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A survey of nectar feeding by spiders in three different habitats

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Abstract

Using cold-anthrone tests, spiders collected in the field were sampled for the presence of plant sugar (fructose). The spiders came from three different habitats: a cotton field, a mixed rape and fava bean field, and a park with flowering woody and herbaceous plants. The percentages of fructose-positive spiders were compared among the different habitats, as well as among the different sexes and ages of *Ebrechtella tricuspidata* (F.) (Araneae Thomisidae). Out of 745 field-collected spiders, 18.7% were positive for fructose, indicating that these spiders feed on plant nectar. Of the 12 families of spiders represented, individuals from 9 families were positive for fructose: Oxyopidae, Thomisidae, Pisauridae, Salticidae, Lycosidae, Tetragnathidae, Araneidae, Nephilidae, and Agelenidae. All members of the other three families (Linyphiidae, Clubionidae and Theridiidae) were negative for fructose. There were no differences for nectar feeding in spiders among the three habitats: 19.3% of individuals from the cotton field, 16.6% from the mixed rape and fava bean field, and 20.0% in park with flowering woody and herbaceous plants tested positive for fructose. For *E. tricuspidata*, significantly more females were positive than males (87.5% versus 42.9%); and immatures tested positive at a lower rate than adults (26.5% and 66.7%, respectively).

Key words: spider, nectar, fructose, anthrone-sulphuric acid.

Introduction

Spiders are generally envisaged as being obligate carnivores (Nentwig, 1987; Foelix, 1996), meaning that they acquire nutrition by feeding on other invertebrates. They are especially known for feeding on other active arthropods, but some spiders eat insect eggs or the eggs of other spiders (Buschman *et al*., 1977; Willey and Adler, 1989; Nyffeler *et al*., 1990; Jackson and Willey, 1994; Cross *et al*., 2009). There are also instances of spiders feeding on dead arthropods (Sandidge, 2003). However, spiders can also expand their food source by feeding on plants. Meehan *et al.* (2009) discovered herbivory in *Bagheera kiplingi* Peckham et Peckham, a Neotropical jumping spider (Salticidae). The spider feeds primarily and deliberately on the tips of an ant-acacia leaflet. Several species of cursorial spiders imbibe nectar as an occasional supplement to animal prey (Jackson *et al.*, 2001), and some juvenile orb-web spiders ingest pollen when recycling their webs (Smith and Mommsen, 1984). In addition, nectaries of plants including floral and extrafloral nectaries (EFNs) are often visited by wandering spiders, including members of Salticidae (Edmunds, 1978), Thomisidae (Vogelei and Greissl, 1989; Beck and Connor, 1992; Pollard *et al.*, 1995), and the fast-moving nocturnal spiders Clubionidae (Ruhren and Handel, 1999), Anyphaenidae, and Corinnidae (Taylor and Foster, 1996; Patt and Pfannenstiel, 2008). When the spiders are near the nectaries, they can prey on nectarivorous insects or can also feed directly on nectar. In these two ways, the spiders can extend their diets to an additional trophic level.

We used the cold anthrone-sulphuric acid method (Van Handel**,** 1972; Li *et al*., 2003; Taylor and Pfannenstiel, 2008), to determine the concentration of fructose in spiders to judge whether they were feeding on nectar. Fructose is a component of sucrose. Fructose, sucrose, and glucose can be found in plant nectar, in different proportions (Nicolson and Thornburg, 2007). A test for fructose can ensure that the sugar is from plants, distinguishing it from glucose. Although the latter is a component of nectar, it also occurs in the blood and lymphatic elements of some spiders (Barron *et al.*, 1999). Reacting with concentrated sulphuric acid, fructose is dehydrated to generate furfural or hydroxymethylfurfural, which can react with anthrone to generate blue-green or blue furfural derivatives. The depth of colour is proportional to the fructose content with a certain scope, so the anthrone generated can be used to assess the amount of fructose present in spiders.

In the present study, we used the cold anthrone-sulphuric acid method to determine the concentration of fructose in individual spiders, including web-building spiders and wandering spiders, collected from three different habitats: cotton field, a mixed rape and fava bean field, and a park with flowering woody and herbaceous plants. *Ebrechtella tricuspidata* (F.) (Araneae Thomisidae), a dominant spider in the fields, was used as an example to compare the difference in nectar feeding among spiders of different ages and sexes.

Materials and methods

Solution preparation

The anthrone reagent was prepared by pouring 380 ml concentrated sulphuric acid into 150 ml distilled water (diluted sulphuric acid), and then mixing 150 mg anthrone with 100 ml the diluted sulphuric acid. We created a series of standard sucrose solutions corresponding to 1, 2, 4, 8, 16, 32, 64, 128, and 256 μg/μl (0.1-25.6% solutions) by dissolving 25.6 g of reagent-grade sucrose in 50 ml of distilled water, adding enough water to make 100 ml of solution, and making eight two-fold serial dilutions (Haramis and Foster, 1983). These solutions were stored at -45 °C. The colorimetric standards for measuring fructose in the spider samples were created by pipetting 1 µl of nine standard sucrose solutions into a test tube and adding two drops of the 1:1 chloroform-methanol solution and 0.5 ml of anthrone reagent. The mixture solutions were held in a 38 °C water bath for 1 h. The colour of the solutions changes from green to green-blue in the presence of fructose, depending on the amount of fructose. We are able to identify fructose content as low as 1 µg.

The collection and preparation of spiders

We collected spider samples early in the evening (18:00-21:00), between November 2008 and September 2009, from three different habitats in Hubei Province, China: a cotton field (CF) at Huazhong Agricultural University; a mixed rape and fava bean field (MRFBF) at the Oil Crops Research Institute, Chinese Academy of Agricultural Sciences; and a park with flowering woody and herbaceous plants (PFWHP) at Hubei University. A sweep net and glass tube (2 × 10 cm) were used to capture the spiders. The collected spiders were killed immediately by immersion in liquid nitrogen, and were stored in a freezer at -86 °C. Because some digestion most likely occurred between collection and complete arrest of the enzymatic activity, our results should provide a conservative measure of nectar feeding in the field. Within a day or two, samples were heat-treated at 80-90 °C for 15 min, using a water bath to drive off all moisture, and were stored for later testing.

The detection of fructose in spiders

To prepare spiders for testing with anthrone, each spider was placed in a 5-ml test tube and moistened with two drops of chloroform-methanol solution to remove cuticular wax. After 20 min, the spiders were gently crushed with a glass stirring rod. Anthrone reagent (0.5 ml) was added, and the tubes were agitated on a vortex mixer, held in a 26 °C water bath for 1 h. The upper, clear liquid was used to compare the colour with the colorimetric standards and to determine the concentrations of fructose in the spiders. Evaluation of the centrifuged and decanted sample by spectrophotometer was not possible because of the presence of spider remains in the sample. Visual inspection without centrifuging allowed us to detect the content of fructose as low as 1 µg. However, we included only readings of more than 2 µg, to ensure that no false positives were recorded. This precaution also contributes to obtain a conservative estimate of fructose-positive spiders. In this experiment, the sample without fructose is a transparent yellow. If green was produced, it indicated only the presence or existence of a combination of fructose and glucose formed by sucrose. Positive spiders either contained the same fructose content as the standard solutions, or as a half of the standard solutions (with glucose).

Data analysis

The percentages of fructose-positive spiders were compared among the three habitats by using significance testing for cross-tabulation tables (2 × 3). Differences in positive percentages between sexes and ages of *E. tricuspidata* were compared by using significance testing for cross-tabulation tables (2 × 2). Chi-squares (χ^2) were calculated in SPSS.PASW.Statistics.v18.

Results

Percentage of nectar feeding by individual spiders

From November 2008 through September 2009, 745 individual spiders were collected and were tested for ingested fructose, including all ages and both sexes. A total of 139 spiders or 18.7% tested positive for fructose (table 1). The fructose contents from 1 µg to 64 µg. To avoid false positives, our analysis included only with 2 µg fructose and above. 83.5% of the samples contained amounts of fructose from 2 µg to 4 µg. The highest readings appeared in two samples of two species: one

Table 1. Percentage of fructose-positive individuals from 12 families of spiders in China (from November 2008 through September 2009).

Families	Species of spider	Percent (no. fructose-positive / no. spiders tested)		
		Adults + subadults	Immatures	Total
Oxyopidae	*Oxyopes sertatus*	48.7% (18/37)	30.0% (3/10)	44.7% (21/47)
Thomisidae	*Ebrechtella tricuspidata*	66.7% (46/69)	26.5% (39/147)	39.4% (85/216)
Pisauridae	*Pisaura ancora*	20.0% (1/5)	0% (0/1)	16.7% (1/6)
Salticidae	*Plexippus selipes*	28.6% (2/7)	0% (0/7)	14.3% (2/14)
Lycosidae	*Pardosa pseudoannulata*	16.7% (8/48)	10.0% (1/10)	13.8% (28/203)
	P. astrigera	14.8% (4/27)	8.3 (1/12)	
	P. laura	13.7%(14/102)	0% (0/4)	
Tetragnathidae	*Tetragnatha squamata*	11.8% (2/17)	0% (0/1)	11.1% (2/18)
Araneidae	*Lariniodes cornuta*	5.3% (2/38)	3.1 (1/32)	6.4% (7/109)
	Eriovixia cavaleriei	11.5% (3/26)	7.7% (1/13)	
Nephilidae	*Nephila clavata*	6.1% (3/49)	0% (0/2)	5.9% (3/51)
Agelenidae	*Agelena labyrinthica*	6.5% (2/31)	2.7% (1/37)	4.4% (3/68)
Linyphiidae	Linyphiidae sp.	0% (0/3)	0% (0/0)	0% (0/3)
Clubionidae	Clubionidae sp.	0% (0/6)	0% (0/2)	0% (0/6)
Theridiidae	Theridiidae sp.	0% (0/4)	0% (0/0)	0% (0/4)
Total				18.7% (139/745)

adult female *E. tricuspidata* (64 µg, Thomisidae) and one adult female *Lariniodes cornuta* (Clerck) (32 µg, Araneidae). The two samples were collected from the MRFBF.

Nectar feeding by spider in different families

Members of 9 of the 12 families were fructose-positive: Oxyopidae, Thomisidae, Pisauridae, Salticidae, Lycosidae, Tetragnathidae, Araneidae, Nephilidae and Agelenidae (table 1). The families Clubionidae, Theridiidae and Linyphiidate had no positive individuals. Of all species tested, 12 were found to feed on nectar: *Oxyopes sertalus* (L. Koch) (Oxyopidae); *E. tricuspidata* (Thomisidae); *Pisaura ancora* (Paik) (Pisauridae); *Plexippus setipes* (Karsch) (Salticidae); *Pardosa pseudoannulata* (Boes et Strand), *Pardosa astrigera* (Koch), *Pardosa laura* Karsch (Lycosidae); *Tetragnatha squamata* (Karsch) (Tetragnathidae); *Eriovixia cavaleriei* (Schenkel), *Larinioides cornuta* (Araneidae); *Nephila clavata* L. Koch (Nephilidae); and *Agelena labyrinthica* (Clerck) (Agelenidae). Although the spiders from nine families tested positive for fructose, there was a wide range in the positive percentage. The highest positive percentage was found in Oxyopidae (44.7%), and the lowest positive percentage occurred in Agelenidae (4.4%).

Nectar feeding by spiders in different habitats

The positive percentage for fructose in the spiders from PFWHP was highest (20.2%), and the spiders from MRFBF had the lowest positive percentage (16.6%). However, the differences in percentage among the three habitats did not reach a significant level ($\chi^2 = 1.0$, df = 2, $P > 0.05$) (figure 1). *E. tricuspidata*, one of the dominant spiders (Shangguan *et al.*, 2001), had similar positive percentages of fructose in the three different habitats ($\chi^2 = 0.4$, df = 2, $P > 0.05$) (figure 2).

Nectar feeding by *E. tricuspidata*

A total of 216 individuals of *E. tricuspidata* were collected from three habitats. Of these, 68.1% were immatures, and 31.9% were adults, which also included those subadults that could be sexed. Of the adults, 30.4% were males and 69.6% were female. Females were significantly more likely to test positive for fructose than males ($\chi^2 = 12.9$, df = 1, $P < 0.001$). 42.9% of the males were positive for fructose (table 2), and 87.5% of the females were positive. 66.7% of adult *E. tricuspidata* were positive for fructose, and 26.5% of the immatures were positive in the three habitats (table 3). The positive percentage for fructose in adults was significantly higher than that in immatures ($\chi^2 = 30.1$, df = 1, $P < 0.001$).

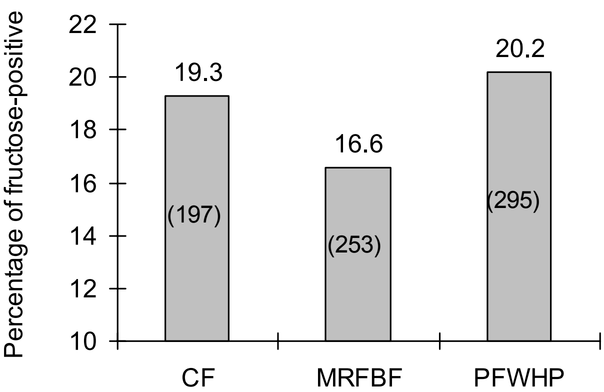

Figure 1. Percentage of fructose-positive individuals of all spiders collected from three habitats. Values in parentheses are number of individuals tested. CF - cotton field; MRFBF - mixed rape and fava bean field; PFWHP - park with flowering woody and herbaceous plants.

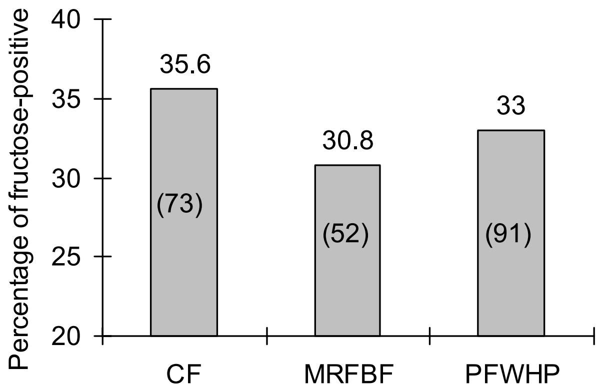

Figure 2. Percentage of fructose-positive individuals of *E. tricuspidata* from three habitats. Values in parentheses are number of individuals tested. CF - cotton field; MRFBF - mixed rape and fava bean field; PFWHP - park with flowering woody and herbaceous plants.

Discussion

Nectar feeding by spiders has been observed in a number of families (Taylor and Foster, 1996; Ruhren and Handel, 1999; Jackson *et al.*, 2001). Our survey showed that about 44.7% Oxyopidae, 39.4% Thomisidae, 16.7% Pisauridae, 14.3% Salticidae, 13.8% Lycosidae, 11.1% Tetragnathidae, 6.4% Araneidae, 5.9% Nephilidae, and 4.4% Agelenidae tested positive for fructose, even using conservative testing methods. The data clearly suggest that nectar feeding is indeed a common activity for these spiders. Many *E. tricuspidata* were caught beneath the flowers of rapes or the stipules of fava beans. These thomisids move slowly and prefer to remain hidden beneath leaves and flowers. For *E. tricuspidata* and other fructose-positive spiders, significantly more adults than immatures were positive for fructose, which may be caused by two reasons. First, immatures may feed on nectar less often than adults or they may feed as often but their fructose content is too low to detect. Second, immatures might also spend more energy pursuing for growth or for oogenesis, which seems to occur only before maturation (Miyazaki *et al.*, 2001; Choi and Moon, 2003; Morishita *et al.*, 2003). Adult female spiders were more likely than males to test positive. The abdomen of females is larger than that of males, which may account for this bias. The different sexes of *E. tricuspidata* may also feed or burn fuel differently. These spiders spend much of the rapidly wandering in the vegetation, but

Table 2. Percentage (%) of fructose-positive females and males of *E. tricuspidata* collected from three habitats.

Sex	Habitats (no. fructose positive/no. spiders tested)			
	CF	MRFBF	PFWHP	Total
Female	89.5 (17/19)	76.9 (10/13)	93.8 (15/16)	87.5 (42/48)**
Male	44.4 (4/9)	25.0 (1/4)	50.0 (4/8)	42.9 (9/21)

** Indicates a significant difference between female and male.

Table 3. Percentage (%) of fructose-positive individuals of different ages of *E. tricuspidata* collected from three habitats.

Age	Habitats (no. fructose positive/no. spiders tested)			
	CF	MRBBF	PFWHP	Total
Adults (or subadults)	71.9 (23/32)	61.5 (8/13)	62.5 (15/24)	66.7(46/69)**
Immatures	29.8 (14/47)	22.9 (8/35)	26.2 (17/65)	26.5(39/147)

** Indicates a significant difference between adults and immatures.

males are more active than females as they search for females to mate. Adult females, however, may be conserving energy to support egg development.

Five non-web-building families (Anyphaenidae, Miturgidae, Salticidae, Thomisidae, and Corinnidae) have been reported to feed on plant nectaries, and a new, cursorial family, the Oxyopidae, was added to the list of nectarivorous spiders by Taylor and Pfannenstiel (2008). However, in the same study, these authors found that none of the lycosids (wolf spiders) tested positive for fructose (Taylor and Pfannenstiel, 2008). In the present study, three species of lycosids (*P. pseudoannulata*, *P. astrigera* and *P. laura*) and one species of pisaurids (*P. ancora*) tested positive. In addition, our experiments demonstrated that members of web-building families also feed on nectar. The spiders from families Tetragnathidae, Araneidae, Agelenidae, and Nephilidae tested positive for fructose. However, the percentage of fructose-positive species of these four web-building families is lower than those of non-web-building families (table 1).

A nectar-feeding spider can either ingest fructose directly or consume prey that has ingested fructose. We did not perform experiments to measure the transfer of fructose to a spider by way of prey, and its importance. We note, however that studies to estimate predation by non-web-building spiders estimate predation to be low, from 0.4-0.8 to 6-8% (Nentwig, 1987). Nyffeler and Sterling (1994) were forced to eliminate thomisids (and salticids) from their analysis of niche breadth and overlap in a Texas cotton crop because they observed too few predation events. The tests for spider and other arthropod predation use serological analyses (Greenstone, 1996) and PCR (Greenstone *et al.*, 2003). These tests are also done after predation. Our tests for ingested fructose took place after the fact, and indeed, only two individuals (*E. tricuspidata*) was found feeding at EFNs (all of which tested positive for fructose). One individual (a clubionid) was observed feeding on prey, and tested negative for fructose.

From a broad biological perspective, if nectar can offer a spider's energy by ingesting fructose, a spider need fewer prey to maintain itself. A spider can, by feeding on flowers, avoid some of the risks and energy costs involved in stalking insects and other motile arthropods (Nelson *et al*., 2001). On plants such as cotton and peach, EFNs may also be more evenly distributed and more easily found than prey. A study of the spider communities in cotton showed that the number of spiders in cotton fields increased with appearance of cotton buds, flowers and other organs (Shangguan *et al.*, 2001). Although at this time a variety of insects attracted by nectar move into cotton fields, we cannot exclude the possibility that the spiders are attracted by the nectar as well. From this view, a question arises as to the final effect of nectar feeding by spiders. Some spiders seem to occupy plants depending on different characteristics, such as all kinds of microclimates, prey, or plant architecture for web attachment sites or shelters (Turnbull, 1973; Uetz *et al.*, 1978; Luczak, 1980; Young and Edwards, 1990; Riechert, 1998; Uetz *et al.*, 1999). Patt and Pffanenstiel (2008) demonstrated that cursorial spiders could detect and respond to nectar odours. Spiders incurred no costs to the plants, but can potentially increase individual plant fitness by reducing damage to reproductive tissues. Temporal conditionality probably occurred because plant productivity exceeded herbivore consumption, thus dampening top-down effects. Specialisation to live on glandular plants may have favored scavenging behaviour in genus *Peucetia* (Araneae Oxyopidae), possibly an adaptation to periods of food scarcity (Jose and Gustavo, 2010). Spiders generally abandoned bromeliads in which three-quarters of the length of the leaves had been removed, although females with egg-sacs remained on these plants (Gustavo and Joao, 2005).

Food is one of the most important factors affecting the growth, reproduction and ecological distribution of the spiders, and the food source is the key factors for rearing and studying them (Amalin *et al.*, 2001; Liu *et al.*, 2002). The behaviour of nectar feeding by spiders provides some references for indoor rearing and for large-scale release of spiders as pest control.

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