

SHORT COMMUNICATION

Cannibalism within nests of the crab spider *Misumena vatia*

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Abstract. About 1% of the nests of a crab spider (*Misumena vatia* [Clerck 1757]) population in coastal Maine, USA, contained apparently cannibalistic individuals. These spiderlings remained in their nests over three times longer than average and attained average masses twice that of non-cannibalistic spiderlings (maximum = four-fold) before dispersing. Parents of the 14 cannibalistic broods came from 10 sites separated from each other by 0.5–10 km and over 23 years; thus, this behavior appears to be widespread and relatively stable, though uncommon.

Keywords: Fitness, local population, Maine, Thomisidae

Recently, cannibalism among just-born young, especially as it relates to possible kin selection (Pfennig 1997; Roberts et al. 2003; Morse 2011), has attracted considerable attention. Many spiders molt into a fully active form within a protective nest or egg sac. However, proclivity toward cannibalism does not seem to have been addressed in offspring prior to emergence from these sites, a period that involves potential interactions only with kin. Under these circumstances, victims of cannibalism would function analogously to trophic eggs (Crespi 1992), enhancing the fortunes of some sibs at the expense of others. Observers could easily miss cannibalism at this point, because it normally would be hidden from view. Here I present evidence from second-instar crab spiders *Misumena vatia* (Clerck 1757) (Thomisidae) strongly suggesting that cannibalism takes place within the nests of a very small minority of broods prior to their emergence.

In the process of obtaining data on several early life history parameters (Morse & Stephens 1996), I collected large adult female *M. vatia* from flowers in fields and roadsides at 18 sites in South Bristol, Bristol, and Bremen, Lincoln Co., Maine (centering on 43°57'N, 69°33'W) during June and July 1987–2009. Adult females of these populations whose mass has increased considerably since molting have almost inevitably mated (LeGrand & Morse 2000). I maintained these individuals in 7-dram vials (5 cm tall, 3 cm diameter) and fed them moths or other insects every other day until they reached a mass at which they would normally lay a clutch of eggs if in the field. I then placed these gravid females on non-flowering common milkweed *Asclepias syriaca* ramets, a favored oviposition site, within bags of white nylon tricot (30 cm tall, 20 cm wide) that confined them to the site, but provided adequate space for them to construct their nests on the distal parts of leaves. Nest building consists of turning under the tip of a leaf, laying eggs within the resulting chamber, filling the remainder of the chamber with flocculent silk and tightly securing the top, bottom and sides with silk to produce the finished nest (Morse 1985). After they laid their eggs and completed their nests, I removed the bags from the milkweed ramets. Subsequently, I visited the nest sites daily to document their status and that of the guarding females (described in Morse 1985, 2007).

During the 1987–1989 seasons I processed especially large numbers of female *M. vatia* (over 200/year) in order to obtain detailed information on several reproductive and developmental parameters. Beginning at 20 days after egg laying I carefully inspected the nests each day for openings in the silk produced by the young, which would usually lead to their departure from the site a few days later (see below). Prior to leaving the nest, spiderlings frequently occupied the entrances of these openings or the nest surface immediately outside them.

In the process of these observations I discovered a small number of nests in which the young did not all depart within a few days of the initial openings. I subsequently noted that individuals at the surface of these openings appeared larger than usual, so I collected, counted and weighed these young and recorded how many days any of them remained in their nests. I compared the prelaying mass of the mothers of the lingering broods, most of which had died or abandoned their nests by this time (Morse 1987), with those from the other nests with similar initial emergence dates, 11–19 August, to control for possible variation resulting from seasonal changes in temperature. I also had available measures of spiderling mass at dispersal (Morse 1993a) and prelaying mass of mothers (Morse 1985, 1987, 2009; Morse & Stephens 1996) from other studies on these populations, which allowed additional comparison.

In addition to the 1987–1989 data, I processed similar broods during 13 subsequent seasons (1990–2000, 2008–2009). Use of the broods in these years did not allow me to obtain some of the supporting data gathered in 1987–1989, thus precluding direct comparisons. During most of these years I reared between 40 and 80 reproductive females. (From 2001 to 2007 I used reproductive females for experiments that did not permit me to obtain any of these data.)

Comparisons between the two types of broods, lingering or directly dispersing, were tested for significance with two-way *t*-tests for the difference between two means. All measures of variance are means \pm 1 SE.

Numbers of nests with large, lingering spiderlings constituted only a minute fraction of the nests that I monitored over this period -1987: 2 of 227 (0.9%); 1988: 3 of 280 (1.1%); 1989: 2 of 271 (0.7%); combined, less than 1% of all nests (Table 1). I probably would not have discovered these individuals without the prodigious effort made during these years to obtain other data (presented elsewhere).

In the nests where spiderlings lingered, only one to five remained at the nests after young had departed from most nests (Table 1). Spiderlings in these nests weighed, on average, twice as much as normally dispersing young (0.6 mg average mass), with a maximum-sized individual (2.33 mg) four times as great. In some instances the differences in mass even suggested that they had preyed on specific numbers of sibs; for instance, one set of remaining young weighed 0.97, 1.25, 1.43 and 1.52 mg (probably one, two, three, and four young, respectively). Other than for their large mass, individuals from these broods did not appear to differ morphologically from spiderlings of the other broods.

These spiderlings have no apparent source of sustenance in the nests or at the entrances to these nests other than their sibs. I have never observed spiderlings feeding on insect prey at the entrances to

Table 1.—Characteristics of putative cannibalistic and non-cannibalistic spiderlings (mean \pm SE), with n 's in parentheses.

Trait	Cannibals	Non-cannibals	df	t	P
Number in nest	2.8 \pm 0.54 (7)	119–368 [‡] (49)	–	–	–
Mass at dispersal (mg)	1.2 \pm 0.05 (17)	0.6 \pm 0.04 (30)	45	9.25	< 0.0001
Time at nest (days)	17.3 \pm 1.76* (7)	5.3 \pm 0.36 (41)	46	12.56	< 0.0001
% nests	0.9 (778)	99.1 (778)	–	–	–
Maximum mass of mother (mg)	216.6 \pm 17.08 (7)	209.5 \pm 3.15 (206)	211	0.41	0.69

* An underestimate because field season ended before all young left two of the nests.

‡ Number of young per nest in these results not measured. Estimate from comparable source (Fritz & Morse 1985).

these openings, either during 1987–1989 or at other times. Their mothers typically place nests a considerable distance away from sites that would attract the small prey upon which they will eventually feed (Morse 1993b). Further, I did not locate any of these experimental sites close to flowers that would attract potential prey.

Upon dissection, the nests contained several corpses (not counted), which were readily distinguishable from the molts of these individuals. Success of eggs is normally extremely high in these nests (94.5%: Fritz & Morse 1985), with the majority of unsuccessful individuals recorded as unhatched eggs, so that few corpses occur in most nests. Judging from the number of molts found in these seven nests, substantial numbers of sibs probably escaped from the nest. However, I have no information on their traits.

The mothers of these putatively cannibalistic broods (henceforth = cannibalistic) did not significantly differ in size from the mothers of the other broods (Table 1) and thus probably did not differ in condition from them. I obtained no other information on the mothers of the cannibals that would separate them from the other females.

Mothers of the seven broods from 1987–1989 came from five sites, which were separated from each other by 0.5 to 10 km. I did not obtain cannibalistic broods from any of these sites in more than one of these three years. Five of the cannibalistic broods hailed from the largest collection sites of females (and presumably the largest populations as well). The other two broods came from the seventh and eighth largest of 18 collection sites. Between 1987 and 1989 minimum yearly counts of reproductive females at the five sites yielding parents of cannibalistic broods ranged from 15 to 127 (48 ± 20.8), and minimum counts of reproductive females at sites not yielding such broods ranged from 1 to 51 (12 ± 3.8) ($t_{16} = 3.08$, $P = 0.007$).

I recorded seven additional cannibalistic broods during 1990–2000 and 2008–2009. Two of these broods came from the same sites as 1987–1989, and the other five came from different sites. Thus, I obtained females with cannibalistic broods from 10 sites. All of the 10 sites yielding the mothers of cannibalistic broods are separated by a minimum of 0.5 km. The records obtained after 1987–1989 suffice to indicate that this trait continues to occur at low frequency in local populations, and to suggest that this frequency has remained relatively constant over time.

It is unclear how often cannibalism occurs among populations of spiders and other organisms at this early developmental stage because of the difficulty of recording under most circumstances. The origin of this trait is also unclear; although it might appear to have a genetic basis in light of its steady recurrence at a low frequency, I have no direct evidence for this hypothesis.

These cannibalistic broods stand in stark contrast to the vast majority of *M. vatia* broods, which show extreme reluctance to cannibalize either brood mates or members of other broods (Morse 2011). Other workers have reported intrapopulation differences in the propensity of early-instar spiderlings to cannibalize. In particular, Hvam et al. (2005) and Mayntz & Toft (2006) propose the presence of cannibalistic morphs in two different species of *Pardosa* wolf spiders, although they do not provide information to verify whether these

traits have a genetic or environmental basis. I know of no such studies that have explored this trait within the nest or egg sac.

The cannibals' mothers do not differ from other females in any parameter I have measured (Morse 1985, 1987, 2009; Morse and Stephens 1996). The collection sites of the cannibals' mothers are scattered through a region that consists primarily of forest and water, unfavorable sites for *M. vatia*, such that only limited gene flow probably occurs, even though the spiderlings balloon readily (Morse 1993a, 2005). Thus, this cannibalistic predisposition is most likely widespread and not the property of a single large regional population.

The pattern seen in *M. vatia* obviously bears considerable resemblance to the cannibalistic morphs in a wide variety of taxa, including some salamanders and fish. Although many of these individuals show striking morphological variation (e.g., Nyman et al. 1993; Michimae & Wakahara 2002; Klemetsen et al. 2003), others do not exhibit morphological variation (e.g., Lanoo et al. 1989). In these instances, cannibalism is presumably an adaptation to temporary and unpredictable conditions, and perhaps most closely resembles the condition seen in *M. vatia*.

Certain spiders (Gundermann et al. 1991) produce trophic eggs, in common with several other groups (Crespi 1992). Others feed on eggs inside the egg sacs or nests (reviewed in Valerio 1974). Although most of these instances relate to egg feeding by first instars, Valerio (1974) reports instances of active second-instar theridiids feeding on eggs, which suggests the feasibility of sib cannibalism (second instars) within the egg sac or nest. The production of relatively small numbers of large young is adaptive under some circumstances (Roff 1992; Stearns 1992), though cannibalism seems an inefficient way of accomplishing such an advantage. Emergence sizes of non-cannibalistic *M. vatia* broods already vary by nearly two-fold (ca 0.4–0.7), a difference that appears to have a genetic basis (Fritz & Morse 1985), so considerable variation exists for selection to act on these populations. However, this variation does not match the size range of the cannibalistic spiderlings in this study, on average double the size of non-cannibalistic spiderlings, with a four-fold extreme. Perhaps the low frequency of these cannibalistic broods is indicative of the usual low fitness (to the parents) of this condition. The increased size of the cannibals probably decreases the probability that they will balloon away from their nest site, thus increasing the probability of this trait concentrating within isolated populations. However, in contrast to this prediction, the phenomenon was uniformly rare but widespread in the present study.

Nest or egg-sac cannibalism could function as a radical alternative to ballooning under temporary and unpredictable conditions, in that it, too, provides a few spiderlings with an early supply of food. However, ballooning young in the study area face a particularly unfavorable probability of success, given the dominance of forest and water in the region.

The low frequency of cannibalism within the nests suggests that under most circumstances it does not yield strong advantages and may even be disadvantageous. Following Hamilton's (1964) argument for inclusive fitness, $-k < 1/r$, where k is the change in fitness of the victim divided by the gain in fitness of the cannibal, with r being the coefficient of relationship of the two individuals, Eickwort (1973)

noted that full sibs with equal initial fitnesses would present the most stringent conditions. Typically, female *Misumena* in these populations mate only once (Morse 2010), and their eggs and newly emerged young are of similar size (Morse 1993a), suggesting that they experience these stringent conditions. In young *Misumena* this advantage could result from reaching a larger size before overwintering, since larger individuals (later instars) appear to overwinter more successfully than smaller ones (Morse 2007). If females mated more than once, conditions would be less stringent. Second matings sometimes occur in the laboratory (Morse 2010), but probably seldom take place in the field in these populations, since densities are low and females aggressively attack males shortly after they first mate (Morse & Hu 2004). Thus, the low frequency of nest cannibalism observed matches the predictions from theory. Unfortunately, I do not know whether the cannibalistic broods resulted from polyandrous mothers.

Although this note involves only a small proportion of the many individuals analyzed, the overall sample size allows me to estimate the frequency of an uncommon trait in both space and time. Since cannibalism is reported from a wide range of taxa (Fox 1975; Polis 1981; Elgar & Crespi 1992) and is frequently compared between sibs and non-sibs, its presence in a species that often exhibits a short period of sociality subsequent to emergence from its natal site (D.H. Morse 2011) provides insight on a species intermediate between social or semi-social forms and forms that never congregate.

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