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Are brown recluse spiders, *Loxosceles reclusa* (Araneae, Sicariidae) scavengers? The influence of predator satiation, prey size, and prey quality

Kenneth L. Cramer: Department of Biology, Monmouth College, 700 E. Broadway, Monmouth, Illinois 61462, USA. E-mail: kenc@monm.edu

Abstract. I examined prey choice of the brown recluse spider (*Loxosceles reclusa* Gertsch & Mulaik 1940) with reference to unusual scavenging behavior originally reported by Sandidge (2003). Because scavenging is an unexpected behavior in normally predatory spiders, I hypothesized that special circumstances must converge for the brown recluse to prefer dead prey over live prey. I offered crickets (*Acheta domesticus*) to brown recluses in several choice experiments. I varied predator satiation (spiders not fed for two or four weeks), prey size (small or large), and prey quality (live, fresh dead, dead 1–2 days, 1 week or 1 month). Overall, recluses preferred live prey over dead, but their choice was influenced by all three variables. Recluses were more likely to scavenge when presented with large live prey paired with dead prey of equal size than when presented with small live and dead prey. Spiders that had fed recently were more likely to scavenge. Finally, recluses preferred dead prey that were freshly killed or less than 24 hours old to items dead for longer periods. My results suggest that scavenging is an opportunistic behavior in recluses that requires specific circumstances that may rarely occur in nature.

Keywords: Brown spider, scavenger, foraging, prey choice

Spiders are generally regarded as obligate predators varying principally in their method of capturing live prey (Coddington & Levi 1991). Originally thought to be non-selective generalists, spiders have also been shown to choose prey in order to meet their current nutritional needs (Greenstone 1979; Mayntz et al. 2005). Such selection has been shown to be important in their growth and survival (Toft 1999; Toft & Wise 1999; Mayntz & Toft 2001). A few exceptions to feeding on active prey have been noted. Some spiders feed on insect eggs (Buschman et al. 1977; Jackson and Blest 1982), nectar (Pollard et al. 1995; Jackson et al. 2001), or pollen (Smith & Mommsen 1984).

Researchers have also observed scavenging by some spiders. Bristowe (1941) observed a gnaphosid feeding on pinned insects and Kullmann (1972) reported that spiderlings of several species would feed on their dead mother. Other researchers have supported lab populations of spiders, especially juveniles, on artificial diets of ground insects (Peck & Whitcomb 1968; Horner & Starks 1972). Knost & Rovner (1975), however, appear to have been the first to conduct experiments on scavenging in spiders. They reported that wolf spiders in the lab would readily consume dead prey and that movement was not a necessary stimulus to induce feeding. Wolf spiders would scavenge even when live prey were available, although the authors did not report on the relative numbers of prey chosen in each category. Although the term "prey" is normally used in reference to live organisms, for simplicity and consistency with earlier literature [e.g., Sandidge 2003], I use the term to refer to both live and dead organisms used for food.

While it may be more common than suspected, little is known about scavenging by spiders in the wild (Foelix 1996). Sandidge (2003) concluded that the brown recluse spider, *Loxosceles reclusa* Gertsch & Mulaik 1940 (Araneae, Sicariidae), was exceptional among wandering spiders because it preferred scavenging over predation and even actively avoided live prey. In the lab he observed that spiders starved for two weeks and offered both live and dead prey simultaneously tended to avoid live prey and instead scavenged on dead prey. He also observed scavenging *in situ* in spiders living in homes. In part because of their preference for scavenging, Sandidge & Hopwood (2005) suggested that brown recluses may be persistent and difficult to control in homes if abundant dead prey are available. Given the apparent rarity of scavenging in spiders and the medical importance of the brown recluse, whose bite can cause severe, necrotic wounds and even systemic reactions (Atkins et al. 1958; Anderson 1998; da Silva et al. 2004), I investigated variables that might promote scavenging in this species.

In the present study I examined three variables that could influence recluse prey choice: predator satiation, prey size and prey quality. I predicted that sated predators would be less likely than nutritionally deprived spiders to attack live prey when dead prey were available; that spiders would be more likely to attack small, rather than large live prey when paired with dead prey of similar size; and that spiders offered only dead prey would prefer more recently killed prey.

METHODS

I used a laboratory population of spiders that was captured from Little Creek Nature Area near Florissant, Missouri, USA (90.291°W; 38.774°N). Spiders were captured from a large pile of lumber in an unheated barn loft. Twenty-six adult male and 35 adult female spiders were housed individually in clear plastic containers (12 × 17 × 6 cm) kept at room temperature under a 12L:12D photoperiod and maintained on a diet of both live and dead domestic crickets (*Acheta domesticus*) offered weekly. Experiments were conducted over a 10-mo period in 2005.

Because brown recluse spiders are a relatively long-lived species (Hite et al. 1966; Eskafi et al. 1977), I was able to use spiders in multiple trials (n = number of trials). To control for possible effects of repeated testing, I randomly assigned spiders to a treatment order to avoid biasing spider choice based on prior experience in another testing situation. To further account for possible bias that could be introduced by

Table 1.—Overview of experimental designs with number of trials and response rates (% spiders feeding).

Treatment design			Sample sizes and response rates		
Starvation period (wk)	Prey size	Prey choice offered	Trials (#)	Spiders feeding (#)	Response rate (%)
2	Large	Live vs. Fresh dead	172	46	27
4	Large	Live vs. Fresh dead	100	61	61
4	Small	Live vs. Fresh dead	87	54	62
4	Small	Live vs. 1-Da dead	28	20	71
4	Small	Fresh dead vs. 1-Da dead	30	20	66
4	Small	7-Da dead vs. 1-Day dead	24	17	71
4	Small	8-Da dead vs. 2-Da dead	24	12	50

repeated testing of the same individual (influence of prior exposure, age, e.g.), I conducted statistical tests for independence of testing order. For spiders tested multiple times (up to 4 times) I used Cochran's Q tests and for spiders tested twice, I employed McNemar's test (Sokal & Rohlf 1969). Spider response was recorded as a categorical variable (choosing live or dead prey) with order of testing as the independent variable. Tests in which the spider did not attack or feed on prey were excluded from this analysis because level of satiation was controlled. I also tested for any influence of sex on choice of prey. If the results for effects of testing order and sex were not significant, I then pooled the data and tested various hypotheses concerning prey choice using a Chi-square test for goodness-of-fit or independence as appropriate. Voucher specimens are housed in the Biology department at Monmouth College, Monmouth, IL.

For prey choice tests I used crickets of two sizes: "large" crickets (4–6 wk old, 11–15 mm body length) and "small" crickets (2–3 wk old, 7–9 mm). Observations showed that the large crickets were well within the size range that the spider's venom could immobilize if they chose to attack. The small size class fell within the range of body lengths of *L. reclusa* used in this study. To kill crickets, I placed them in a freezer (-20° C) for approximately 24 h prior to testing and thawed them to room temperature before testing began. I also "aged" different groups of dead crickets by leaving them in ventilated containers at room temperature for 1, 2, 7, or 8 da (= day) and 4 wk. For all tests, I used forceps to place dead and live prey in the center of the plastic containers housing individual recluses.

I observed feeding behavior in a darkened room under low light beginning at roughly 18:00 h. During the first 15 min of testing, I observed spiders continuously and then checked every 15 min for the next 2 h for evidence of feeding. Because recluses will feed for ≥ 1 h on a given prey (Hite et al. 1966) this method ensured that no feeding in the first 2 h was missed. More than 90% of the spiders had made a choice of prey within the first 30 min. After 18 h of testing, I removed any uneaten prey. In the few instances when feeding occurred overnight after the initial 2-h observation period, I confirmed prey choice by examining prey remains under a dissecting scope. Feeding was easily confirmed by noting loss of volume and collapse of the exoskeleton due to fluids being withdrawn. I conducted seven principal experiments in which I varied predator satiation, prey size and prey quality (Table 1). In all results where spiders were tested multiple times, the number of trials (n) is followed by the number spiders tested in parentheses.

Effect of satiation level.—I replicated portions of Sandidge's (2003) study by offering a choice of large live and large dead crickets to spiders that had been starved for 2 wk (n = 172 [51]). Due to the low rate of feeding in these tests, I modified Sandidge's (2003) design and starved spiders for 4 wk (n = 100 [47]), comparing the results of the two tests. Because the response rate increased dramatically, I starved spiders for four weeks in all other experiments.

Effect of prey size.—To compare with above experiments offering only large prey, I offered spiders small dead and small live prey (n = 87 [47]). In separate tests, I offered spiders either small live (n = 24) or large live prey (n = 23) alone rather than simultaneously to control for the possibility that spider avoidance of large crickets could cause them not to feed on small crickets placed in the same enclosure.

Effect of prey quality.—Spiders that had been starved for four weeks were offered the following choices of small crickets: live and 1-da dead (n = 28); fresh dead and 1-da dead (n = 30); 1-da dead and 7-da dead (n = 24); 2-da dead and 8-da dead (n = 24). Finally, prey that had been dead for 1 mo were offered alone to spiders (n = 23).

RESULTS

Spider choice was independent of testing sequence. For spiders feeding in at least two sequential experiments (n = 48), choice of prey was entirely independent of prior experience (Q = 0, P = 1.00). Likewise, prey choice was independent of prior exposure for spiders feeding in three sequential experiments (n = 27, Q = 0.15, P = 0.93) and four sequential experiments (n = 12, Q = 5.0, P = 0.17). Similarly, male and female spiders fed at the same rate and chose prey in the same proportions in all tests of live vs. dead prey (Chi-square test: $X^2_1 = 0.586$, P = 0.90) and in comparisons of dead prey of varying quality (Chi-square test: $X^2_1 = 3.515$, P = 0.32). Thus, the results are based on data pooled for both sexes.

Effect of predator satiation.—Spiders starved for 2 wk and offered large dead and large live crickets (as in Sandidge 2003) fed in only 27% of the 172 trials; the majority ignored both live and dead prey (Chi-square test: $X^2_1 = 45.06$, $P < 0.0001$). Only one spider fed on both prey. This individual was excluded from the choice comparisons as were spiders in other experiments that fed on both prey (except as noted). Of the spiders that fed on a single prey, 58% chose live prey but this preference was not significant (Fig. 1). An additional 12 spiders attacked and killed live prey but did not feed on the cricket.

After withholding food from spiders for 4 wk and offering large prey, 60% of the spiders fed and a clear majority (70%)

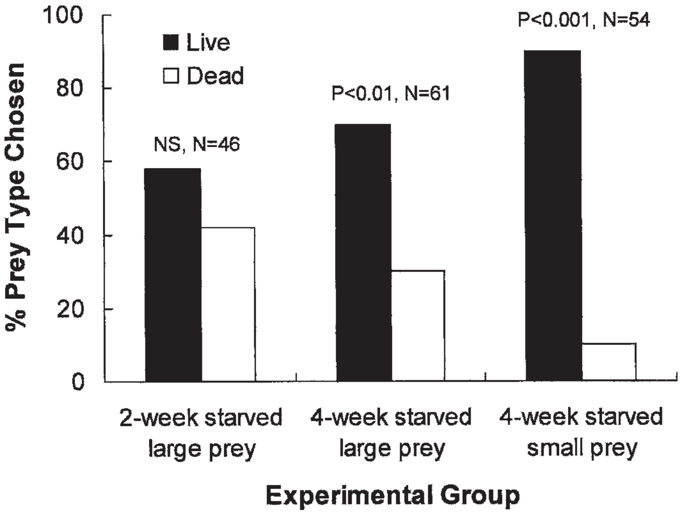

Figure 1.—Effects of satiation and prey size on scavenging by brown recluse spiders. Percentage of live vs. dead prey chosen by spiders deprived of food for 2 or 4 wk and offered large or small prey. NS = non-significant, $P > 0.05$. n = sample size.

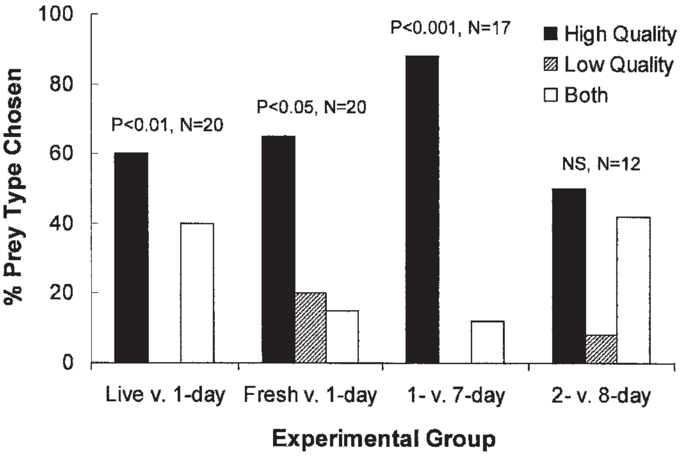

Figure 2.—Effects of prey quality on scavenging by brown recluse spiders. Percentage of high vs. low quality prey chosen by spiders deprived of food for 2 wk and offered small prey. NS = non-significant, $P > 0.05$. n = sample size.

preferred to feed on live prey (Chi-square test: $X^{2}_{1} = 8.0$, $P = 0.005$; Fig. 1). A significant number of spiders (18% of those feeding) fed on both live and dead prey. In all tests below, spiders were not fed for 4 wk prior to testing to increase response rate.

Effect of prey size.—When offered small live and small dead crickets, 62% of the spiders fed; a response rate similar to when they were presented with large crickets. However, 90% chose the live prey exclusively, a highly significant preference (Fig. 1). This preference was significantly stronger than when spiders were offered large crickets (Chi-square test: $X^{2}_{1} = 5.59$, $P = 0.018$). Many spiders (24%) fed on both live and dead prey, as they did when presented with large prey, but in every case they attacked and fed on live prey first. The percent feeding on both prey items was significantly greater in spiders that were not fed for 4 vs. 2 wk (Chi-square test: $X^{2}_{1} = 8.756$, $P = 0.003$). Only two spiders (3.6% of spiders showing some response) attacked but did not feed on small live prey compared to 17% in the two tests with large crickets (Chi-square test: $\mathrm{X}^{2}_{1} = 6.21$, $\mathrm{P} = 0.013$). Finally, when spiders were offered a single small or large cricket alone, far more spiders attacked and fed on small (74%) than large (17%) crickets (Chi-square test: $X^{2}_{1} = 14.81$, $P = 0.0001$).

Effect of Prey Quality.—When spiders had a choice of live prey vs. prey dead for 1 day, none ate only the dead prey, showing a clear preference (100%) for live prey (Chi-square test: $X^{2}_{1} = 12.0$, $P = 0.0005$; Fig. 2). Many spiders in this group fed on both live and dead prey, usually choosing the dead prey after feeding on the live specimen. Nonetheless, including spiders that chose both prey still results in a significant preference (71%) for live prey (Chi-square test: $X^{2}_{1} = 5.14$, $P = 0.023$).

When offered two classes of dead prey, fresh and 1-da dead, 60% of the spiders fed and the majority (76%) preferred the fresher prey item (Chi-square test: $X^{2}_{1} = 4.76$, $P = 0.029$; Fig. 2). Including spiders that chose both prey obscures this preference (Chi-square test: $X^{2}_{1} = 3.52$, $P = 0.061$), but the fresher prey was almost always fed on first. Spiders also preferred to scavenge 1-da old prey vs. 7-da old prey (Chi-square test: $X^{2}_{1} = 15.0$, $P = 0.0001$; Fig. 2). Once the prey had been dead for ≥ 2 da, spiders seemed less able to discern any difference in prey quality. Only 50% of the spiders fed when offered 2 or 8-da old dead prey. While most fed only on 2-da rather than 8-da old prey the difference was suggestive but not significant (Chi-square test: $X^{2}_{1} = 3.57$, $P = 0.059$; Fig. 2). More spiders also fed on both prey rather than refusing one as they did in the 1- vs. 7-da comparison.

Finally, when 1-mo old dead crickets were offered to spiders, none of them fed on this item even though no other choice was available. Eighteen of the 23 spiders left their retreats and searched for food, but none fed, even after being starved for 4 wk.

Overall, spiders followed a hierarchy in prey selection by favoring live over dead, small over large, and fresh over more decayed dead prey. Further, less satiated spiders were more likely to feed on both live and dead prey, but fed on live prey first. More satiated spiders were more likely to attack, but not feed, on crickets, especially large ones.

DISCUSSION

Predator satiation.—Less than 30% of spiders starved for 2 wk fed when offered prey and even a 4-wk starvation period only produced an average 60% feeding response over all trials. Such low feeding rates may be a reflection of the low metabolic requirements of brown recluses, especially in laboratory situations. Recluses will remain motionless for extended periods and a recluse starved for 2 wk is probably not energetically stressed. Carrel & Heathcote (1976) found that *Loxosceles* and the closely related spitting spiders (*Scytodes*) had lower than expected heart rates for their size compared to the other spiders they studied. The remarkable ability of recluses to do without food or water for long periods and their impressive longevity for a small invertebrate also attest to their low metabolic requirements (Hite et al. 1966; Eskafi et al. 1977). Recluses live an average of 2 ys (with one female living nearly 5 yr) and can survive 2–3 mo without food (Eskafi et al. 1977). A recluse that is not energetically or nutritionally stressed may be less likely to attack large, live prey because the risk of damage to itself outweighs the potential energy gain.

Prey size.—Recluses preferred live prey similar to their own body size even though their venom is capable of immobilizing much larger prey. Like Sandidge (2003), I also noted that recluses would often retreat from or ignore large, live crickets in their enclosures and would feed on dead crickets instead. Generalist predators with limited visual acuity, such as many wandering spiders, often use size as an initial screening device to determine the suitability of prey (Foelix 1996). Spiders may benefit by ignoring large, potentially dangerous prey if there are safer resources available like fresh, dead prey. Jackson et al. (2002) showed that the jumping spider *Portia* adjusts its attack strategy depending on prey vulnerability in order to reduce risk to itself. Wigger et al. (2002) found that the wandering spider *Cupiennus* injects more venom in prey that are difficult to subdue or dangerous, a behavior that Malli et al. (1999) demonstrated was dependent on the intensity and duration of the prey's struggle but independent of prey size. Sandidge's (2003) results are also consistent with the hypothesis that brown recluses avoid more dangerous prey. In his study, spiders were more likely to attack live over dead prey when offered slow-moving larval prey such as waxworms (*Achroia grisella*) and mealworms (*Tenebrio molitor*). Conversely, he observed the highest rates of scavenging when spiders were offered much more active and potentially more dangerous crickets as live prey.

Level of satiation is also likely to influence the size of prey a spider is willing to attack. Brown recluses may be more willing to take risks on large prey if they have not fed recently and have a lower response threshold to the stimulus of a moving prey. The fact that recluses more often attacked and bit, but did not feed on, large prey rather than small prey suggests that these behaviors may have been defensive rather than predatory and supports my interpretation that large prey are viewed as a threat rather than an opportunity. When spiders encountered small live prey, they were much more likely to attack even if relatively satiated.

Prey quality.—Quality of prey, defined here as a hierarchy based on age of the dead specimens (and live prey assumed to be of better quality than dead), also clearly influenced prey choice by recluses. Recluses preferred fresh dead prey rather than prey dead even for as little as 24 h. After 2 da of decay their ability to distinguish declining quality of dead prey appeared diminished. Wolf spiders showed a similar preference for fresher dead prey (Knost & Rovner 1975). My results suggest that unless fresh, dead prey is common in the natural habitat of recluses, scavenging is an unlikely option compared to predation. Prey choice will also depend on the relative availability of live and dead prey in their natural habitat, about which next to nothing is known.

I was unable to replicate the degree of scavenging observed by Sandidge (2003) in choice tests identical to his experimental design (2 wk starvation, relatively large dead and live crickets, same-sized enclosures, etc.). Whereas his spiders chose dead over live crickets 75% of the time, only 42% preferred dead prey in this study. Modifying Sandidge's (2003) design slightly by offering small crickets to less satiated spiders reduced rates of scavenging to only 10%. Thus, Sandidge's (2003) experimental design (large live prey, a fresh, dead alternative prey, and a relatively satiated spider) may have contributed to the high rates of scavenging he observed.

Another explanation for our differing results may be the origin of our test populations. Mine were collected from a semi-natural setting, a barn loft in a nature preserve in Missouri whereas Sandidge (2003) used spiders captured principally in homes in Kansas (personal communication). Synanthropic populations may have more opportunities for scavenging or there simply may be natural variation among populations in their tendency to scavenge. In particular, the high populations of recluses observed by Sandidge (2003) and reported by others (Vetter & Barger 2002) in some homes may make competition for live prey especially intense, increasing the profitability of scavenging. Lastly, in both studies, feeding on dead prey may not indicate that recluses necessarily scavenge in the wild. Spiders often return later to feed on prey they have killed earlier and this behavior could easily manifest itself in the lab where prey have been previously killed by the experimenter rather than the spider.

Brown recluses will scavenge under the right conditions. However, in this study brown recluses preferred live prey in nearly all circumstances. Larger live prey, greater satiation, and fresher dead prey all increased the likelihood of scavenging. We will need to learn more about quality and availability of prey to brown recluses *in situ* to determine if they are preferential or opportunistic scavengers.

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