pairs had a more rapid decline in longevity than solitary spiderlings and the second remaining spiderling (Fig. 2), suggesting that these spiderlings were dying earlier than we would expect given their nutritional resources. However, the remaining spiderlings in pairs did not show any overall benefit to

cannibalizing because the longevity of solitary and remaining spiderlings did not differ (Fig. 2).

We found that nectar as an alternative food source greatly reduced cannibalism in the early instars, with only 33% mortality for paired spiderlings with nectar available (and 50% of pairs exhibiting no cannibalism) compared to 90% mortality for paired spiderlings without an alternative food source. Food limitation is considered the single most important factor promoting cannibalism because hunger increases foraging activity and risk taking during foraging (Wise 2006). It may be that nectar feeding resulted in lower hunger levels, deterring spiderlings from cannibalizing. Because both water and fructose were available to spiderlings, our data suggests that nectar is actively being chosen as an alternative, less risky food source to conspecifics, resulting in a drastic decrease in cannibalism. An alternative explanation for the lower rates of cannibalism in the presence of fructose may be that spiderlings are using this resource to increase their energy levels and avoid being cannibalized by evading the potential cannibal. However, this hypothesis seems unlikely because hungry spiders display increased aggression and risk taking behavior (Petersen et al. 2010); both spiderlings in a pair were likely to consume nectar and reduce their hunger and aggression levels.

Our findings are congruent with other studies that have shown cannibalism is less likely to occur when spiders are satiated and similar in size (Vanacker et al. 2004; Rickers & Scheu 2005; Wise 2006; Peterson et al. 2010). In a natural setting, spiderlings that take advantage of nectar sources may be able to reduce the frequency of cannibalistic events, creating an opportunity for spiderlings to grow at varying rates depending on their access to nectar. If body size ratios increased after several instars, the potential for cannibalism may increase. Studies have shown with increasing size variation, there is an increased propensity for cannibalism (Hvam et al. 2005; Petersen et al. 2010).

A longer observation period might show interactions we fail to see in only two weeks, particularly in the fructose treatments because of the high percentage of survival at the end of the experiment. Other experiments related to food sources and survival of spiderlings have used 6 to 27 weeks of observation, showing longer term effects that we are unable to see in 14 days (Toft & Wise 1999; Mayntz & Toft 2001; Oelbermann & Scheu 2002). However, these experiments were performed with wolf spiders, *Pardosa amentata* and *Pardosa lugubris* (Walckenaer, 1802), which can survive longer (12–21 days) than *O. salticus* (9.5 days) when being starved with access to water. Lynx spiders may hatch with less fat reserves than wolf spiders, making them unable to survive for comparable periods of time to wolf spiders. This makes our shorter period of time more appropriate to the specific study species used.

Cannibalism rates among different species of spiderlings are comparable to the 90% mortality after 14 days we observed in water treatments. In *P. palustris* (Linnaeus, 1758), there was 95% mortality among juveniles with no alternative food source besides conspecifics (Rickers & Scheu 2005). A rate of cannibalism of 70% after 14 days of starvation was seen in *P. agrestis* (Samu et al. 1999). Dwarf spiders, *Oedothorax gibbosus* (Blackwall, 1841) (Linyphiidae), showed 61–90% mortality after 20 days (Vanacker et al. 2004). Variation

occurs from inconsistent methods in experimental design, but all studies resulted in over 60% mortality. When given access to nectar, lynx spiderling mortality reduced to 33% after 14 days, considerably less than other groups without the addition of an alternative food source.

Ultimately, this study adds to the growing body of evidence of spider nectivory (Nyffeler et al. 2016), particularly in spiderlings when nutrient resources in the early life stages is crucial to survival. In the lynx spider, and species with similar lifestyles, nectar feeding may play an essential role in the first meal of many spiderlings. Nectar feeding provides the essential nutrients to increase the longevity of spiderlings while also reducing costly cannibalistic behaviors.

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