Do cannibalism and kin recognition occur in just-emerged crab spiderlings?

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Abstract.   Most spiders are aggressive, socially intolerant predators; however, broods develop inside a common site and thus should benefit from restraining aggression at this time and until they disperse. I tested single and mixed-brood groups of *Misumena vatia* (Clerck 1757) (Thomisidae) spiderlings that had just emerged from their nests to determine whether they cannibalized other young under crowded conditions comparable to the immediate area of their nests, and if so, whether they distinguished between sibs and non-sibs. Young *M. vatia* provide an interesting test case, since some broods remain in close contact for a short period of time after emerging from their nests. Mortality remained low over one month in provisioned young under crowded conditions, and no cannibalism occurred in these individuals. Cannibalism remained low in most broods of unprovisioned young, even though most of them eventually starved over this time. Just-emerged spiderlings placed in the field for three days and then run similarly also showed initially low tendencies toward cannibalism. However, larger free-ranging spiderlings that overlapped in size with provisioned spiderlings in the study cannibalized freely when confined similarly to the other spiderlings in this study. During this period the spiderlings showed no clear evidence of distinguishing between sibs and non-sibs.

Keywords: Crowding, *Misumena vatia*, starvation, Thomisidae

Cannibalism, the ingestion of all or part of a conspecific (Pfennig 1997), occurs naturally in a wide range of animals (Pfennig 1997; Osawa 2002; Hvam et al. 2005). However, its impact within populations typically has elicited only limited attention (Fox 1975; Polis 1981; Elgar & Crespi 1992), and it remains relatively poorly understood (Wilder & Rypstra 2010. Yet, cannibalism may play an important role in regulating both even-aged and size-structured populations whose large individuals prey on small ones (Polis & McCormick 1987; Fagan & Odell 1996). Cannibalism may even occur within a cohort (Klingenberg & Spence 1996; Wagner & Wise 1996). For instance, Wagner & Wise (1996) found that intracohort cannibalism in a litter-dwelling wolf spider population played the major role in engendering density-dependent control, and Hvam et al. (2005) obtained similar results with another wolf spider.

Most spiders are highly predatory, socially intolerant animals and in many instances will kill one another if confined (Foelix 1996a; Wise 2006), behavior consistent with the normally solitary existence of the vast majority of species. A critical stage thus takes place immediately after they emerge from their natal sites, when spiderlings of diverse species remain in sibling groups prior to dispersing. Relatively few spiders provide parental care (Foelix 1996a), which might decrease cannibalism, although social and subsocial spiders remain together and may discriminate between kin and non-kin (Evans 1999; Bilde & Lubin 2001; Beavis et al. 2007). Since they start their independent lives with a large yolk sac spiderlings have little initial need to cannibalize, though they may readily take prey at this time. Studies examining whether spiderlings of solitary species routinely attack each other at this time have reported differing results. In one such study Roberts et al. (2003) found that second-instar wolf spiders *Hogna hellulo* (Walckenaer 1837) exhibited both kin recognition and a reluctance to cannibalize kin, in contrast to other wolf spiders (Wagner & Wise 1996; Hvam et al. 2005).

A reluctance to cannibalize could be general or specific to the brood (Hvam et al. 2005). Recognition of one's offspring or sibs may assume considerable selective significance in directing predation away from closely related individuals. Although widely distributed among animals, kin recognition is seldom reported among solitary arthropods (Hepper 1991; Faraji et al. 2000). Some apparent examples of kin recognition may simply reflect a response to general similarity, making discrimination a more appropriate term (Hvam et al. 2005; Wise 2006). For instance, a group of siblings may be of similar size, but differ in size from members of other conspecific broods, predisposing the larger to cannibalize the smaller (Chapman et al. 1999).

Similar size and the consequent substantial danger of attempting cannibalism may inhibit this behavior within a brood without evoking kin recognition (Chapman et al. 1999; Wise 2006). In some species cannibalism only occurs as the animals approach starvation (Evans 1999; Bilde & Lubin 2001). However, Roberts et al. (2003) found no increase in cannibalism among individuals of different size or in starved *H. hellulo* sibs. Differences may also vary with sex and stage (Agarwala & Dixon 1993; Joseph et al. 1999; Osawa 2002). Individuals that remain together (social insects and social spiders) usually exhibit restraint, as do certain other arthropods without rapid, highly developed dispersal (e.g., phytoseiid mites: Faraji et al. 2000; Schausberger & Croft 2004).

Several of the studies on cannibalism and kin recognition have taken place in the laboratory under crowded conditions that the participants would seldom if ever experience for more than a brief period under natural settings (e.g., Wagner & Wise 1996; Rickers & Scheu 2005; Dobler & Kölliker 2010). However, they take on considerable interest because they simulate brief, but potentially important, stages of the life cycle and may thus illuminate conditions that occur naturally in the field.

The crab spider *Misumena vatia* (Thomisidae), an aggressive solitary species, provides an interesting opportunity to address questions of cannibalism and kin recognition early in life. Individuals remain within their natal nests until part way through their second instar and normally disperse soon after,

but occasionally remain together immediately outside their nest for a day or more before dispersing (Morse 2007). Thus, they occur temporarily in extremely crowded situations, both inside and outside of their nest. These conditions thus resemble those of crowded laboratory experiments and provide the basis for the experiments presented here. Specifically, I ask, 1) do recently emerged spiderlings cannibalize at this stage, 2) does food (or its absence) affect these results, and 3) do recently emerged spiderlings exhibit kin recognition? Preferentially cannibalizing non-kin would provide evidence for Question 3.

METHODS

The species.—Female *Misumena* lay a single large clutch of 75–300+ eggs in a nest constructed by turning under the distal end of an elliptical leaf and tightly binding the resulting domicile with silk (illustrated in Morse 1985, 2007). Although mothers guard their nests for a considerable period, they provide no active protection for their young after the latter emerge from the nest (Morse 1985), in contrast to spiders that shelter their offspring for several days (e.g., wolf spiders: Rovner et al. 1973). The young emerge from their nests about 26 days after egg-laying, having by then undergone one molt (Morse 1985). Shortly before leaving their nests the young second instars begin to make holes through the silk in the nest that allow them access to the exterior and routinely occupy these exits or even venture outside. Usually they abandon their nests within a few days after construction of the nest holes (Morse 1987, but see Morse 2011). Occasionally they congregate for up to a day or more immediately outside a nest hole, but usually they disperse within a day after final emergence, either by walking or on lines to nearby hunting sites, often goldenrod (*Solidago* spp.) inflorescences, or by ballooning greater distances if they do not quickly find hunting sites (Morse 1993). Spiderlings' normally rapid dispersal suggests their vulnerability at this time, and cannibalism represents one such possible danger.

However, unequivocally demonstrating cannibalism presents a possible problem. *Misumena* do not masticate their prey, and I could not find wounds on the victims. Crab spiders make microscopic holes, only about 50 µm × 50 µm in rectangular wounds made by adult female *Xysticus cristatus* (Clerck 1757), which quickly fill with rapidly drying hemolymph upon withdrawal of the chelicerae (Foelix 1996b). Holes made by *Misumena* spiderlings will make much smaller holes than mature *Xysticus*.

Spiderling *Misumena* typically only take live prey (D.H. Morse, pers. obs.), such that observations of spiderlings feeding on conspecifics probably represent cannibalism events. Further, early-instar *Misumena* feed much longer on conspecifics than on similar-sized *Drosophila melanogaster*, collapsing the conspecifics' abdomens, so that they become concave (rather than convex), a condition seen in each instance of cannibalism or apparent cannibalism (feeding upon conspecifics), including two observations of successful attacks (D.H. Morse pers. obs.). The long feeding times also heighten the probability of observing apparent cannibalism in the process of monitoring, maintaining and observing the spiderlings. I obtained minimum feeding times for seven instances of apparent cannibalism. The apparent cannibals had already begun to feed on their victims in each of these observations, so the actual times necessarily exceeded those recorded.

Experiments.—I used members of 31 broods of spiderlings as the primary subjects in this study. All came from experimentally mated parents, using virgin females to ensure full sibship of brood members.

In order to test for cannibalism, the effect of food upon the propensity to cannibalize, and kin recognition, I used 14 pairs of broods. For each pair, I set up two treatments with 10 siblings, with or without food, and two treatments of mixed broods, five spiderlings each, with or without food. In addition to these 14 complete designs (28 broods), I included three incomplete designs (three broods) where appropriate. Since broods emerged sequentially over a few weeks, I assigned pairs on the basis of which broods emerged at nearly the same time.

All individuals of each brood had emerged from their nests within the preceding two days and had not fed before I set up the experimental groups, using individuals selected haphazardly from the broods. I marked each individual with either red or blue powdered micronite dye to identify it to brood, the colors randomly designated by brood. Previous studies indicate that the dye does not affect their behavior (Morse 1993, 2000a. I housed all the groups in cylindrical 7-dram vials (5 cm tall, 3-cm diameter) at natural day lengths and provided them with a small (2 cm²) square of paper toweling, moistened every other day. This enclosure provided them with a space comparable in size to the congregating sites immediately outside their natal nests (Morse 2007). Individuals in the provisioned groups received one *Drosophila melanogaster* per test member every other day. Second and third instars grow rapidly on this diet (Morse 2000b). I inspected all groups daily, as well as at other random times, for deaths or molts. On average this work required approximately an hour per day in each year I ran these experiments (2001, 2002, 2007, 2008, 2010), during which I simultaneously made observations on the spiderlings.

I weighed individuals from 12 of these broods at the start of the study, but did not subsequently weigh them in order to avoid further observer effects. For the same reason I did not again mark any individuals that had molted or whose color had become so faint that it hindered recognition. In most instances this strategy confined brood identity of the mixed groups to the second instar; many individuals molted once or occasionally twice during the study.

I also ran a control to test the possible effect of maintaining multiple individuals in a confined space, rearing 20 spiderlings individually (one per vial) from each of 17 broods for one month in similar vials and providing them with one *Drosophila* every other day, similarly to the experimentals. I then compared their month-long survival with that of the experimental groups. None of these individuals came from the afore-mentioned 31 broods.

In addition to the above-mentioned groups of spiderlings tested, I ran three additional groups of spiderlings in 2010 in order to gather additional insight into the role of cannibalism. I elaborate upon them in the following three paragraphs and refer to them in quotation marks in order to minimize confusion.

I observed two pairs of these experimental broods, set up as described above, intensively ("intensively-observed group"),
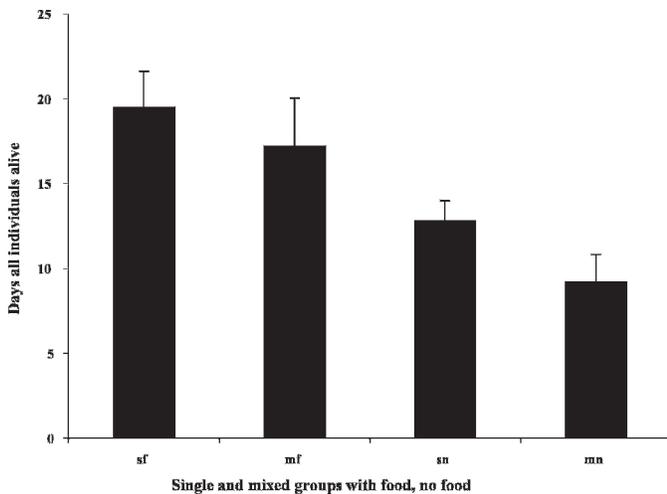
Figure 1.—Number of days that all individuals of one- and two-brood groups survived with and without food, mean + SE. Abbreviations: sf = single brood with food, mf = two-brood group with food, sn = single brood group without food, mn = two-brood group without food.
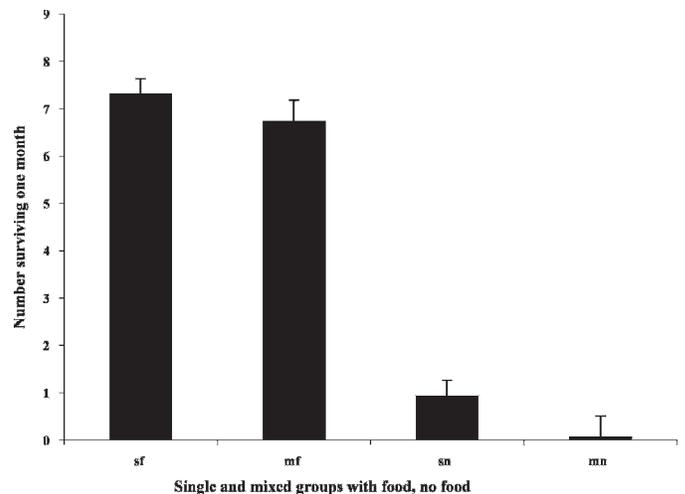

Figure 2.—Survivorship of *Misumena vatia* spiderlings in one- and two-brood groups with and without food over a month after emergence from their nests, mean + SE. Symbols as in Figure 1.

an extra hour or more per day, in addition to the time involved in maintenance. I thereby accumulated a large number of spider-hours, since all of these groupings (12 vials) could be observed simultaneously.

I also released six entire color-marked broods (three pairs) into the field on goldenrod *Solidago canadensis*. Three days later I collected 15 individuals of each brood ("field-experienced group") and established them in 7-dram vials, as in the previous experiment: 10 individuals each of both broods and five individuals of both broods in a third set. I also watched these broods approximately one hour each day over a 30-day period. All but five of the 90 individuals captured for this experiment exceeded the mean mass of their broods when released (0.78 ± 0.02 vs. 0.48 ± 0.01 mg). Thus, most had probably captured one or two prey over this time and were not in a starved condition. When collected in the field, none of the individuals were spaced as densely as those in their nests or in the 7-dram vials. Since I wished to concentrate on the conditions most likely to elicit cannibalism, I did not establish sets of provisioned individuals in either this or the following (next paragraph) manipulation.

I also collected larger spiderlings ("large group") of unknown parentage from goldenrod and established seven sets of six individuals each, matched for size. I lowered numbers of individuals per 7-dram vial to six in light of their relatively large size. These individuals ranged from 1.19 to 5.50 mg and probably had been exposed to field conditions for one to three weeks. I maintained these spiderlings for 15 days.

One might question the effect of the confined conditions to which I exposed the spiderlings. However, the volume of the vials resembles their exposure immediately before emerging from their nest and the numbers that accumulate on the under surface of their nest immediately after emergence (Morse 2007). Thus, the main effect of confining the newly emerged spiderlings was to preclude dispersal. Although members of more than one brood would seldom mix at a dispersal site,

early instars of different broods often accumulate at rich hunting sites soon after, not infrequently in high densities (Morse 1993).

Analysis.—I tested comparisons between broods with two-way ANOVAs or *t*-tests for the difference between two means. I used *G*-tests of independence or goodness of fit for 2×2 comparisons and a binomial test for a one-sample comparison. All tests are two-tailed, and all measures of variance are means ± 1 SE.

RESULTS

Survival.—A majority of the provisioned spiderlings survived for the entire 30-day experimental period (Fig. 1). Unprovisioned spiderlings lived for varying periods, but members of several broods died within a week of the start of the experiments (Fig. 1). Overall, the model comparing provisioned and unprovisioned individuals was significant ($F_{3,92} = 6.10$, $P < 0.001$). Provisioned and unprovisioned individuals differed highly significantly in survival time ($F_1 = 13.78$, $P < 0.001$). Single-brood groups survived marginally longer than two-brood groups ($F_1 = 3.57$, $P = 0.062$), but the interaction term was not significant ($F_1 = 0.02$, $P = 0.88$).

The same pattern occurred in the number of single-brood and two-brood groups of individuals alive at the end of a one-month run (Fig. 2), with a highly significant overall model ($F_{3,92} = 124.74$, $P < 0.0001$). A majority of provisioned individuals survived for a month, but very few unprovisioned individuals survived that long ($F_1 = 340.88$, $P < 0.0001$), and again the numbers from the one-brood group marginally exceeded those from the two-brood group ($F_1 = 3.26$, $P = 0.074$). Again, the interaction term was not significant ($F_1 = 0.02$, $P = 0.74$).

Survival of the separated spiderlings to one month (16.9 ± 0.52 of 17 broods = 84.5%) significantly exceeded that of the one-brood groups (72%: Fig. 2) ($t_{30} = 2.42$, $P = 0.022$), largely the consequence of the uncharacteristically low survival in two of the one-brood sets. (A non-parametric Mann-Whitney *U* test yielded a similar result: $P = 0.028$).

Initial mass did not affect survival in single-brood groups with food ($t_{15} = -0.64$, $P = 0.53$ for days that all individuals survived; $t_{15} = -0.42$, $P = 0.68$ for the number of individuals surviving one month). Neither did it significantly affect survival of those without food ($t_{15} = -0.94$, $P = 0.36$ for days that all individuals survived; $t_{15} = -1.85$, $P = 0.086$ for the number surviving one month), although a trend occurred toward large individuals surviving longer than small ones. I did not test two-brood groups in this way because after a molt I could not identify them to brood.

Cannibalism.—I observed only two probable instances of cannibalism among the provisioned spiderlings, both involving the deaths of males that had molted into the antepenultimate stage (Instar 4), at which point they differ markedly from the females. Both females (from different broods) fed on male sibs on Day 28. The spiderlings' tendency to take only live prey suggests that the females had killed their male sibs.

Five unprovisioned spiderlings lived to the end of these 30-day experiments, over twice the mean survival period (Fig. 2), probably by feeding on other individuals. As the sole remaining individuals, they had no other resources. Two came from single-brood groups and three from two-brood groups. Two of the latter survivors probably fed on fellow brood members and one on a member of the other brood. One of these five individuals weighed more after 30 days than at the beginning of the run.

I observed nine instances of probable cannibalism in the set of four "intensely-observed" broods, all spiderlings feeding on other individuals or fresh corpses found with conspicuously shrunken (concave) abdomens, the typical condition of conspecifics after being fed upon by spiderlings. Other spiderlings that had recently died did not have conspicuously concave abdomens. With one early exception, all these instances of apparent cannibalism in the "intensely observed" broods occurred only after two weeks or more, by the time that considerable numbers of unprovisioned spiderlings began to starve. All nine of these individuals came from the unprovisioned group ($P = 0.004$, binomial test), seven of them from the 40 individuals in the single-brood vials, not significantly different from the two out of 20 individuals in the mixed-brood vials ($G = 0.62$, $P > 0.3$, G-test). One of the two mixed-brood losses involved individuals from the same brood, but I could not identify the brood of the other one. Five of the nine apparent cannibalism events came from just one of the six vials of unprovisioned spiderlings (a single-brood vial), suggesting a predisposition toward cannibalism in one of the broods, though this relationship did not differ statistically from that in the other vials ($G_1 = 1.56$, $P > 0.2$, G-test). However, one individual probably made most of these kills. It weighed 1.01 mg after 18 days, well over twice the mean mass of its brood at emergence from their nest (0.45 mg).

I observed two successful cannibalistic attacks by the six broods of "field-experienced" spiderlings, both eventually resulting in corpses with collapsed (concave) abdomens. I recorded 18 instances of cannibalism or apparent cannibalism from these six broods, not significantly different from the nine instances in the four intensively-observed broods of the preceding test ($G = 0.19$, $P > 0.5$), though the latter group was unusual in terms of its high apparent frequency of cannibalism. However, apparent cannibalism in the "field-experienced" spiderlings significantly exceeded that of the entire set of 31 broods used in the main set of experiments ($G = 12.50$, $P < 0.001$).

The "field-experienced" group tended to commence cannibalizing more quickly after the initiation of the experiment than the "intensively-observed" group, even though almost all had fed previously, judging from their increase in mass since release. Six of 18 events took place before 14 days, vs. one of nine in the naïve group ($G = 2.80$, $0.1 > P > 0.05$). Nine of the 22 individuals from the "field-experienced" group that survived for 30 days weighed more than the mean mass at Day 1 (0.78 mg), consistent with cannibalism. Three of the 18 events took place between broods vs. 15 within broods, a trend toward favoring sib cannibalism ($G = 3.09$, $0.1 > P > 0.05$). Of the three instances in the mixed broods, one occurred within-brood, one between-brood, and the other undetermined.

In contrast to the other groups, the "large" spiderlings experienced high apparent cannibalism from the start, even prior to the time at which I provided *Drosophila* to any groups of provisioned spiderlings. They cannibalized 19 of the 42 individuals within the first two days, evenly across the seven vials, and the number surviving had declined to seven by the end of Day 15, all fatalities apparently resulting from cannibalism. Mortality of these "large" spiderlings significantly exceeded that of both the "intensely observed" group ($G = 18.47$, 37.91 at two and 15 days, respectively) and the "field-experienced" group ($G = 97.14$, 23.28 at two and 15 days, respectively) ($P < 0.001$ in each instance).

Cannibals fed on their victims for a long period. I obtained minimum feeding times for seven of these cannibalization events in the "intensely observed" and "field-experienced" groups, which averaged over five and one-half hours (331 ± 64.4 min). Actual times probably considerably exceeded this figure, because all individuals had already begun feeding when first found.

Kin recognition.—The experiments provided no clear evidence of kin recognition, as recognized by differential survival or cannibalism rates in the mixed-brood experiments presented in the preceding sections. A few observations do provide possible anecdotal evidence for kin recognition. All five individuals of one brood in a mixed brood vial died on the second day, a pattern not repeated elsewhere. Since these individuals all came from one brood, and no other cohort of sibs died at the same time, cannibalism seems plausible. The trend for cannibalizing sibs in the "field-experienced" broods suggested a preference for sibs, though no such pattern emerged elsewhere, making the evidence in support of kin recognition, at most, equivocal.

Prey capture.—Provisioned spiderlings used in these experiments captured prey from the start of these experiments, each day collectively killing all of the flies presented them. Although the observational regime did not permit me to establish whether each individual captured a *Drosophila* on the first day, the ability of all individuals of some provisioned groups to survive to the end of the experiments, combined with the relatively rapid mortality of most unprovisioned groups, indicated that most of the spiders captured prey. Some individuals fed on a fly in tandem (not quantified), typically from the opposite ends of the victim. Failure to attack other

spiderlings was thus not related to a generalized reluctance to attack under these confined conditions.

DISCUSSION

Survivorship of provisioned single-brood and two-brood groups did not differ significantly over their first month, either in time to first mortality or mean survival time, though a weak trend occurred for single-brood groups to exceed two-brood groups. Although more solitary controls survived for a month than in provisioned groups, the modest differences between them could represent a stress factor associated with crowding, rather than cannibalism (Dobler & Kölliker 2010). A likely exception among the provisioned individuals, the demise of two precocious males, could result from the discrete changes occurring in some males at their last molt in the experiment (striping of legs, etc.: Hu & Morse 2004). These males would normally not experience cannibalism at this point, since they would not have remained in close contact with their female sibs. This putative cannibalism probably did not result from a behavioral change by the males, because they do not differ in activity from other immatures at this time and exhibit no signs of sexual activity (Sullivan and Morse 2004). However, the likely fate of those males resembles the differential treatment accorded sex and stage by various ladybird beetles (Agarwala & Dixon 1993; Joseph et al. 1999; Osawa 2002).

The unprovisioned spiders living in groups suggest that cannibalism is relatively uncommon in most, though not all, newly emerged *Misumena* broods, with the majority of them dying of apparent starvation. Although the simultaneous demise of all five members of a brood in a mixed group seems most likely attributable to cannibalism, it probably did not result from impending starvation, which facilitates cannibalism in some species (Evans 1999; Bilde & Lubin 2001) and likely accounted for most of the cannibalism of unprovisioned individuals recorded in this study.

If cannibalism occurred frequently, I should have recorded more potential examples among the 31 broods of just-emerged spiderlings. Although the observational regime did not permit continual surveillance, the spiderlings feed on prey (Erickson & Morse 1997; Morse 1999), especially conspecifics (this paper), for long periods, so that I would likely have regularly observed such events, had they frequently occurred. Observations of spiderlings feeding on other spiderlings likely represent cannibalism, since the spiderlings do not regularly scavenge dead organisms (Morse 2007). Dobler & Kölliker (2010) have, however, noted that all studies of this sort record very few actual observations of cannibalism, even if it is likely prevalent. Only constant surveillance will quantify this potential factor definitively. In fact, my only two observations of spiderlings successfully attacking and killing conspecifics occurred during extended observation periods. The larger number of apparent cannibalism events in the set of four "intensively-observed" broods probably results from the characteristics of these individuals, rather than a difference in procedure. Instances of one spiderling feeding on another are conspicuous and unlikely to be missed. Other results (Morse 2011) indicate considerable differences among broods in the propensity to cannibalize.

The reluctance to cannibalize even held in the unprovisioned "field-experienced" broods, although cannibalism commenced marginally sooner than in the comparison group of four "intensively-observed" broods and significantly sooner than in the just-emerged spiderlings. Still, no cannibalism occurred before the sixth day, thereby demonstrating a continuing reluctance to cannibalize either sibs or non-sibs.

The behavior of the "field-experienced" group differed strikingly from that of the randomly captured "large" spiderlings, whose numbers nearly halved over the first two days. These results suggest that a separation of more than three days is required to remove completely the inhibition to cannibalize. Although the "large" group of spiderlings cannibalized freely, provisioned spiderlings showed no tendency to cannibalize during the experimental period (30 days), over which time they overlapped with the "large" field-captured spiderlings in both mass and probable age.

Thus, the "field-experienced" group (in the field for three days) showed a possible reduced inhibition to cannibalize, and the "large" spiderlings, in the field for an estimated one to three weeks, showed no apparent inhibition to cannibalize. These results suggest that in most instances inhibition to cannibalize lasts for a few days, considerably longer than the spiderlings normally remain together, and that it declines over time until it disappears, as in the "large" spiderlings tested.

The low frequency of apparent cannibalism in the first half of the month-long observation period is consistent with other studies in which equivalent' participant size decreases cannibalistic tendencies (Chapman et al. 1999). The wolf spider *Pardosa agrestis* (Westring 1861) only cannibalizes victims half or less than half its size (Samu et al. 1999). However, some species do regularly cannibalize similar-sized conspecifics (Klingenberg & Spence 1996; Wagner & Wise 1996).

Clearly, factors other than size play a role in deterring cannibalism in these spiderlings, because both *Drosophila melanogaster* and the spiderlings' frequently abundant prey in the field, a small dance fly (Empididae) (Morse 1993, 2000a), are similar in size to the young spiderlings (Morse 2000b), though totally different in appearance. The spiderlings readily attack the flies immediately after emerging from their nests and they also attack *Drosophila* in the laboratory at this time (Morse 2000a).

In most instances the spiderlings appeared to treat sibs and non-sib conspecifics similarly. Though these data do not eliminate the possibility of kin recognition, the majority of these results strongly suggests that they typically interact similarly with sibs and non-sibs.

LITERATURE CITED

Agarwala, B.K. & A.F.G. Dixon. 1993. Kin recognition and larval cannibalism in *Adalia bipunctata* (Coleoptera: Coccinellidae). European Journal of Entomology 90:45–50.

Beavis, A.S., D.M. Rowell & T. Evans. 2007. Cannibalism and kin recognition in *Delena cancerides* (Araneae: Sparassidae), a social huntsman spider. Journal of Zoology 271:233–237.

Bilde, T. & Y. Lubin. 2001. Kin recognition and cannibalism in a subsocial spider. Journal of Evolutionary Biology 14:959–966.

Chapman, J.W., T. Williams, A. Escribano, P. Caballero, R.D. Cave & D. Goulson. 1999. Fitness consequences of cannibalism in the fall armyworm, *Spodoptera frugiperda*. Behavioral Ecology 10:298–303.

Dobler, R. & M. Kölliker. 2010. Kin-selected siblicide and cannibalism in the European earwig. Behavioral Ecology 21:257–263.

Elgar, M.A. & B.J. Crespi. 1992. Cannibalism: ecology and evolution among diverse taxa. Pp. 1–12. *In* Cannibalism: Ecology and Evolution Among Diverse Taxa. (M.A. Elgar & B.J. Crespi, eds.). Oxford University Press, Oxford, UK.

Erickson, K.S. & D.H. Morse. 1997. Predator size and the suitability of a common prey. Oecologia 109:608–614.

Evans, T.A. 1999. Kin recognition in a social spider. Proceedings of the Royal Society of London B 266:287–292.

Fagan, W.F. & G.M. Odell. 1996. Size-dependent cannibalism in praying mantids: using biomass flux to model size-structured populations. American Naturalist 147:230–268.

Faraji, F., A. Janssen, P.C.J. van Rijn & M.W. Sabelis. 2000. Kin recognition by the predatory mite *Iphiseius degenerans*: discrimation among own, conspecific, and heterospecific eggs. Ecological Entomology 25:147–155.

Foelix, R.F. 1996a. Biology of Spiders. Second edition. Oxford University Press, New York.

Foelix, R.F. 1996b. How do crab spiders (Thomisidae) bite their prey? Revue Suisse de Zoologie, hors série: 203–210.

Fox, L.R. 1975. Cannibalism in natural populations. Annual Review of Ecology and Systematics 6:87–106.

Hepper, P.G., ed. 1991. Kin Recognition. Cambridge University Press, Cambridge, UK.

Hu, H.H. & D.H. Morse. 2004. The effect of age on encounters between male crab spiders. Behavioral Ecology 15:883–888.

Hvam, A., D. Mayntz & R.K. Nielsen. 2005. Factors affecting cannibalism among newly hatched wolf spiders (Lycosidae, *Pardosa amentata*). Journal of Arachnology 33:377–383.

Joseph, S.B., W.E. Snyder & A.J. Moore. 1999. Cannibalizing *Harmonia axyridis* (Coleoptera: Coccinellidae) larvae use endogenous cues to avoid eating relatives. Journal of Evolutionary Biology 12:792–797.

Klingenberg, C.P. & J.R. Spence. 1996. Impacts of predation and intracohort cannibalism in the water strider *Gerris buenoi* (Heteroptera: Gerridae). Oikos 75:391–397.

Morse, D.H. 1985. Nests and nest-site selection of the crab spider *Misumena vatia* (Araneae, Thomisidae) on milkweed. Journal of Arachnology 13:383–390.

Morse, D.H. 1987. Attendance patterns, prey capture, changes in mass, and survival of crab spiders *Misumena vatia* (Araneae, Thomisidae) guarding their nests. Journal of Arachnology 15:193–204.

Morse, D.H. 1993. Some determinants of dispersal by crab spiderlings. Ecology 74:427–432.

Morse, D.H. 1999. Attack sites of newly-emerged crab spiders *Misumena vatia* (Araneae, Thomisidae) on their prey. Journal of Arachnology 27:171–175.

Morse, D.H. 2000a. Flower choice by naïve young crab spiders and the effect of subsequent experience. Animal Behaviour 59:943–951.

Morse, D.H. 2000b. The effect of experience on the hunting success of newly-emerged spiderlings. Animal Behaviour 60:827–835.

Morse, D.H. 2007. Predator Upon a Flower. Harvard University Press, Cambridge, Massachusetts.

Morse, D.H. 2011. Cannibalism within nests of the crab spider *Misumena vatia*. Journal of Arachnology 39:168–170.

Osawa, N. 2002. Sex-dependent effects of sibling cannibalism on life history traits of the ladybird beetle *Harmonia axyridis* (Coleoptera: Coccinellidae). Biological Journal of the Linnean Society 76:349–360.

Pfennig, D.W. 1997. Kinship and cannibalism. BioScience 47:667–675.

Polis, G.A. 1981. The evolution and dynamics of intraspecific predation. Annual Review of Ecology and Systematics 12:225–251.

Polis, G.A. & S.J. McCormick. 1987. Intraguild predation and competition among desert scorpions. Ecology 68:332–343.

Rickers, S. & S. Scheu. 2005. Cannibalism in *Pardosa palustris* (Araneae, Lycosidae): effects of alternative prey, habitat structure, and density. Basic and Applied Ecology 6:471–478.

Roberts, J.A., P.W. Taylor & G.W. Uetz. 2003. Kinship and food availability influence cannibalism tendency in early-instar wolf spiders (Araneae: Lycosidae). Behavioral Ecology and Sociobiology 54:416–422.

Rovner, J.S., G.A. Hagashi & R.F. Foelix. 1973. Maternal behavior in wolf spiders: the role of abdominal hairs. Science 182:1153–1155.

Samu, F., S. Toft & B. Kiss. 1999. Factors influencing cannibalism in the wolf spider *Pardosa agrestis* (Araneae, Lycosidae). Behavioral Ecology and Sociobiology 45:349–354.

Schausberger, P. & B.A. Croft. 2001. Kin recognition and larval cannibalism by adult females in specialist predaceous mites. Animal Behaviour 61:459–464.

Sullivan, H.L. & D.H. Morse. 2004. The movement and activity patterns of adult and juvenile crab spiders. Journal of Arachnology 32:276–283.

Wagner, J.D. & D.H. Wise. 1996. Cannibalism regulates densities of young wolf spiders: evidence from field and laboratory experiments. Ecology 77:639–652.

Wilder, S.M. & A.L. Rypstra. 2010. Males make poor meals: a comparison of nutrient extraction during sexual cannibalism and predation. Oecologia 162:617–625.

Wise, D.H. 2006. Cannibalism, food limitation, intraspecific competition, and the regulation of spider populations. Annual Review of Entomology 51:441–465.