Spider Nectarivory

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VIRTUALLY ALL SPIDERS SUSTAIN THEIR SURVIVal, growth, and reproduction by eating insects and other arthropods, including other spiders. A few exceptional spiders even prey on small fish, birds, amphibians, and reptiles. Many webmakers eat and thus recycle their webs, but this activity in itself results in no exogenous nutritional gain. At least some temperate-zone orb-weaving spiderlings, however, *do* enjoy a net gain by coincidentally ingesting captured pollen grains along with the web, substantially increasing the spiderlings' survival (Smith & Mommsen 1984). Web recycling and pollen grains aside, most arachnologists perceive spiders as exclusively carnivorous and as generalist predators with a taste for diverse living arthropods and even an occasional willingness to feed on dead ones (Foelix 1982, Riechert & Harp 1987, Wise 1993).

Well-versed in this knowledge of spider carnivory, in 1984 we encountered wandering spiders in Costa Rica whose behavior challenged this time-honored view. During four nocturnal collections of nectar-feeding mosquitoes at the coastal research site of Llorona, Corcovado National Park, on the Osa Peninsula, we observed quick and agile spiders crawling among the spiked inflorescences of the pantropical Indian almond, *Terminalia catappa* L., a common beachfront tree. This is nothing unusual for wandering spiders. Many are active only at night, and those on the Indian almond were most likely to encounter nectar-feeding prey if they moved rapidly among the small white florets in an efficient search pattern. But to our surprise, these spiders were clearly busy with the flowers themselves. They buried their mouthparts deep within each floret, held still for a few seconds, then dashed to the next, seeming to work the flowers for nectar as do bees, moths, and other common nectar feeders.

Our suspicion that these spiders might be feeding on nectar was reinforced when, during the same field work, we saw similar sorts of spiders on the seaside shrub *Hibiscus tiliaceus* L. This pantropical plant has showy yel-

Culex nigripalpus, the mosquito vector of St. Louis encephalitis in Florida, feeding from the cup-like extrafloral nectary on a petiole at the base of a castor bean leaf in Vero Beach, FL.

Hibana velox feeding from paired extrafloral nectaries at the base of a castor bean leaf in Vero Beach, FL. At night, exploring spiders moved rapidly over the surfaces of the plant and paused chiefly when disturbed or after encountering these nectaries.

low flowers, a likely source of nectar. But more important, it also has at least three prominent extrafloral nectaries located on the underside of each heart-shaped leaf near the petiole. These nectaries are small longitudinal slits, one on the base of each main leaf rib. The plants grow so tall and the leaves are so large that it is easy to stand beneath the higher branches of a single shrub and observe a number of extrafloral nectary slits at the same time. In addition, each nectary is clearly marked by a sooty fungus associated with the sugar it secretes. During the day, ants dominated these nectaries. At night, the most abundant visitors were nectar-feeding mosquitoes, which placed their proboscises directly into the slits. But also during the night, between sundown and around 2200 hours, we saw the same sorts of wandering spiders as we saw on *Terminalia* flowers. They splayed their legs, flattening themselves against the leaves, and pressed their mouthparts into the nectary openings. There were no opportunities to photograph these nervous subjects, and we lacked the required permits to take voucher specimens.

For these spiders to assume such unnatural looking postures at these nectaries suggests clearly that they were not there by chance. For them to be at extrafloral nectaries, as well as in flowers, discounts the argument that they may have been seeking only insects hidden inside the flowers or seeking pollen grains, which are known to be nutritious. Finally, it seems unlikely that these spiders sought water at the nectaries; the foliage in this soggy environment was usually wet from daily afternoon and evening downpours. Floral and extrafloral nectars, however, contain not only water; they provide a rich source of sugars and often contain significant amounts of amino acids, lipids, vitamins, and other potential nutrients (Baker & Baker 1975, 1983; Koptur 1992).

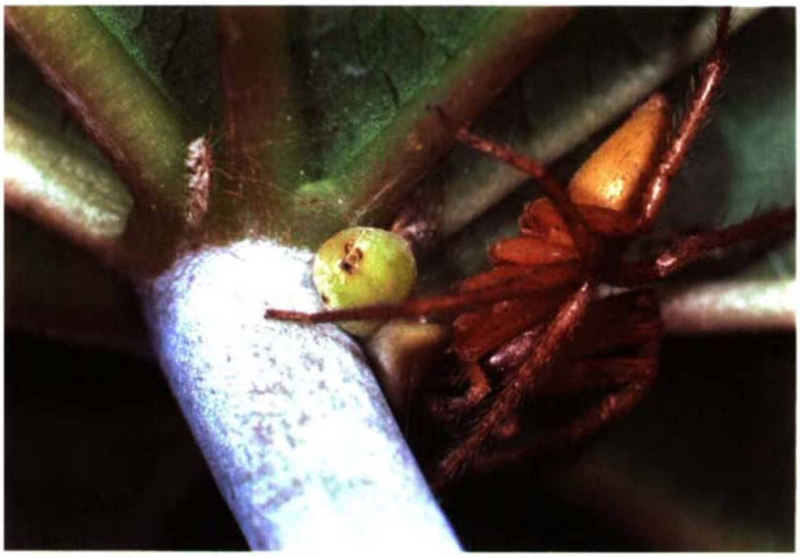
In 1986 and 1987, during several nights of mosquito work near a tidal marsh in Vero Beach, FL, once again we saw both sexes of subtropical wandering spiders apparently feeding on nectar, this time on *Eupatorium serotinum* Michaux, a common thoroughwort with tiny white florets forming flat-topped clusters. These spiders behaved like those in Costa Rica, wandering quickly from floret to floret, thrusting their mouthparts into each. In just over an hour, we watched nine spiders inserting their mouthparts into a succession of florets. And, as in Costa Rica, we found Florida spiders at extrafloral nectaries—in this case on the common castor bean (castor-oil) plant, *Ricinus communis* L.—once again precluding the possibility that they were responding to, or feeding on, pollen or insects hidden in the flowers. The extrafloral nectaries of castor bean are large, obvious, cup-shaped structures located on the petiole along its length and at its terminus on the underside of each huge leaf. On every night that we searched, we saw many immature and adult spiders of both sexes (as confirmed by collection) with their mouthparts pressed to the nectaries, and there seemed to be a greater variety of species than we had seen in Costa Rica. The four species identified from Florida are placed in three closely allied families of spiders: (1) Anyphaenidae: *Hibana* (=*Aysha*) *velox* (Becker); (2) Clubionidae: *Chiracanthium mildei* L. Koch; and (3) Corinnidae: *Trachelas volutus* Gertsch; *Trachelas similis* F. O. Pickard-Cambridge. These families are generally referred to as *running spiders* or *sac spiders*, because they hide during the day in small nests of their own making, often in rolled up leaves or under loose tree bark. All were extremely sensitive to disturbance and had quick running and jumping capabilities, making photographs and collections difficult.

Among the spiders collected from Florida castor bean nectaries, a female *H. velox* deposited an egg cluster from which we collected 48 spiderlings to test the effects of a sugar diet on survival. Individual spiderlings were isolated in small plastic containers at 27°C and 80% RH. Half received water only and the other half received water and a 25% sucrose solution. Aside from a few that died early by accidental crushing or miring, the mean age at death of the sucrose group was 40.4 days (range, 26–56) and for the water group it was 18.7 days (range, 16–27), a significant reduction. Thus, the availability of a sucrose solution, in addition to water, more than doubled the longevity of these spiderlings, which hatch from egg sacs typically deposited in vegetation. If these spiderlings take nectar in the field when the vegetation in which they hatch has nearby floral or extrafloral nectaries or honeydew, then sugar's contribution to spiderling survival might be substantial.

We observed yet another case of apparent nectar feeding by tropical running spiders in eastern Panama in 1988. At a research station on Majé Island in Lake Bayano, we collected large numbers of mosquitoes from the domestic cashew tree, *Anacardium occidentale* L. Although the trees were covered with small pale blossoms, almost every nonquiescent mosquito, chironomid, and other nectar-feeding insect was probing small areas of apparently undifferentiated plant surface at the angles of the cashew panicle branches. On each of the seven nights of collecting, we saw several spiders pressing their mouthparts to these same places, which are known to be the sites of nectar-bearing trichomes (Wunnachit et al. 1992). All of the spiders collected were *Hibana* (=*Aysha*) *similaris* (Banks) (Anyphaenidae), including immatures and adult males and females. Some of these individuals were observed on the trees for over an hour. They moved quickly among the panicle nectaries, pausing at each one for at least one to two seconds while touching their mouthparts to the surface. They also explored the flowers and flower buds themselves but did not pause there. One spider was observed to capture and eat two small insects probing the nectar sites; it then ceased wandering.

The anecdotal and experimental spider literature reveals, here and there, single observations of spiders indulging in catholic tastes (Nentwig 1987). Crab spiders have been observed to drink the excess molting fluid from their exuvial legs immediately after ecdysis (Dondale 1965). Experimental spiders have been noted to eat sausage, banana (Decae 1986), other meats, and fruit preserves (Bonnet 1924); their longevity has been doubled when allowed access to the pollen on flowers in addition to water (Vogelei & Greissl 1989); and they have been raised on artificial laboratory diets of milk and egg yolk, although their growth was slowed (Peck & Whitcomb 1968). More telling, however, is what spiders eat in nature. Particularly relevant to our own work are the singular observations of the ant-mimicking jumping spider *Myrmarachne foenisex* Simon (Salticidae) feeding on honeydew from coccids in Zaire (Collart 1929a, b) and of *M. legon* Wanless taking nectar from extrafloral nectaries in Ghana (Edmunds 1978). Why have there been so few of these observations? Two possibilities are that investigators seldom follow wandering spiders continuously up in the herbaceous and arboreal vegetation to see what they consume and that few studies of visitors to extrafloral nectaries are conducted at night, when so many wanderers are most active.

The above observations suggest that if some tropical and subtropical spiders are nectar feeders, then, because plant nectar and spiders are practically ubiquitous, some temperate species probably are nectar feeders too. This, in fact, is the case. During field studies in Virginia of crab spider courtship behavior, Pollard et al. (1995) observed that males of *Misumenoides formosipes* (Walckenaer) fed on the floral nectar of Queen Anne's lace (*Daucus carota* L.), goldenrod (*Solidago* spp.), and chicory (*Cichorium intybus* L.). The nectar feeding in this case may even be critical to the male's mating success: mature



H. velox with chelicerae pressed onto the surface of a castor bean extrafloral nectary in Vero Beach, FL. The source of the webbing around the nectaries, which has ensnared a psyllid, is unknown.

C. ocossa feeding on the nectar-bearing trichomes at a panicle branch of the cashew tree on Majé Island in Lake Bayano, Panama. This mosquito, a vector of Venezuelan encephalitis in Central America, and several other mosquito species and other insects concentrated their probing activities at these spots, at which wandering spiders also nearly always paused and touched their mouthparts.

H. similaris, its mouthparts applied to the nectar-bearing trichomes at a panicle branch of the cashew tree on Majé Island in Lake Bayano, Panama. These spiders paused and apparently fed at these spots as they wandered over the plant. They also quickly explored the flowers, located at the tips of the branches, but did not pause to probe them.

males, whose bodies are minuscule compared to those of the females, and who spend most of their time on the flowers engaged in courting females rather than catching prey, may find that the small amounts of nectar in the tiny florets provide a significant source of energy. Laboratory experiments showed that these males preferred a 30% sucrose solution to water and would still imbibe sugar after they would no longer drink water. Males given access to Queen Anne's lace inflorescences for 1 hr every 1–2 days lived about 13 days, almost 3 days longer than those given water only. Also in the laboratory, Vogelei & Greissl (1989) showed that newly emerged *Thomisus onustus* Walckenaer spiderlings, deprived of prey but with continuous access to 30% sucrose solution, lived about four months—three and six times as long as those maintained on pollen only and water only, respectively.

Of hundreds of observations of female crab spiders in the field, only once was a female observed to feed on nectar (Pollard et al. 1995), whereas our nectary collections of running spiders in the tropics and subtropics consisted of both sexes. Perhaps this is because the nectaries we observed are much more productive in relation to the spider body sizes or because sugar is more critical to the nutritional economy of both sexes of these high-strung foragers. As for our own observations in temperate regions, we have one anecdote. A potted tropical hibiscus located outdoors in Columbus, OH, had an enormous drop of viscous nectar hanging from one of its foliar nectaries. While one of us watched, a local pale wanderer, presumably a clubionid or relative, discovered the nectar, stopped, and in clear unobstructed profile, drank the entire drop.

Analyses of spider energetics, competition, and distribution have always taken into consideration the numbers and types of prey available to spiders. Occasionally, the type or distribution of vegetation is considered important, as it might serve as support for webs, as refugia, or as a food source for the insects that spiders catch. Certainly those studies that examine plant life in a spider's environment do not consider the vegetation as a direct source of food for juvenile or adult spiders. It may be, however, that some immature and adult spiders are routinely gathering carbohydrates, amino acids, lipids, and vitamins from the ubiquitous and energy-rich nectar and honeydew found on plants. If true, it calls into question those studies that consider only prey among a spider's foods when evaluating the nutritional resources of a study site.

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