How Dietary Plant Nectar Affects the Survival, Growth, and Fecundity of a Cursorial Spider *Cheiracanthium inclusum* (Araneae: Miturgidae)

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ABSTRACT We measured the effects of plant nectar consumption on *Cheiracanthium inclusum* (Hentz) (Miturgidae), an agriculturally important spider. Newly emerged spiderlings were reared on the eggs of *Helicoverpa zea* (Boddie) at four prey densities, 1, 5, 25, or 125 eggs, three times a week, with or without nectar. Nectar came from the extrafloral nectaries of Indian almond, *Terminalia cattapa* L. (Combretaceae). The addition of nectar to prey (1) allowed spiderlings on the 1-egg diet to survive longer and molt many more times; (2) allowed virtually all of the spiderlings on the 5-egg diet to become small adults and 50% to mate and reproduce versus those without nectar, none of which matured to adulthood; and (3) increased fecundity of females on 5-egg and 25-egg diets to the level of females fed five times the amount of prey. These results show that spiders that feed on nectar increase their fitness with increased survival, growth, and fecundity, particularly when density of prey is inadequate or marginal.

KEY WORDS allocation, foraging, *Helicoverpa zea,* nutrition, starvation

Adequate nutrition is necessary for any organism to fulfill its fitness potential. An organism that can expand its diet a trophic level, therefore, is also likely to increase its fitness. As obligate carnivores, spiders most often prey on other arthropods, including pest species, and assessments of spider diets and their contribution to natural pest control usually focus on spiders as predatory secondary consumers. Recognizing that some spiders also feed on plant products in addition to prey, Coll and Guershon (2002) have identified some spiders as both primary and secondary consumers. They cite in particular juvenile orb weavers that gain nutrition from ensnared pollen grains that the spiders incidentally eat when they consume and recycle their webs (Smith and Mommsen 1984) and all ages and both sexes of fast-moving cursorial spiders (Clubionidae, Anyphaenidae, and Corinnidae) observed in the field feeding from floral and extrafloral nectaries (EFNs) (Taylor and Foster 1996). Observations of spiders feeding on nectar have been interpreted as isolated or unusual events, but the accretion of evidence suggests nectar feeding as a general phenomenon. Members of large families of spiders have been noted to feed on nectar, such as prey-deprived crab spiderlings (Thomisidae) that lived much longer in the presence of flower nectar (Vogelei and Greissl 1989) and male crab spiders observed to feed on nectar between bouts of courtship on Queen Anne's lace (Pollard et al. 1995). Jumping spiders (Salticidae) observed gathering nectar at the EFNs of a wild legume preferred plants with EFNs to those without (Ruhren and Handel 1999), and laboratory experiments showed that 91 species of jumping spiders preferred sucrose to water (Jackson et al. 2001). In the field, systematic collections of cursorial spiders from cotton plants, which contain EFNs (Butler et al. 1972), showed one in four spiders to be positive for plant sugar (i.e., fructose), with females more often positive than males (Taylor and Pfannenstiel 2008).

Beyond nectar's contribution to survival, Taylor and Bradley (2009) showed that dietary nectar increased molting in newly emerged prey-deprived *Cheiracanthium mildei* (Miturgidae) and sustained their energy-demanding nocturnal foraging. In this experiment, we followed the effect of dietary nectar on the entire life history—from emergence to functional maturity and reproductive output—of a closely related active forager *C. inclusum* (Hentz) (Araneae, Miturgidae). A common predator in agricultural crops in the United States, such as apple (Bajwa and Aliniazee 2001), grape (Costello and Daane 1998, Roltsch et al. 1998), and cotton (Whitcomb et al. 1963, Agnew et al. 1982), *C. inclusum,* like *C. mildei,* is quiescent during the day in a lightly woven silk resting cell and active during the night searching for prey. Along with other ecologically similar (i.e., non–web-building cursorial) spiders, *C. inclusum* occupies vegetation and visits EFNs (Taylor and Foster 1996, Taylor and Pfannenstiel 2008).

To study nectar's contribution to the fitness of *C. inclusum,* we reared spiderlings to adulthood on eight diets: 1, 5, 25, or 125 *Helicoverpa zea* eggs three times a week (Pfannenstiel 2008) with or without extrafloral nectar. In particular, we asked four questions regard-

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ing the presence of nectar at each level of prey. (1) Can nectar reduce the time required to reach adulthood? (2) Can nectar increase a spider's size? (3) Can nectar increase a spider's fecundity? (4) Do the newly emerged offspring of nectar-fed females survive starvation longer than the offspring of females without nectar?

Materials and Methods

Spiders, Containers, and Diets for Immatures. Spiders were obtained from laboratory-reared *C. inclusum* collected from cotton and maintained at the U.S. Department of Agriculture–Beneficial Insects Research Unit (USDA–BIRU) in Weslaco, TX. One hundred sixty spiderlings from five egg masses collected from five individual females were evenly distributed among eight diets: four levels of prey, with and without extrafloral nectar.

Spiders received the eggs of the corn earworm *Helicoverpa zea* (Boddie) (=*Heliothis zea*) (Lepidoptera: Noctuidae), which *C. inclusum* eats in crops (Nyffeler et al. 1990). *H. zea* eggs were supplied by USDA–BIRU. Allotments of 1, 5, 25, or 125 eggs were provided three times a week, with nectar (+N) or without (−N). Nectar was collected from the EFNs of Indian almond (*Terminalia cattapa*) grown in the Ohio State University greenhouse. Nectar was collected with a microspatula, scraped into glass collecting bottles, and stored at −45°C. Serial dilutions on a Reichert-Jung refractometer showed the EFN sugar concentration of *T. cattapa* to be 87.5%. A 1- to 2-μl aliquot of nectar was placed with a microspatula into a dimple drilled into a plastic "feeder" (1 by 2.5 cm). Nectar was refreshed three times a week, along with prey. When 75% of the spiders on the 1-egg/+N diet had molted three times, they were switched to 69% sucrose, which has been shown to have an effect equivalent to the EFN used here (Taylor and Bradley 2009). This substitution was necessary to conserve plant nectar for fecundity experiments; spiders on the 1-egg diets were not expected to mature.

Individual spiders occupied 125 by 15-mm plastic petri dishes, turned upside down so that the spider wove its sac in the solid, uppermost part (=bottom) of the dish. Opening the dish rarely caused disturbance. Cotton water wicks (0.5 in) in each dish were remoistened three times a week when eggs and nectar were replaced. Spiders were reared in incubators with a 14:10 light:dark cycle, 24°C, and a relative humidity range of 48–82%. Spiders were rotated among the shelves and checked daily for mortality and molting.

Containers and Diet for Reproductive Females. When females reached functional maturity (determined by the presence of a fully sclerotized epigynum), they were mated with nonsibling males, either wild caught or from the 25- or 125-egg feeding groups. After mating, each female was housed in an upside-down 150 by 25-mm plastic petri dish to accommodate a more generous diet of eggs and a glass shell vial for the spider to deposit her egg mass. Immediately after mating, all females were placed on the same diet of 250 eggs, three times per week (Monday, Wednesday, Friday) to allow any female, regardless of her historical nutritional status, to develop the eggs that she had generated presumably before she matured (Miyazaki et al. 2001, Choi and Moon 2003, Morishita et al. 2003). After egg deposition, food was withheld while the female guarded her eggs and until the spiderlings emerged. This cycle was repeated for each female for three egg masses.

Estimates of Body Size and Offspring Survival. We estimated body size by carapace width (measured with a microscope ocular micrometer), a sclerotized part of the spider that, unlike the abdomen, is not affected by a spider's current nutritional state (Dondale 1961, Hagstrum 1971). We measured the carapaces of adults only, eliminating individuals on 1 and 5 eggs/−N diets.

At emergence, 15 spiderlings randomly selected from each of 92 egg sacs (remaining individuals were frozen and counted) received water only and were monitored daily for survival.

Data Analysis. All comparisons were conducted with Minitab 15 (2007; Minitab, Inc.). To measure offspring survival, we pooled the data for all of the females on each diet and used Kaplan-Meier survival analysis. All other comparisons used Mann-Whitney U tests, appropriate for nonparametric data with small sample sizes. α was set at 0.05. For unplanned multiple comparisons, we reduced α to reflect the total number of planned and unplanned comparisons (k) as per the Bonferroni procedure (α/k) (Moore and McCabe 1999).

Results

For every parameter tested (growth, size, fecundity, and offspring survival), spiders fed five eggs with nectar differed significantly from their counterparts without nectar, because none of the spiders on the 5 egg/−N diet molted to adulthood (Figs. 1–4). Formal statistical comparisons were impossible within this group. Spiders fed one egg lived longer and underwent many more molts if they also received nectar. Nectar contributed to the fecundity and growth rate of spiders on the 25-egg diet. Measures of offspring survival showed mixed results, although starved offspring of females fed 125 eggs with nectar lived longer than offspring of similarly fed females without nectar.

Time to Reach Adulthood. In the 5-egg diet, nectar made the difference whether spiders reached adulthood or not. Nineteen of the spiders fed 5 eggs/+N matured to adulthood. Conversely, none of the spiders fed 5 eggs/−N reached adulthood. Spiders on the 25-egg diet also reached adulthood significantly sooner if they also received nectar (Mann-Whitney, $U = 497.5$, $P = 0.02$; Fig. 1).

None of the spiders fed only one egg reached adulthood. Among those that also received nectar, however, 12 molted seven times and two molted nine times. (One individual survived an unexpected 505 d.) By comparison, all of the spiders fed one egg without nectar died before, during, or days after their second molt. All of the spiders fed 125 eggs reached adult-

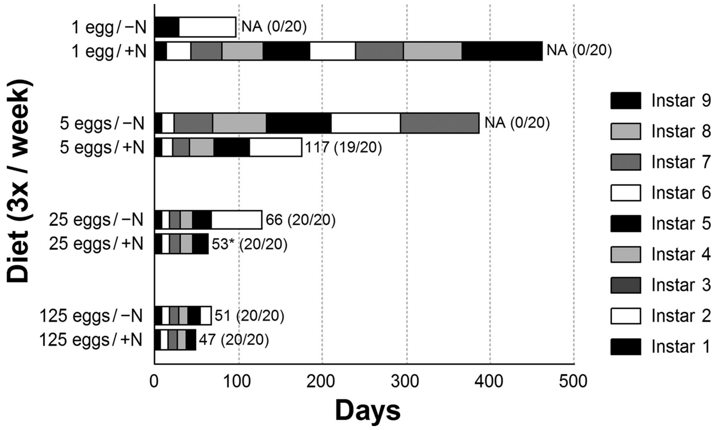

Fig. 1. The effects of dietary plant nectar on the number of days for *C. inclusum* ($n = 20$) to reach adulthood. Diets are four densities of prey (moth eggs) with (+N) or without (–N) nectar. Number of days (median) to adulthood are at ends of bars. Numbers in parentheses are spiders that reached adulthood. On three diets (1egg/+N; 1 egg/–N; and 5 eggs/–N), formal analysis was not applicable (NA) because spiders survived but did not molt to adulthood. The x-scale concords with bar segments, which indicate mean instar duration and instar number.

hood. Nectar did not affect their rate of maturation (Mann-Whitney, $U = 458.5, P = 0.19$). All comparisons were planned and within diets. α was 0.05.

Body Size. Only by adding nectar to five eggs were both males and females able to reach adulthood (Fig. 2). Comparisons within the 25- and 125-egg diets showed that adding nectar made no statistical difference in body size for males or females (25 eggs: males, Mann-Whitney $U = 104.5$, $P = 0.67$; females, Mann-Whitney, $U = 83.5$ $P = 0.28$; 125-eggs: males, Mann-Whitney $U = 92.0$, $P = 0.21$; females, Mann-Whitney $U = 64.0$, $P = 0.47$). Comparison across diets of males and females fed 5 eggs with males and females fed 25 eggs/−N showed the marginally fed (five eggs) adults to be relatively and notably small (males, Mann-Whitney $U = 53.0$, $P = 0.0017$; females, Mann-Whitney $U = 47.0$, $P = 0.0007$).

Figure 2 shows mean (rather than median) body sizes for clarity, because all of the body widths were normally distributed except for females on the 125 egg/+N diet, which could not be normalized, precluding parametric analysis. Multiple unplanned comparisons were adjusted by $k = 6$; $\alpha = 0.008$.

Reproductive Competence. Although spiderlings in the 5-egg diet reached sexual maturity only if they also received nectar, reproductive competence was not guaranteed. Three of the 11 males had either malformed palps or palps that pulled away completely during their final molt. Six males fed 5 egg/+N contributed to 10 matings, producing seven viable egg masses (two of these males produced zero egg masses). These males were mated with healthy, well-fed females reared especially for the purpose of not confounding potential male reproductive incompe-

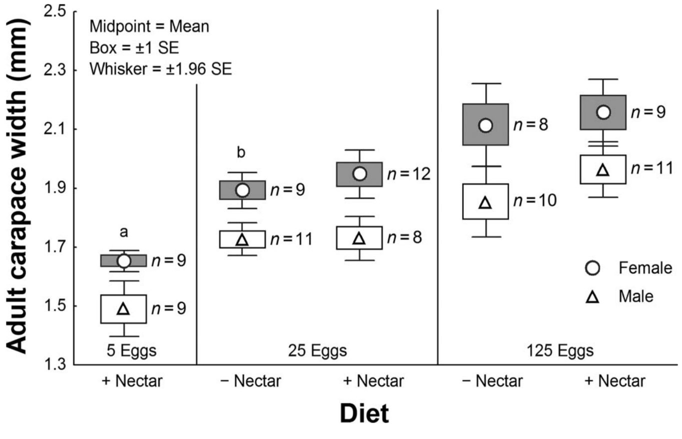

Fig. 2. The effects of dietary plant nectar on mean carapace widths (mm) of adult male and female *C. inclusum* reared on diets of four densities of prey (moth eggs) with (+N) or without (–N) nectar. Three diets, 1 egg/+N; 1 egg/–N; and 5 eggs/–N, did not produce adults for comparison. Planned comparisons within the other two levels of prey showed no statistical effects. Different lowercase letters indicate significant differences (unplanned comparisons) across diets (alpha corrected for multiple comparisons).

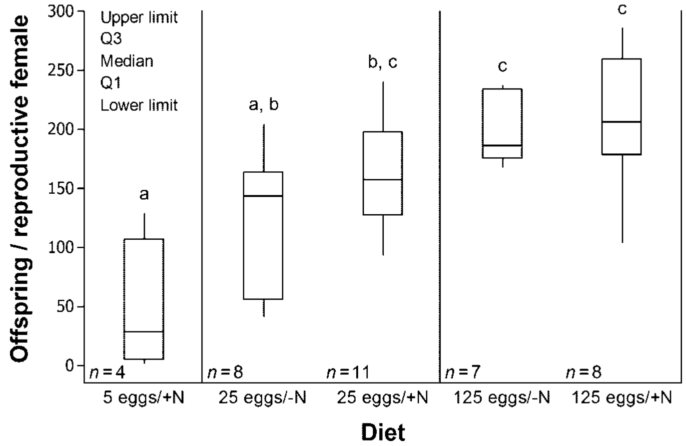

Fig. 3. The effects of dietary plant nectar on mean offspring production per reproductive female *C. inclusum* reared on diets of four densities of prey (moth eggs) with (+N) or without (-N) nectar. Three diets, 1 egg/ +N; 1 egg/-N; and 5 eggs/-N, did not produce adults for comparison. Planned comparisons within the other two levels of prey showed no statistical effects. Different lowercase letters indicate significant differences for females across diets (α corrected for multiple unplanned comparisons).

tence with female incompetence on such a low-prey diet. Likewise, all nine of the females on this diet (5 eggs/ +N) were mated with well-fed males; four of the nine laid egg masses. We intentionally mated, however, one male and one female on the 5 eggs/ +N diet, and she produced three viable egg masses, which was the only female among the four reproductive females on the diet to produce multiple masses.

Female Fecundity. Females on the 5-egg diet reproduced only if they also received nectar, four of which produced 188 offspring (Fig. 3). In planned comparisons within the 25- and 125-egg diets, nectar had no statistical effect on female fecundity (25 eggs: Mann-Whitney $U = 62.0$, $P = 0.15$; 125 eggs: Mann-Whitney $U = 51.0$, $P = 0.60$).

In unplanned comparisons across diets, however, reproductive output of females on the 5-egg/ +N diet was comparable to output of females on the 25-egg/ −N diet (Mann Whitney $U = 14.0$, $P = 0.05$, although this should be regarded with caution because Bonferroni's correction is conservative and without the correction $\alpha = 0.05$). Likewise, females provided nectar on the 25 egg/ +N diet were able to produce numbers of eggs statistically comparable to females on the 125 egg/ −N diet (Mann Whitney $U = 89.0$, $P = 0.17$), whereas females fed 25 egg/ −N compared with 125 egg/ −N produced statistically fewer eggs (Mann-Whitney $U = 40.5$ $P = 0.008$; Fig. 3). Multiple comparisons were adjusted by $k = 5$; $\alpha = 0.01$.

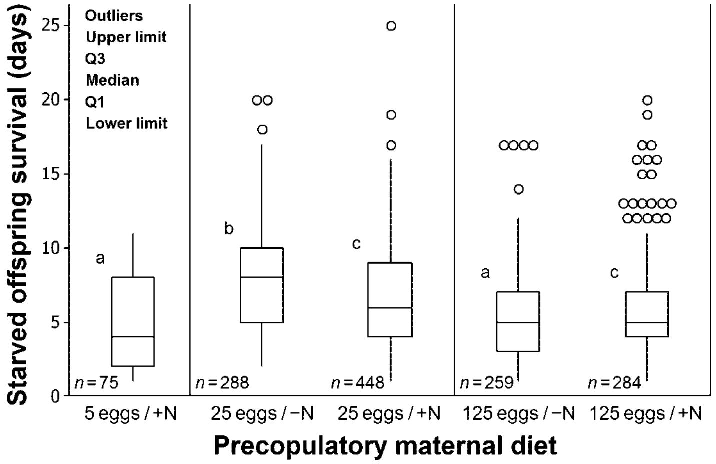

Fig. 4. The effects of maternal dietary plant nectar on starved offspring survival (fed water only) of *C. inclusum*. Maternal diets were four densities of prey (moth eggs) with (+N) or without (-N) nectar. Three diets, 1 egg/ +N; 1 egg/-N; and 5 eggs/-N, did not produce offspring. Boxes with medians depict Kaplan-Meier survival analysis. Different lowercase letters indicate significant differences across diets (α corrected for multiple unplanned comparisons).

Offspring Survival. Figure 4 shows the mixed results of offspring of females who did and did not receive dietary nectar. Because females fed 5 eggs/−N did not mature to adulthood, the offspring of females fed 5 eggs/+N unequivocally survive longer than offspring of females without nectar. In planned comparisons, the addition of nectar made no significant difference to the offspring of females on the 25-egg diet. In fact, unplanned comparisons showed that the females fed 25 eggs/−N produced offspring that survived longer than the offspring of all five other groups (all *P* value comparisons = 0.000). However, in a planned comparison, nectar added to the maternal diet of 125 eggs produced offspring that statistically lived longer than those without nectar (Mann-Whitney $U = 67{,}078$, $P = 0.003$). The unplanned comparison of offspring of females fed 5 eggs/+N showed their survival to be comparable to the offspring survival of females fed 125 eggs/−N (Mann-Whitney $U = 12003$, $P = 0.448$). Multiple unplanned comparisons were adjusted by $k = 7$; $\alpha = 0.007$.

Discussion

Spiders in nature are generally thought to be prey limited (Miyashita 1968, Anderson 1974, Nentwig 1987, Nyffeler et al. 1987, Wise 1993, Nyffeler and Sterling 1994), which makes our findings of spiders benefiting from feeding on plant nectar all the more relevant. Our experiment showed for the first time that dietary nectar can help a spider reach sexual maturity and increase its number of offspring. Added to a marginal diet of prey (five *H. zea* eggs three times a week), nectar allowed maintenance, growth, and reproduction among virtually the entire sample of *C. inclusum*, which the diet of prey alone could not. In addition, the reproductive output of these marginally fed females was comparable with females fed five times the amount of prey (5 versus 25 eggs). Likewise, the addition of nectar to a diet of 25 eggs increased female fecundity to a level comparable with that of females fed 125 eggs. These results lead us to this hypothesis: under conditions of limited prey, for a spider whose foraging method seems to require considerable energy, plant nectar confers benefits similar to a five-fold increase in prey. (We reiterate here that to assess how many eggs a female could develop on the 5-egg diet, we were compelled to increase the diet post copulation. Oogenesis in spiders is not well understood, and based on scant information we presumed that females did not develop new eggs in response to the increased diet we provided them after mating. To have maintained females on their restricted diets throughout egg development and through the time of egg deposition risked females being too malnourished to develop whatever eggs they had generated [in response to the level of prey] and laying nothing at all).

Some miturgids, anyphaenids, thomisids, and oxyopids, provided the opportunity, are already known to feed on nectar in the field (Taylor and Pfannenstiel 2008). When living in agricultural crops such as cotton, which produce nectar at EFNs (Wäckers et al. 2001), spiders have an additional and ubiquitous source of food, and, as consumers of nectar directly, they derive more energy from nectar's simple carbohydrates than would be obtained through their nectarivorous prey. As regular consumers and beneficiaries of nectar meals, some spiders position themselves among the ranks of other predaceous arthropods, such as larval lacewings (Limburg and Rosenheim 2001), mites (van Rijn and Tanigoshi 1999), and bigeyed bugs (Yokoyama 1978) that increase their longevity with nectar during prey deprivation. Furthermore, the simple carbohydrates that compose the bulk of plant nectar (Percival 1961, Baker and Baker 1975, 1983) can fuel the activity of spiders (Taylor and Bradley 2009), allowing them to allocate the more valuable nutrients of prey to growth and reproduction.

Because it is an active forager presumably with high energetic demands, *C. inclusum* lends itself well to an experimental diet such as this, which can satisfy the spider's energetic and nutritional requirements separately with different, quantifiable diets. The dietary nectar provided from the EFNs of Indian almond was nearly identical to the concentration of sugars (87.2%) from the EFNs of castor bean (*Ricinus communis*) (Baker et al. 1978) and the EFNs of cashew (77.7%; *Anacardium occidentale*) (Wunnachit et al. 1992). Both castor bean and cashew are sites of earlier observations of spider feeding, in addition to Indian almond itself (Taylor and Foster 1996). The nectar was delivered imprecisely and presumably to saturation to examine what benefits nectar could contribute to prey-saturated and particularly to prey-limited diets. The amount of prey, therefore, was tightly controlled, taking advantage of the ability of *C. inclusum* to reach normal functional maturity on a monotypic diet of *H. zea* eggs (Pfannenstiel 2008). That *C. inclusum* can mature on another single-species diet has been suggested elsewhere (Amalin et al. 2001), although this is the first experiment to take advantage of and apply a diet that can be so reliably and precisely meted out. Additionally, spiders could mature on this diet in 51 d, about one half of what had been previously established for *C. inclusum* (95 d for males, 125 d for females) on what was assumed to be a natural, nutritious (albeit laboratory provided) mixed-prey diet (Peck and Whitcomb 1970).

Contributing to the perception that spiders are generally prey limited, Miyashita (1968) concluded that food for field-collected lycosids was "considerably limited" over the long term, because their carapace widths resembled the widths of laboratory-reared spiders fed every fourth day as opposed to every second day or every day. In the short term, Anderson (1974) determined field-collected lycosids and filistatids to be "starving," because their abdominal width/cephalothorax width ratios were equal to or less than the ratios of experimental starvation groups of the same species in 46 and 50% (respectively) of the samples. If spiders that have been observed at nectaries are in fact starving or prey limited, nectar feeding in the field may be very important to these species. It may also be, however, a mistake to generalize what we know about nutrition in lycosids to other spiders. In particular, lycosids are unlikely to feed on nectar (Taylor and Pfannenstiel 2008), and what is perceived to be a normal nutritional status for them may poorly represent the normal nutritional status of spiders that do feed on nectar. If, for example, some cursorial spiders rely on nectar more than we recognize, we risk assuming prey requirements of a spider whose requirements may be much lower. Among animals that specialize on sugary, protein-dilute foods, for example, there is an association with relatively low protein requirements, apparent in nectar-feeding and frugivorous birds (Witmer 1998). Perhaps spiders that feed on nectar should also be studied for having protein requirements that are lower than expected. For example, lycosids and other spiders, on the one hand, are well known to require a mixed prey diet to survive and mature (Uetz et al.1992). *C inclusum,* however, is able to develop normally and even more rapidly on a diet solely of *H. zea* eggs than on a diet of mixed prey. This indicates something important about the food (*H. zea* eggs) or about the spider (or both). In fact, the precise dietary delivery system of nutrients (moth eggs) and sugar in this experiment could help ascertain the nutrients and calories that are no more than absolutely necessary for *C. inclusum* to reach adulthood.

The "small adults" produced on the 5-egg diet were substantially smaller than adults in the next diet regimen (25 eggs; Fig. 2) and may represent a decision of the spider to molt to adulthood in a prey-deprived situation (Forrest 1987). This phenomenon of spiders molting to small adulthood after food deprivation is well documented (Turnbull 1962, Wise 1976, Miyashita 1986, Higgins 2000), although the fecundity of these small females is not. Higgins, for example, presumed that smaller females would naturally lay fewer eggs than larger females and be relatively less fit. Turnbull assumed his tiny female linyphiids to be clearly fully mature but "sterile," although he does not say with whom he mated his females to conclude this; he did not mate any of the males in his study. In our study, we discovered that only by intentionally mating a small female with a small male did a small female reproduce three healthy egg sacs and 129 of the 188 offspring produced by small adults. These numbers are comparable with females on the next highest prey diet (25 eggs), and the starved offspring survived as long as offspring of females having received 25 times the amount of prey (125 versus 5 eggs). Before we collected these results, we intentionally mated all other small adults (male and female) with spiders of normal size based on our own (mistaken) preconceptions that small adults would have trouble reproducing and that mating them with one another would confound our ability to decipher their individual reproductive capabilities. The presence of sexually incompetent males with pale, soft palps and chelicerae (normally dark, hard structures) suggested inadequate protein (Dalingwater 1987) and seemed to support this decision. However, in our efforts to reduce confounding variables ("smallness" and possible protein deficiency), we may have guaranteed the reproductive failure of small adults and ultimately severely underestimated their reproductive potential.

To conclude that a spider is "starving," researchers should establish that it cannot reliably maintain itself, grow, or reproduce. Body size has been used as an indicator of starvation (or prey limitation), but our study shows that body size is not a reliable indicator. Although the body size of the "small" C. *inclusum* (on the 5-egg regimen) was substantially smaller than the next feeding regimen (25 eggs), their reproductive outputs were statistically comparable. This output may have been much greater had we allowed small individuals to mate with one another. Small adults or small juveniles, therefore, may be mistakenly determined as "starving," when, in fact, at low densities of prey, they are simply on a slower track to adulthood and reproduction. Furthermore, unless we know for each species what is normal development in nature, what is perceived as "limited," "slow," and "small" in the laboratory may actually be typical or common in the field.

In his study of the effects of caloric restriction on the bowl and doily spider (*Frontinella pyramitela = F. communis*), Austad (1989) faced this very conundrum of having to know first what was calorically "normal" for spiders in the field before he could consider his caloric regimen "restricted." He cogently presents the problem: "the relation between feeding regimes proffered in the laboratory and those available in nature is rarely known. Therefore it is unclear whether laboratory experiments are comparing overfed with normally fed individuals, or normally fed versus food-restricted individuals" (p. 84). Indeed, Turnbull faced the same problem in his efforts to underfeed his linyphiids to keep them from sexual maturation, and overfed them (Turnbull 1962). Austad's laboratory study showed that, in *F. pyramitela,* as occurs in many other taxa, low caloric intake contributed to longevity and eventual maturation to adulthood. He concluded from field studies, however, that the effects of caloric restriction in *F. pyramitela* could not play out in nature, because the natural lifetime of the spider is not nearly long enough, shortened by predation rather than senescence. To apply these findings of a short life and early death to *C. inclusum* and other cursorials that nectar feed, however, may be a mistake. For example, *F. pyramitela* is a diurnal sedentary webweaver; by contrast, *C. inclusum,* is a lightning-quick nocturnal forager that spends much of its life in a cryptic, lightly woven resting cell. By evading predation, *C. inclusum* may actually reach senescence in the field (unlike any of Austad's field *F. pyramitela*) so that its nutritional status in the field may be tied to its natural life span. That is, small spiders in the field that some might identify as "starving," may actually be engaged in a secondary strategy—to stay small and reproduce. With the availability of nectar for some, adulthood may come later but necessitating far fewer prey than was ever previously imagined. Matings between these small individuals may be more common and more reproductively fruitful than previously thought, however, meaning that predation lost to nectar feeding may be regained with increased numbers of offspring.

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