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Plant nectar increases survival, molting, and foraging in two foliage wandering spiders

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Abstract. We predicted that because plant nectar is high in energy, it is likely to provide multiple benefits to spiders that spend a substantial amount of energy foraging. In three laboratory experiments, we tested the effects of dietary extrafloral nectar on the survival, molting, and activity of two foliage wanderers, *Cheiracanthium mildei* L. Koch 1864 (Miturgidae) and *Hibana velox* (Becker 1879) (Anyphaenidae), both highly active, quick-moving nocturnal foragers. Extrafloral nectar contributed significantly to survival and molting in prey-deprived *H. velox*. On a marginal diet of prey (one *Drosophila* adult on alternate days) offered to spiders as soon as they emerged, 97% of *C. mildei* underwent their first molt if they also received nectar, compared to 7% of controls without nectar. On a marginal diet of prey (one *Drosophila* adult on alternate days) offered to spiders starting two days after their emergence, 78% of the spiders also receiving nectar molted, compared to 0% of controls without nectar. Video recordings of activity showed that prey-deprived groups of *C. mildei* maintained their active nocturnal foraging for many days on nectar, whereas controls became increasingly quiescent until they died. Non-web-building spiders that feed on nectar may utilize its energy for foraging and thereby allocate the nutrients of prey to maintenance and growth.

Keywords: Diet, extrafloral, fitness, nutritional allocation, *Cheiracanthium mildei*, *Hibana velox*

As obligate carnivores, spiders are presumed to acquire their energy for maintenance, growth, and reproduction from captured prey. Attesting to their levels of activity (and resulting energetic needs), some wandering spiders encounter and eat insect eggs (Buschman et al. 1977; Nyffeler et al. 1990; Miliczky & Calkins 2002; Pfannenstiel 2004) and the eggs of other spiders (Willey & Adler 1989). As generalist predators, spiders are useful models for investigating invertebrate nutrient-specific selective foraging (Mayntz et al. 2005), but not all spiders should be presumed to be exclusively carnivorous or to get all of their energy from prey lipids. Coll & Guershon (2002) identify "true omnivory" (i.e., feeding on both plants and prey) in spiders, citing members of two families in particular: an araneid that feeds on pollen grains in the juvenile stage, which the spiderlings trap and eat incidentally when they eat and recycle their webs (Smith & Mommsen 1984), and an anyphaenid that feeds on plant nectar (Taylor & Foster 1996).

Compared to feeding on pollen grains, nectar feeding is a more directed behavior, which has been reported among all ages of spiders and among a number of different families. Independent observations of members of Thomisidae (crab spiders), Salticidae (jumping spiders), and the active, fast-moving Anyphaenidae, Miturgidae, and Corinnidae—all wanderers in foliage —suggest that all feed at the floral and extrafloral nectaries (EFNs) of plants (Edmunds 1978; Vogelei & Greissl 1989; Pollard et al. 1995; Ruhren & Handel 1999; Jackson et al. 2001). Applying what Singer & Bernays (2003) might call a "behavioral perspective," Taylor & Pfannenstiel (2008) sampled spiders they deemed most likely to feed regularly on nectar from the EFNs of cotton plants and determined that one out of four were positive for ingested fructose, a plant-derived sugar. The survey also added members of Oxyopidae to the list of families that nectar feed. Considering that the hunting success rate for some wandering spiders is thought to be low (Miyashita 1968; Anderson 1974; Nentwig 1987; Nyffeler et al. 1987; Nyffeler & Sterling 1994), we propose that plant sugars may be of direct benefit and help fuel the cursorial life of these spiders, allowing the valuable nutrients of prey to be allocated to the more complex metabolic processes of maintenance, growth, and reproduction.

Plant nectars contain primarily carbohydrates and water (Percival 1961), but also amino acids, lipids, vitamins, and minerals (Baker & Baker 1975, 1983; Koptur 1992). Nectar is exuded at floral nectaries, but unless a flower's corolla is shallow, nectar is more accessible to spiders' small mouthparts by way of extrafloral nectaries (EFNs), nectar-bearing tissues or structures that reside anywhere on a plant outside of a flower. EFNs often occur on leaves or leaf petioles, and take many forms, such as slits, cups, bowls, or undifferentiated tissue. Arthropods, particularly ants, often visit these open, accessible EFNs (Bentley 1977). Spiders observed at nectaries are non-web-building wanderers that inhabit vegetation, and their degree of activity and nectar feeding may be correlated. Searching for prey requires wandering, and frequent wandering means a greater likelihood of encountering EFNs and plant nectar. Plant nectar, which contains mostly sugar, could repay the energetic costs of wandering. The active foragers, *Cheiracanthium mildei* L. Koch 1864 (Miturgidae) and *Hibana velox* (Becker 1879) (Anyphaenidae), run throughout the vegetation at night, making them good candidates to investigate the energetic contributions of nectar. Both of these spiders have been observed at plant nectaries (Taylor & Foster 1996).

Three laboratory experiments tested the effects of extrafloral nectar on the survival, molting, and activity of newly emerged spiders. *Hibana velox* was the subject of initial survival tests. *Cheiracanthium mildei*, which is ecologically similar, was more easily obtained and the subject of later experiments. The experiments tested 1) the effects of nectar and two concentrations of sucrose on the survival of individually housed *H. velox*, 2) the effect on molting in *C. mildei* by adding nectar to a marginal diet of prey (*Drosophila melanogaster*), and 3) the effects of nectar on the nocturnal running activity of small groups of prey-deprived *C. mildei*.

METHODS

Spiders.—Experimental *H. velox* were offspring of adults collected in 1994 in Alachua County, Gainesville, FL, USA; experimental *C. mildei* were offspring of adults collected in Franklin County, Columbus, Ohio, USA. Egg sacs were either collected in the field with adult females (which guard them) or produced by females maintained in the laboratory on a varied insect diet (mainly house flies and mosquitoes). Adults lived in 7-liter clear acrylic cages (15 × 21 × 27 cm) with a screened opening at one end and a sleeved opening at the other.

Experiments were conducted in a laboratory rearing room maintained on a 16:8 h light:dark diel cycle at ca 27° C and 80% relative humidity. Spiders were checked daily for molting and mortality. Each experiment or trial began within 12 h of spiderlings' emergence from their egg sacs, which was considered Day 0. "First molt," therefore, refers to a spider's first molt post-emergence.

Spiders were housed individually in clear, lidded, plastic containers, 5.2 cm diam. × 3.6 cm. Each container had four holes: two 12-mm, mesh-covered holes top and bottom; and two opposing 17-mm holes in the side wall, one mesh-covered and the other corked for introduction of prey and for changing the fluid wells of feeders. Feeders were small rectangles of plastic (1 × 2.5 cm) with a dimple (i.e., fluid well) drilled near each end (large dimple for water, small for nectar). Twenty of these small containers, composing an even mix of controls and treatment individuals, filled a large, clear, plastic 30 × 25 cm lidded box. Two boxes fit on a large plastic tray, lightly dusted with sifted sulfur to repel mites. Boxes were rotated daily.

Spiders in the activity trials were housed in small 7-cm-square plastic lidded boxes, each with four 17-mm holes, one on each side, three mesh-covered and one corked for introduction of spiders and for refilling fluid wells and changing feeders. Each box held four feeders, totaling eight fluid wells. For the control, all eight wells contained water; for the treatment, four wells contained water, and four contained nectar. Control and treatment boxes were placed side-by-side in a lidded clear plastic box, 35 × 24 cm and filmed with an RCA closed circuit TC7011 infrared-sensitive camera under continuous red light illumination, which does not disturb the spiders (Peck & Whitcomb 1970).

Diet.—In all experiments, water was available ad libitum. All containers that held spiders also held at least one feeder. In controls, both fluid wells of the feeder contained water. In treatment groups, the large well of the feeder contained water, and the small well contained either nectar or sucrose. Water also was available from soaked No.1 (9 mm) cotton dental balls. Ambient relative humidity was high, and smaller containers were kept in large boxes to keep water wells from drying out. The constant availability of free water ensured that spiders did not take nectar solely to obtain water. Sucrose and nectar, because of their viscosity, were delivered with a micro spatula in the smallest transferable amount, between 1–2 µl, smeared into the smaller fluid well of the plastic feeders.

Water, sucrose, and nectar were changed daily. Prey consisted of live, vestigial-winged *Drosophila melanogaster* maintained on instant (blue) *Drosophila* medium (Carolina Biological Supply). Diets combining prey and nectar were offered separately on alternate days to ensure that spiders were willing and able to consume nectar directly, rather than by way of prey that had ingested nectar.

All nectar was extrafloral to avoid introduction of pollen as a possible source of protein (Smith & Mommsen 1984). For the first trial of the first experiment with *H. velox*, extrafloral nectars were collected and combined from various greenhouse plants, such as *Hibiscus* and orchids. The nectar was slightly diluted to an unknown concentration to ease handling. For the second trial and all of the following experiments, nectar was undiluted and came solely from *Terminalia cattapa* (Indian almond, also growing in the university greenhouse), which produces copious nectar at EFNs on the base of the leaf near the petiole. Nectar from *T. cattapa* EFNs was 87.5% sugar constituents (variety unknown) determined from serial dilutions and a Reichert-Jung refractometer. The nectar was collected with a microspatula and stored at −45° C.

Experiments.—*1. Survival:* Two trials compared survival in individually housed *H. velox* on diets of water only, sucrose, or extrafloral plant nectar. For each trial, spiders from a single egg sac were divided among the control and two treatments. Both trials included a sucrose treatment to distinguish contributions of carbohydrates from possible contributions of other nectar components, such as amino acids or lipids. In the first trial, sucrose was relatively "low" (25%), in the second trial, "high" (69%), to more closely imitate the high sugar concentration of extrafloral nectars. Individuals were checked daily for mortality.

2. Molting: Two trials compared molting in individually housed *C. mildei* receiving marginal diets of prey (*Drosophila*) with and without nectar from *T. cattapa*. For each trial, spiders from a single egg sac were divided between the control and the treatment. In both trials, spiders were fed a single *Drosophila* adult on alternate days until the spider molted. On days without *Drosophila*, spiders received water (controls) or nectar. In the first trial, *Drosophila* were introduced on Day 1. In the second trial, introduction of *Drosophila* was delayed until Day 3. Nectar-fed spiders on the delayed *Drosophila* diet received nectar for the first two days. Spiders were part of the trial until they molted once.

3. Activity: Because both *H. velox and C. mildei* wander energetically in vegetation at night and are inactive during the day, we filmed two groups of cohabiting spiders at night in the laboratory, one with and one without access to nectar. Both had access to water ad libitum. For both replicates spiders from a single egg sac were divided between the control and treatment. From tapes, we quantified nightly activity as the number of spiders simultaneously running during a one-minute period at 10-min intervals, for 54 periods covering crepuscular light and the eight hours of scotophase. The mean of these 54 periods represented that night's activity.

Analysis: We analyzed data with *Statistica* for Windows (2000), StatSoft, Inc. Survival analysis (Kaplan-Meier) employed log-rank tests, which were adjusted for multiple comparisons, for which the calculated comparison-wise error rate of 0.008 is based on $K = 3$ treatments (Hardin et al. 1996).

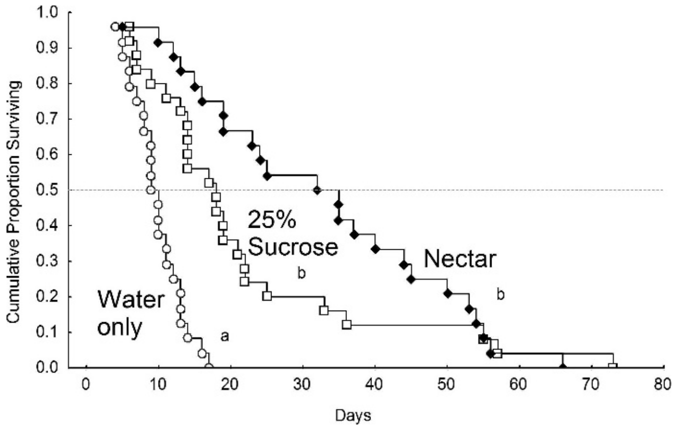

Figure 1.—Survival estimates for *Hibana velox* fed water only ($n = 24$), 25% sucrose ($n = 25$), or extrafloral nectar ($n = 24$). Curves with different letters are significantly different (adjusted pair-wise comparison).

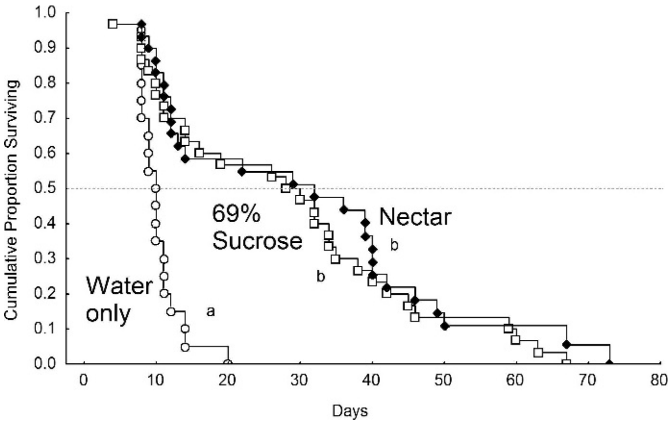

Figure 2.—Survival estimates of *Hibana velox* fed water only ($n = 20$), 69% sucrose ($n = 30$), or extrafloral nectar ($n = 30$). Curves with different letters are significantly different (adjusted pair-wise comparison).

We used chi-square tests to compare molting and the Mann-Whitney *U*-test to compare nocturnal activity.

RESULTS

1. Survival.—In the first trial, prey-deprived spiders survived significantly longer than water-only controls if they received 25% sucrose (log-rank test statistic = 3.71, $P = 0.0002$), or if they received nectar (log-rank test statistic = 4.39, $P = 0.0001$). The 25% sucrose and nectar treatments were not significantly different (log-rank test statistic = −1.43, $P = 0.1566$) (Fig. 1). The second trial produced similar results. Spiders survived longer than water-only controls if they received 69% sucrose (log-rank test statistic = 3.36, $P = 0.0008$), or if they received nectar (log-rank test statistic = 3.66, $P = 0.0003$) (Fig 2). The 69% sucrose and nectar treatments were not significantly different (log-rank test statistic = 0.770, $P = 0.4412$) (Fig. 2). Molting occurred in all of the groups except the controls of Trial 2 (Table 1).

2. Molting.—Both trials ended when all of the spiders in the nectarless control died, Day 15 for the first trial and Day 16 for the second. Nectar added to a marginal diet of prey (one *Drosophila* adult on alternate days) significantly increased the numbers of spiders that underwent their first molt whether the *Drosophila* diet began on Day 1 (97% vs. 7%) or Day 3 (78% vs. 0%). Delaying the introduction of prey, however, had a significant effect on the ability to survive the process of molting. Among the 97% (29/30) of spiders that molted receiving nectar and *Drosophila* on Day 1, 100% survived the molting process. Among spiders receiving nectar from Day 1 and *Drosophila* first on Day 3, 78% (38 /49) initiated molting, but only 47% of the sample survived the molting process, a significant decrease in survival (multiple comparison χ^2: prey on Day 1, $n = 30$; prey on Day 3, $n = 49$, $P < 0.001$).

Whether they received nectar or not, individual spiders on average consumed the same number of prey daily before an individual died or molted, calculated from the total number of *Drosophila* consumed in the experiment/total spider days survived. In the first trial, spiders with nectar ate 0.32 *Drosophila* daily and those without, 0.30 *Drosophila* (94 prey/294 d; 74 prey/243 d, respectively). In the second trial, spiders with nectar ate 0.26 *Drosophila* daily, and those without, 0.23 *Drosophila* (122 prey/466 d; 62 prey/265 d, respectively).

3. Activity.—The trials ended when any of the spiders died, which occurred in the nectarless control on Night 5 in the first replicate and on Night 4 in the second replicate. Comparisons of the total number of intervals of activity (270 for Replicate 1, 216 for Replicate 2) between the control and the nectar treatment show that nectar contributes significantly to the spider's running, in absence of prey (Mann-Whitney *U*: Replicate 1, $n = 270$ for both treatments, $Z = -12.709$, $P < 0.001$; Replicate 2, $n = 216$ for both treatments, $Z = -13.377$, $P < 0.001$). On Day 1, there was no significant difference in activity between spiders with and without nectar. On successive nights, spiders without nectar became increasingly quiescent until they died (Fig. 3). Individuals could not be distinguished from one another, and seven individuals at most could be distinguished running simultaneously, making the estimate of spider activity conservative.

Table 1.—Survival (mean ± 1 SE) and molting of *Hibana velox* in two trials of survival on diets of water only, sucrose, or nectar. Significantly more spiders molted than their water-only controls if they received nectar or 69% sucrose (χ^2, *$P < 0.05$, **$P < 0.001$).

Trial	Diet	Survival (d)	Range (d)	1st molt	*n*
1	Water only	9.8 ± .7	4–17	17%	24
1	25% sucrose	22.0 ± 3.4	6–73	28%	25
1	Nectar	32.6 ± 3.6	5–66	50%*	24
2	Water only	10.4 ± .7	8–20	0%	20
2	69% sucrose	28.4 ± 3.4	4–67	63%**	30
2	Nectar	28.1 ± 3.5	8–73	52%**	30

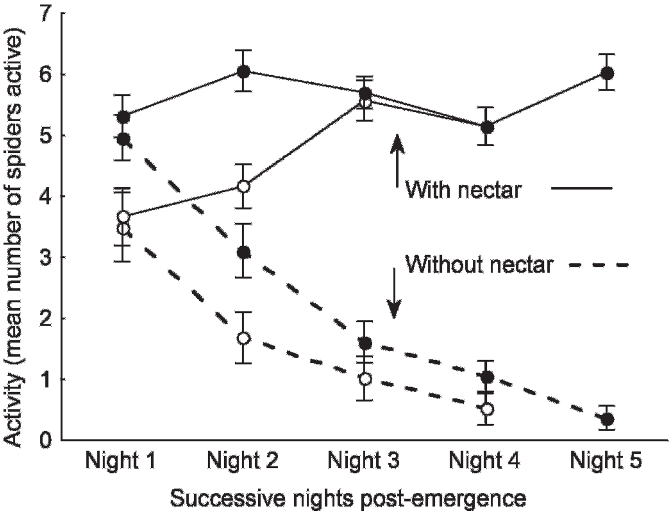

Figure 3.—Nocturnal activity of eight or nine cohabiting, newly emerged, prey-deprived *Cheiracanthium mildei*, with or without nectar. Replicate 1 (solid circles) without nectar, *n* = 8; with nectar, *n* = 8. Replicate 2 (open circles) without nectar, *n* = 9, with nectar, *n* = 9. "Activity" is the mean number of spiders simultaneously running during a one-minute period at 10-minute intervals for 54 periods. Points are means ± SE.

DISCUSSION

In the lives of spiders, vegetation is considered important as a support for webs, as refugia, or as a food source for the insects that spiders catch (Turnbull 1973; Hatley & MacMahon 1980; Greenstone 1984; Uetz et al. 1999). Only recently have researchers considered the possibility of vegetation as a direct food source, and some spiders as true omnivores among terrestrial invertebrates. Taking this recognition one step further, we investigate why nectar feeding should be a likely activity among some spiders and for the first time measure the direct biological benefits to spiders that nectar-feed.

Why nectar feeding is a likely activity.—The likelihood that nectar can and does play a role in the energy budget of some spiders is unsurprising. Nectar's value as a dietary source of energy has been well established for nectarivorous insects, such as bees and butterflies; and predaceous arthropods other than spiders have been shown to survive periods of prey deprivation by feeding on plant nectars (Yokoyama 1978; Hagen 1987; van Rijn & Tanigoshi 1999; Limburg & Rosenheim 2001). Cursorial spiders that wander in vegetation with EFNs are likely to encounter nectar, which they have the potential to detect with "gustatory" hairs on their tarsi (Barth 2002). *Cheiracanthium mildei*, for example, oriented immediately to sugar and inserted its mouthparts as soon as a foretarsus touched it (RMT personal observation). Encountering nectar, spiders are predisposed to ingesting their food in liquid form, given their form of extra-oral digestion (Cohen 1998), which may also help them ingest nectars that can be too viscous for other nectar feeders to handle (Wäckers et al. 2001). Spiders respond positively to nectar, shown by preference tests (Jackson et al. 2001) and by their willingness to ingest chemicals, such as LSD, caffeine, and strychnine, if they are delivered in a sucrose solution (Christiansen et al. 1962; Witt 1971). And, both spiders that have been analyzed for digestive enzymes (a tarantula and an agelenid) possess the enzyme sucrase (Pickford 1942; Mommsen 1977), which can digest nectar

Concentration of sugars at EFNs.—Our experiments show that even when water was available, spiders still drank nectar when offered. *Hibana velox* without prey survived significantly longer and had a significantly higher incidence of molting than water-only controls if they had access to nectar or to the high (69%) concentration of sucrose (Table 1). Such high concentrations of sugar are not unusual in EFNs. The sugar concentration of *T. cattapa* extrafloral nectar that we determined to be 87.5% is nearly identical to the concentration of sugars (872 mg/ml) from the EFNs of castor bean (*Ricinus communis*) (Baker et al. 1978), and is similar to the concentration of sugar (77.7%) exuded at the EFNs of cashew (*Anacardium occidentale*) (Wunnachit et al. 1992). *Hibana velox* has been observed feeding at both of these species (Taylor & Foster 1996). Other *Hibana* spp. and *C. inclusum* have been observed at the EFNs of cotton (Taylor & Pfannenstiel 2008), which produce nectars with a sugar concentration between 62% (Wäckers et al. 2001) and 86% (Butler et al. 1972).

Nectar fulfills energy requirements.—In experiments providing *C. mildei* with *Drosophila* on Day 1, 97% of the spiders molted if they also had access to nectar, compared to 7% of controls without nectar. In experiments measuring activity, nectar contributed significantly to the energetic needs of *C. mildei*, conferring not only survival but also allowing them to keep up their frenetic running all night, every night that they were filmed. These results offer an opportunity to tease apart how these spiders are allocating nectar and prey-derived nutrients and can begin to address Uetz's (1992) question, "Is energy the sole currency involved in spider foraging, or do nutrients play a critical role?"

Both nectar and pure sucrose contributed to a higher incidence of molting in prey-deprived *H. velox* (Table 1), suggesting that it was the sugar component of nectar that contributed most to molting. Molting is an energy-depleting event that can increase respiration three-fold (Stranzy & Perry 1987). Nearly half of the components of a spider's cuticle, however, consist of proteins (Dalingwater 1987). Because sucrose contributed to the same incidence of molting as nectar, but molting requires not only carbohydrates but also protein for new cuticle, it appears that sugars fulfilled much of the energetic demand of sustained nocturnal locomotion (i.e., foraging), survival, and ecdysis (the molting event), allowing the protein contained in yolk reserves and prey to be allocated primarily to growth and/or new cuticle deposition. This may explain why *H. velox* provided with nectar but no prey survived long but did not grow (only some undergoing a single molt: Table 1), and why *C. mildei*—a larger spider at emergence with perhaps fewer reserves— provided with a marginal amount of prey but deprived of nectar, died early without molting. That is, a marginal amount of prey divided between activity and growth could not support both. The addition of nectar substantially changed the outcome: on average, both control and treatment *C. mildei* ingested nearly identical amounts of prey (0.30 vs. 0.32, and 0.23 vs. 0.26 *Drosophila*/spider/day in trials 1 and 2, respectively), but molted only if their diet was supplemented with nectar, suggesting that they were at the margins of their nutritional requirements. Nectar feeding, by providing the energy for activity, may allow spiders to subsist on marginal amounts of prey, and, depending on the minimum amount required to reach functional maturity, might substantially reduce a spider's prey requirements. Spiders that can reduce their prey intake also are likely to reduce the energy and risk associated with attacking and subduing prey.

It is not clear why *C. mildei* receiving their initial *Drosophila* on Day 3 underwent a first post-emergent molt after consuming fewer prey than when *Drosophila* were introduced on Day 1. The consequences of delaying the introduction of prey by two days are dire: a 53% reduction in first-molt survival. This hints at some possible protein requirement for normal development within the first two days of spiderling emergence, or perhaps some developmental timeline triggered by the presence of protein in the diet. Fulfilling either of these requirements would make nectar-fueled survival and hunting all the more valuable.

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