Extended Survival of Spiders (Aranaeae) Feeding on Whitefly (Homoptera: Aleyrodidae) Honeydew[1]

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Abstract Honeydew produced by homopteran insects, such as aphids, whiteflies, and mealybugs, can be abundant in some crops and may represent an important food resource for spiders and other honeydew-feeding natural enemies. Woolly whiteflies (*Aleurothrixus floccosus* [Homoptera: Aleyrodidae]) are common in south Texas citrus, and spiders consistently compose a large percentage of the predatory arthropods in citrus and may benefit from honeydew resources. Feeding on woolly whitefly honeydew was assayed for its contribution to spider survival for five species from different arachnid families. When provided with whitefly honeydew, survival of all five species was significantly better than when provided water alone. However, the level of improvement in survival varied significantly among species. Honeydew supplementation increased survival by 73.5% for *Apollophanes punctipes* (Cambridge, O. P) (Philodromidae) (32.1 versus 18.5 d on water alone), 266.7% for *Cesonia bilineata* (Hentz) (Gnaphosidae), 352.6% for *Dictyna* sp. near *bellans hatchi* (Dictynidae), 130.9% for *Thiodina sylvana* (Hentz), and 1,102.5% for *Hibana futilis* (Banks) (Anyphaenidae) (48 versus 4 d on water alone).

Key Words honeydew, nonprey resources, spider

In habitats that harbor homopteran insects, such as aphids, whiteflies, or mealybugs, honeydew produced by these insects may be abundant and represent an important nutrient resource for spiders (Pfannenstiel and Patt 2012). Woolly whiteflies (*Aleurothrixus floccosus* [Homoptera: Aleyrodidae]) can be common in south Texas citrus, and spiders consistently compose a large percentage of the predators in citrus grown there (R. Pfannenstiel, unpubl. data). Nocturnal cursorial spiders in the families Anyphaenidae and Miturgidae have been documented to commonly feed on extrafloral nectars in cotton (Taylor and Pfannenstiel 2008) and observed to feed on floral nectars and honeydew sugars (Pfannenstiel and Patt 2012). Anyphaenidae and Philodromidae were also observed feeding on whitefly honeydew on citrus leaves (R. Pfannenstiel, pers. obs.). The availability of these sugar resources provide significant benefit for development and reproduction when spiders are prey-limited (Taylor and Pfannenstiel 2009) or for survival and foraging in the absence of prey (Pfannenstiel and Patt 2012, Taylor and Bradley 2009). Spiders have generally been considered to be food-limited (Nentwig 1987, Nyffeler

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and Sterling 1994, Wise 1993), so the availability of these resources might significantly facilitate colonization, retention, and population growth of spiders in both natural and agricultural settings. Crops where honeydews or extrafloral nectars are available appear to show higher densities of important spider predators (Pfannenstiel 2005, 2008a), and this may improve biological control of crop pests (Lundgren 2009). A small number of studies have documented spider feeding on floral and extrafloral nectar (Jackson et al. 2001, Taylor and Foster 1996, Taylor and Pfannenstiel 2008, Vogelei and Greissl 1986), but little is known of the value of sugar feeding for most species and honeydew feeding has only been documented for two species (Lundgren 2009, Pfannenstiel and Patt 2012).

In south Texas as well as other citrus-growing regions, whiteflies can produce prodigious amounts of honeydew. Because spiders appeared to be the dominant predator taxa in south Texas citrus (R. Pfannenstiel, unpubl. data), five common spiders were tested for the beneficial effects of feeding on whitefly honeydew in comparison to water alone. The spiders represented five families in the Araneae: *Apollophanes punctipes* (Cambridge, O. P) (Philodromidae), *Cesonia bilineata* (Hentz) (Gnaphosidae), *Dictyna* sp. nr. *bellans hatchi* (Dictynidae), *Hibana futilis* (Banks) (Anyphaenidae), and *Thiodina sylvana* (Hentz) (Salticidae). These spiders vary significantly in their searching behavior. It was hypothesized that the honeydew would be of greatest benefit to those spiders with the highest perceived energetic needs, particularly the nocturnal running spiders.

Materials and Methods

Spiders were collected from citrus trees in the lower Rio Grande Valley of Texas during a study examining predator complexes in dooryard and abandoned citrus groves. Adult and juvenile spiders of several of the more frequently observed species were collected and maintained in the laboratory on frozen *Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae) eggs using methods described by Pfannenstiel (2008b). When egg masses became available from either field-collected adult females or from females mated in the laboratory, they were assigned to this study. Egg masses were maintained at 26 ± 1°C with a 14:10 (light:dark) photoperiod and observed daily until spiderling emergence. On emergence spiderlings were divided into two treatments: *Aleurothrixus flocossus* (Maskell) (Homoptera: Aleyrodidae) honeydew or a water control. Individual spiderlings were placed in a 90 × 15–mm plastic petri dish with moistened dental wicks. A coverslip (22 × 22 mm) with about 5 μl of water placed on top (water control) or a coverslip with *A. flocossus* honeydew was added to each dish. The coverslips were changed weekly and the dental wicks were rehydrated twice weekly.

Aleurothrixus floccosus honeydew was collected directly from whitefly-infested citrus leaves. Leaves containing *A. flocossus* colonies were removed from the five citrus trees in the author's yard in Weslaco, TX. The five trees consisted of a grapefruit (*Citrus* × *paradisi* Macfayden), a sour orange (*Citrus* × *aurantium* L.), and three sweet oranges [*Citrus* × *sinensis* (L.) Osbeck] of indeterminate parentage. The trees were observed late at night (typically 10 p.m. to 6 a.m.) while illuminated with a hand lamp. *Aleurothrixus flocossus*–infested leaves were checked for the availability of honeydew. Honeydew collections were best when it was not too cold (at about 13–15°C the whiteflies seemed to stop feeding) and moderately humid (>65–75**%** relative humidity). When humidity was low, water evaporated from the honeydew, leading to high viscosity, which hampered collection. Leaves containing either a high density of honeydew or large honeydew droplets were collected. Each leaf was examined under a dissecting microscope, and honeydew collected with the end of a straightened paper clip. When the end of the paper clip was touched to the honeydew droplets, the droplet would stick to the end and could then be easily transferred by streaking onto plastic slide coverslips. Each coverslip was streaked with honeydew collected directly from at least two whitefly nymphs and carefully placed into a large 150 × 25–mm plastic petri dish. The amount of honeydew was not measured, but between 1 and 3 μl of raw honeydew was likely applied to each coverslip. Petri dishes containing coverslips were placed in a freezer at −20°C. While in the freezer and after placement in the petri dish, the water evaporated from the honeydew, leaving a sugar residue with variable amounts of moisture. This freezer did not have fans, which might have caused sublimation of the frozen honeydew. Collections were made until a several-month supply of honeydew-streaked coverslips was stored within the freezer before beginning the experiment. coverslips with honeydew were kept frozen until used.

Newly emerged spiderlings from each of the five species were placed individually into 90 × 15–mm plastic petri dishes with a moistened dental wick and randomly assigned to each feeding treatment. Each dish contained a plastic coverslip streaked with whitefly honeydew or reverse-osmosis water. Between addition of the coverslips with water and hydration of the dental wicks, spiders in the controls were exposed to free water about 3 d per week. Spiders were maintained at 26 ± 1°C with a 14:10 (light:dark) photoperiod and observed daily until death. Because the number of eggs per mass could vary considerably among species, the number of individuals set up per cohort varied widely. Typically, the same numbers of spiders were set up for each treatment except toward the end of the study, when small variations were made in the attempt to stabilize sample sizes.

Survival of each spider species on honeydew versus water alone was compared by pairwise analysis with PROC LifeTest (SAS Institute 2000) with $\alpha = 0.05$. Statistical analyses only evaluated differences for each species between honeydew and water. The baseline survival of each species was different so the relative value of sugar feeding was also hypothesized to vary among species with the most value being gained by species with high movement rates and likely high energetic needs such as *H. futilis*. Both the log-rank and Wilcoxon statistics (χ^2) were examined because the log-rank test is more sensitive to larger survival times while the Wilcoxon statistic gives more weight to early survival times (SAS Institute 2000).

Results and Discussion

Feeding on whitefly honeydew significantly extended the survival of all spider species tested here beyond that possible on water alone ($P < 0.0001$) for both Wilcoxon and log-rank tests for all comparisons (Table 1). Spider survival varied on water alone (Fig. 1, Table 1). Because their survival varied on water alone the

Table 1. Survival summary of five spiders feeding on wooly whitefly honeydew vs. water.

	Fed Water		Fed Honeydew			χ^2 Values for Comparison Vs. Water**	
Species (Family)	Mean ± SE Days Survived* (n)	Range (days)	Mean ± SE Days Survived (n)	Range (days)	% Survival Extension	Wilcoxin Test	Log-Rank Test
Apollophanes punctipes (Philodromidae)	18.5 ± 0.7 (34)	12–30	32.1 ± 3.3 (28)	14–67	73.5	14.6	19.3
Cesonia bilineata (Gnaphosidae)	9.6 ± 0.6 (24)	7–18	35.2 ± 2.2 (24)	16–59	266.7	44.6	54.9
Dyctina sp. near *bellans hatchi* (Dictynidae)	9.5 ± 0.3 (22)	8–15	43.0 ± 2.9 (43)	10–89	352.6	67.2	74.6
Hibana futilis (Anyphaenidae)	4.0 ± 0.2 (21)	3–5	48.1 ± 3.4 (20)	21–92	1102.5	36.6	42.2
Thiodina sylvana (Salticidae)	8.1 ± 0.3 (17)	6–11	18.7 ± 0.7 (24)	12–24	130.9	42.7	49.4

* Survival results for water are separated with pairwise comparisons using Proc LifeTest ($\alpha = 0.01$).

** For comparisons of each species fed on honeydew vs. water, both the Wilcoxin and the Log-Rank tests are included because they weight the significance tests to different parts of the survival curves. In all comparisons, statistical significance was $P < 0.0001$.

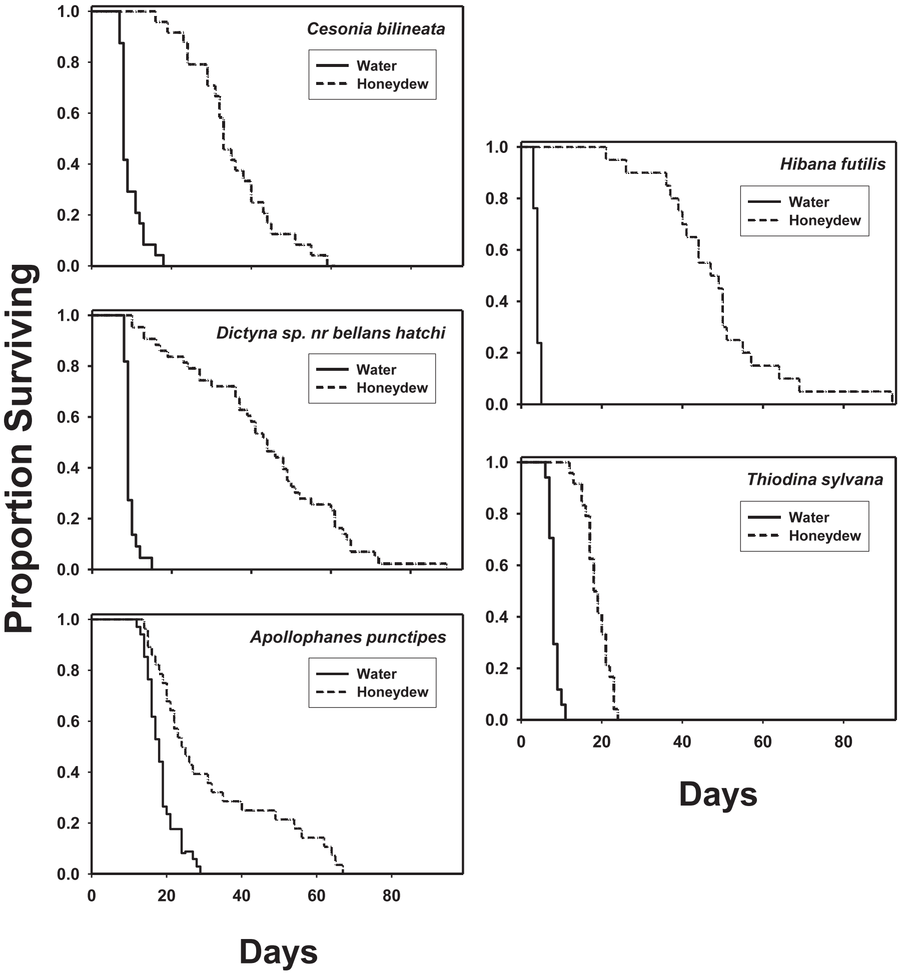

Fig. 1. Survival of spiderlings of five spiders common in south Texas citrus when fed woolly whitefly honeydew versus water alone.

percentage of improvement in mean survival between honeydew and water was calculated for each spider species. The mean improvement in survival ranged from 73.5% for *A. punctipes* to 1,102.5% for *H. futilis* (Table 1). Maximum survival for a spider feeding on honeydew ranged from a relatively short 24 d for *T. sylvana* to around 90 d for both *Dictyna* sp. nr. *bellans hatchi* and *H. futilis*. Extension of survival did not correspond as well to perceived spider activity level as I had hypothesized. *Hibana futilis* exhibited the largest improvement in survival from honeydew feeding; however, among the other spiders, one of the less-active spiders *Dictyna* sp. nr. *bellans hatchi* had relatively high improvement in survival while the actively searching *T. sylvana* exhibited the smallest improvement in survival with honeydew feeding.

Evaluation of honeydew feeding over a range of spider families found significant improvements in survival as well as significant differences in the survivorship response. It is evident that spiders are well adapted to locate, feed upon, and utilize the sugars found in nectars and honeydew (Patt and Pfannenstiel 2009, Taylor and Pfannenstiel 2008). For example, inclusion of extrafloral nectar or sucrose in the diet of prey-limited spiders enhanced their survivorship, development, and fecundity (Pfannenstiel and Patt 2012, Patt et al. 2012, Taylor and Bradley 2009, Taylor and Pfannenstiel 2009). Contact with sucrose induced localized searching behavior in *H. futilis* (Patt and Pfannenstiel 2009), a spider that can learn to recognize and remember novel nectar odors (Patt and Pfannenstiel 2008). Although it has been demonstrated that honeydews, nectars, and their sugar components can be nutritionally beneficial for spiders, our understanding of the details of this benefit across taxa is extremely limited. Here we begin to look at the variability in response of spiders to honeydew. Survival of spiders feeding on honeydew was markedly improved over that observed on water alone for all five spider species. A previous study of feeding by *Cheiracanthium inclusum* (Hentz) (Araneae: Miturgidae) on mealybug honeydew demonstrated a percentage of improvement in survival greater than all of the spiders in this study except *H. futilis* (Pfannenstiel and Patt 2012). In that same study, *H. futilis* was observed to vary in its survival on sugars representative of nectars and honeydews. The other spiders in this study are from taxa for which sugar feeding has not been studied; there are no comparable data. Here significant differences in the response of spiders in five families to honeydew from a single whitefly species were found. Whether the variation in spider response to this honeydew was because of variable response to its specific constituent sugars or to sugars in general is yet to be determined. It would be interesting and significant to test these same spiders for their responses to extrafloral nectars or to a subset of the constituents of *A. flocossus* honeydew.

This study demonstrates the value of honeydew in the absence of prey or other food resources, In that sense, the extension in survival is a “worst-case” scenario in the absence of prey. Studies in which prey or alternate resources are provided in addition to sugars showed that spiders readily feed on and benefit from multiple resources (Patt et al. 2012, Schmidt et al. 2013, Taylor and Pfannenstiel 2009). Field studies of sugar feeding by spiders observed that under nonmanipulated conditions, high percentages of spiders are feeding on sugars when prey are presumably available (Chen et al. 2010, Taylor and Pfannenstiel 2008).

The data presented here are from spiders that vary considerably in their search strategies. *Dictyna* sp. near *bellans hatchii* builds small diffuse space webs on leaves or twigs and *H. futilis* is a nocturnal runner and moves almost constantly during the nighttime hours in search of prey, yet their survival patterns were similar. *Cesonia bilineata* probably searches in a manner similar to *H. futilis* and from observations made during this study may move even faster. *Thiodina sylvana* is an active visually orienting hunting spider during the daytime whose motions are generally slow and deliberate versus the more constant motion of *H. futilis* and the gnaphosids. The benefits gained from feeding on honeydew sometimes, but not always, matched expectations of which spiders might benefit. It was expected that the sugars would benefit the running spiders the most because of their perceived energetic needs and would benefit the others less. The only web-building spider in this study, *Dictyna* sp. nr *bellans hatchi*, constructs a relatively small web that is neither sticky nor reconsumed and whose construction is suspected to be energetically less intensive than those produced by other web-building spiders such as the araneids.

Although spiderling size was not measured as part of this study, there may be some correlation between spiderling size and the relative value of sugar feeding. The spiders with the greatest observed survival improvement were ones that appeared to be smaller. Species with larger spiderlings, such as *A. punctipes* and *T. sylvana*, showed smaller relative improvements in this study. Sugar feeding may be more important to spider species that produce smaller spiderlings, such as *Dictyna* sp. nr *bellans hatchi* or *H. futilis*, which have fewer resources on emergence from the egg sac. The sugar composition of honeydews also can be a major determining factor for their nutritional value (Wäckers 2005). However, in some situations, reduced performance on honeydews can be due to its viscosity, not its constituent sugars (Faria et al. 2008).

Despite the variability in benefits from honeydew and nectar feeding by spiders, the consistent positive response of spiders to sugar feeding across many families suggests that sugars represent an important resource for spiders in general. Previously published reports have demonstrated that spiders from many families feed on sugars (Chen et al. 2010, Jackson et al. 2001, Taylor and Foster 1996, Taylor and Pfannenstiel 2008); however, the specific benefits to survival, development, and foraging behavior have been demonstrated for only a few families (Pfannenstiel and Patt 2012, Taylor and Bradley 2009, Taylor and Pfannenstiel 2009). The availability of sugar sources may be of particular importance to spiderlings, who have a limited window of time in which to find resources or die. Alternatively, the availability of sugars enhances development and reproduction when prey are limited (Patt et al. 2012, Taylor and Pfannenstiel 2009).

The finding that the diet of spiders extends beyond that of prey and includes a variety of nonprey resources such as nectars, honeydews, yeasts (Patt et al. 2012), and pollens (Ludy 2004, Peterson et al. 2010, Pfannenstiel 2012, Vogelei and Griessl 1989) alters how we must look at the suitability of various crops and habitats for colonization and population growth by these spiders. Utilization of nonprey resources may be of particular importance for spiders colonizing annual crops where prey resources early in the season may be scarce. For the spiders studied here, survival of spiderlings was extended for weeks, if not months, when feeding on honeydew. Extended survival should make it much more likely that the spiders would locate prey and subsequently develop to adulthood, hopefully leading to improved control of crop pests. For many predators (including spiders) to be of benefit in controlling annual crop pests, individuals must colonize the crop soon after emergence and then develop and reproduce during a relatively short growing season (Yeargan 1998). Under conditions of prey scarcity, the availability of an abundant resource, such as extrafloral nectar or honeydew, may be instrumental in allowing spiders to establish, build populations, and contribute to pest control later in the season. Spider association with plants producing extrafloral nectar has been documented to benefit the plants (Ruhren and Handel 1999, Whitney 2004). Investigation of the role that sugar availability plays in spider colonization of crop habitats and whether it consistently influences the predator's impact on pest insects is critical to understanding the role of sugars in functional and numerical responses of predators in crops.

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