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

ATTENDANCE PATTERNS, PREY CAPTURE, CHANGES IN MASS, AND SURVIVAL OF CRAB SPIDERS *MISUMENA VATIA* (ARANEAE, THOMISIDAE) GUARDING THEIR NESTS

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ABSTRACT

Crab spiders *Misumena vatia* typically guard their nests after laying eggs. Individuals that disappeared from their nests before their young emerged had similar laying dates, pre- or post-laying mass, egg mass, or reproductive effort to those that remained. They included both individuals that actively left the sites and ones that died.

Spiders lost mass constantly through the guarding period, but total losses in the field did not approach those from the laboratory and were unlikely to be the primary source of mortality. Few spiders caught prey during this time, and those captures had little effect on the rate of loss. Small day-to-day fluctuations in mass were largely a result of changes in moisture availability.

INTRODUCTION

The period between which an animal lays its eggs or gives birth and the resulting young become independent is likely to be a time of high vulnerability to these offspring. Not surprisingly, many species protect their reproductive investment during this stage (reviewed by Morse 1980). If an animal produces only one clutch of offspring, the period takes on particular importance. However, a variety of possible trade-offs exists between parental care and reproductive effort (mass of eggs or offspring/mass of parent before laying or birth), if care is not obligate. Animals with a low reproductive effort might guard the eggs or young more effectively than those making a high effort. Individuals that hunted during this period might thereby improve their body condition and thus be able to defend offspring more effectively at other times. Surprisingly, very little information exists on how individuals of a population that differ in their reproductive effort, reproductive output (mass of eggs or newborn offspring), and related variables respond to these differences subsequent to reproduction (e.g., Stearns 1977, 1980). It is thus important to obtain basic behavioral information about individuals that exhibit different reproductive attributes at this stage. In addition to filling vital gaps in our understanding of post-reproductive behavior, such information may eventually even provide valuable insight about the forces dictating the evolution of semelparous and iteroparous reproductive systems.

Here I describe the patterns by which semelparous crab spiders, *Misumena vatia* (Clerck) (Thomisidae), guard their egg masses. I have discussed other aspects of the life history of this species in detail elsewhere (Morse and Fritz 1982, 1987; Morse 1984, 1985a; Fritz and Morse 1985). These spiders vary in their patterns of attendance at their nests, and they also vary in several attributes related to reproduction: date of laying, mass before and after laying, mass of eggs, and reproductive effort (Fritz and Morse 1985). Specifically I concentrate here on activity and length of attendance at the nests, prey capture, changes in mass during the period of attendance, and survival while at the nests. The results allow me to test the hypothesis that the spiders adjust their nest attendance in a way that accommodates for differences in pre-reproductive success (prey capture: Morse and Fritz 1982) and reproductive success (size of egg mass: Fritz and Morse 1985). Earlier (Morse submitted), I established that guarding increases reproductive success of these nests, largely by lowering the frequency of loss to ichneumonid and dipteran egg predators. Further, large spiders guard more successfully than smaller ones.

All of these results assume additional interest in that differences in body size and egg mass size are a consequence of differences in foraging success and, earlier, in hunting-site decisions (Morse and Fritz 1982; Fritz and Morse 1985). Thus, it is possible to relate the behavior observed about the nest to a few earlier key events in the life cycle and determine if these earlier events strongly influence subsequent performance.

MATERIALS AND METHODS

Adult female *Misumena* reach 10 mm in total length and biomasses of 200-400 mg or more (maximum recorded = 515 mg) prior to egg laying. Before laying their eggs they are sit-and-wait predators at flowers that attract large numbers of insects. Nest-attending females used in this study were observed during the summers of 1980-1985 in Bremen, Lincoln Co., Maine, USA. All of these individuals had hunted on common milkweed (*Asclepias syriaca* L.) flowers, their commonest mid-summer haunt in this region (Morse 1981; Morse and Fritz 1982).

In the study area, a large field with several milkweed clones (described in Morse 1981), spiders almost always built their nests on milkweed leaves (Morse 1985a). A spider about to lay its eggs first rolls under the tip of a medium-sized leaf and secures it with silk. Subsequently, it lays its eggs within the enclosure formed and secures the extremities of the leaf with silk until they are tightly opposed. It then usually rests on the under side of the nest, the former upper side of the leaf tip. Eggs are laid at night. I have described and illustrated the nests and their precise locations in detail elsewhere (Morse 1985a). Subsequently, the spiders guard these nests, sometimes until the young emerge from the nest in the second instar nearly a month later (Morse 1985a), often dying soon after (Gertsch 1939; Levi and Levi 1968).

Spiders were individually numbered on the posterior part of the abdomen with indelible ink prior to egg-laying and subsequently monitored and weighed regularly. As soon as they laid their eggs, they were weighed again, allowing calculation of the mass of the eggs and permitting an estimate of reproductive output and effort. Silk production amounts to only about 1% of the mass of the eggs (Fritz and Morse 1985) and was therefore not included in the calculations.

In 1980 and 1981 the egg masses were collected shortly after laying, weighed, and then dissected to measure egg number (Fritz and Morse 1985). Those parent spiders were brought into the laboratory at that time and, after counting and weighing, kept with their eggs in individual open-topped containers at 18°C-22°C until the eggs hatched. I returned the eggs to their egg sacs after handling; however, since this procedure required collecting the leaves and opening the sacs, the humidity of the eggs' environment was undoubtedly lower than those of egg sacs in the field. A randomly chosen sample of these adult spiders were subsequently weighed every few days, as were a few individuals similarly maintained in 1982.

In 1982-1985 virtually all of the individuals were monitored in the field. Those studied during 1982-1984 were weighed every other day prior to egg-laying, as soon as they laid their eggs, and thereafter every third day, always being returned immediately to their nests. On other days they were censused, and observations made of their location, behavior, and any evidence of prey captured. Information on survival and predation by adult spiders were taken at the time. Treatment of the spiders was similar in 1985, except that they were weighed only once subsequent to egg-laying.

In 1983, 21 spiders were confined to their nest-sites in large bags of white nylon tricot (25 cm wide x 30 cm long, (0.3 mm x 0.3 mm mesh)) as soon as they laid their eggs. They were then monitored similarly to the other spiders. Since ambient temperatures within the bags scarcely differed from those immediately around unmanipulated nests ($\bar{x} \pm \mathrm{SD} = 0.1 \pm 0.1$°C, $N = 18$ measurements), these individuals provided a control against which to compare the biomass changes, survival and nest-abandonment of the other individuals monitored in the field.

Sizes of samples differ widely in the results, since many of the spiders were used in other studies that made them appropriate for analysis of only certain of the variables reported here.

RESULTS

Behavior of spiders attending nests.—Spiders usually remained on the under side of their nest, the most likely point of entrance to it by insect predators. During daily censuses in 1982-1985, I saw spiders on top of their nests only 65 times (usually in full sunlight during mid-morning) and in other nearby locations (up to 7 cm away from their nests) 37 times (in 3914 observations on 220 spiders); in all other instances they occupied the under side of the nest. Thus, in only 2.6% of the observations did individuals fail to attend in the commonest way. These were only occasional acts by the spiders exhibiting them, observed in 62 (31%) of the spiders for which census data existed. No individual was observed away from the under side of the nest more than five times. Of individuals seen away from their nest, 65% ($N = 37$) subsequently abandoned that nest, compared to 47% ($N = 183$) never seen away from it ($G = 4.84$, $df = 1$, $P < 0.05$). Individuals seen away from nests and those not seen away from nests did not differ in size before or after egg-laying, size of egg mass, or reproductive effort, however (Table 1).

Effect of handling on adults disappearing from egg masses.—If handling caused spiders to leave their egg masses, the disappearances recorded would be partly or totally an artifact. In that instance, numbers of disappearances recorded on the

Table 1.—Size and reproductive characteristics of spiders that were seen off nest one or more times and ones always seen on next.

Variable	Seen away from nest one or more times $\bar{x} \pm$ SD	N	Not seen away from nest $\bar{x} \pm$ SD	N	t^1 or z^2	P
Size before egg laying (mg)	253.3 ± 65.5	32	220.0 ± 75.6	161	1.005^1	>0.3
Size after egg laying (mg)	77.9 ± 21.1	35	75.2 ± 20.8	182	0.703^1	>0.4
Size of egg mass (mg)	154.0 ± 49.1	32	146.0 ± 58.8	161	0.710^1	>0.4
Reproductive effort (%)	65.1 ± 5.4	32	64.7 ± 7.8	161	1.310^2	>0.1

[1] t-tests, two tailed (df $=N$-2)

[2] Wilcoxon pairs test, two-tailed

days immediately following weighings should exceed those of other days. In 529 spider-days (number of spiders x number of days censuses during 1982-1984), eight spiders (1.5%) disappeared from their egg masses between weighing and the next census one day later. Fourteen (1.3%) disappeared on the other days, which totaled 1092 spider-days. These two measures do not differ ($G = 0.14$, $df = 1$, $P > 0.7$, G-test); therefore, I conclude that the weighing procedure did not affect the tendency to abandon egg masses. These results are in accord with my observations that randomly-discovered *Misumena* nests often are unattended; i.e., disappearances occur naturally.

Characteristics of disappearing and remaining adults.—Almost one-third of the spiders disappeared from their nests before their young began to emerge (Table 2). Their lengths of attendance ranged from four days to individuals that disappeared only shortly before the young began to emerge ($\bar{x} \pm$ SD = 14.9 ± 9.4 days). Spiders that disappeared from their egg masses did not differ from those that guarded their egg masses until juvenile emergence (Table 2) in date of egg laying, mass before or after egg-laying, reproductive effort, mass of clutches, or rate of loss in mass subsequent to laying (Table 2).

Length of attendance.—Thirty-nine of the 71 spiders (55%) attending nests that I monitored through the dispersal phase of the young remained until the young

Table 2.—Characteristics of crab spiders that disappeared and remained on their egg masses until young emerged.

Variable^1	Disappeared from egg masses $\bar{x} \pm$ SD	N	Remained on egg masses $\bar{x} \pm$ SD	N	t^3 or z^4	P
Date of laying^2	211.3 ± 11.6	53	214.4 ± 9.3	131	1.921^3	>0.05
Size before egg-laying (mg)	215.6 ± 73.5	42	219.1 ± 71.2	118	0.266^3	>0.7
Size after laying (mg)	72.7 ± 17.3	53	75.6 ± 21.5	131	0.873^3	>0.3
Size of egg mass (mg)	144.2 ± 58.2	42	143.4 ± 54.6	118	0.095^3	> 0.9
Reproductive effort (mass of eggs/ mass of spider before laying) (%)	65.3 ± 8.0	42	64.4 ± 7.0	118	1.254^4	>0.2
% loss/day between egg-laying & disappearance: % loss/day of a random sample of spiders remaining	0.6 ± 0.8	18	0.8 ± 0.7	18	1.220^4	>0.1

[1] Variables 1-4 did not differ significantly among the years 1982-1985 ($P > 0.5$ in one-way ANOVA for variables 1-3; $P > 0.5$ in a Kruskal-Wallis one-way ANOVA for variable 4)

[2] Julian date: 211 = 31 July, 214 = 3 August

[3] t-tests, two tailed (df = N−2)

[4] Wilcoxon pairs tests, (two-tailed)

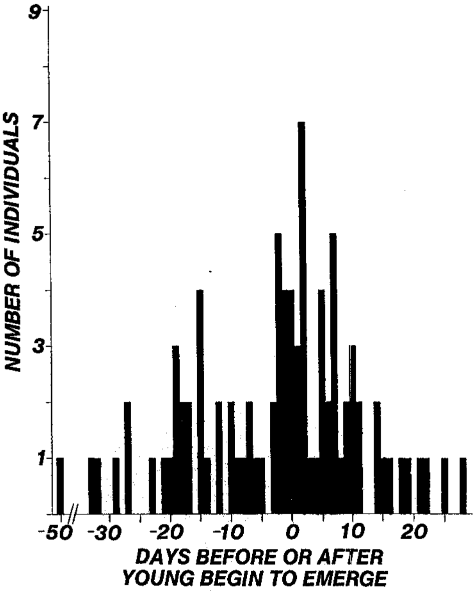

Fig. 1.—Number of adult spiders that ceased guarding their nest before and after the first spiderlings began to emerge. Day of first emergence is 0, negative numbers on abscissa refer to adult spiders that left before the first spiderlings emerged, positive numbers on abscissa refer to adults that remained after the first spiderlings emerged.

began to emerge from their nests (Fig. 1). Their length of stay was not significantly related to pre-laying body mass, or reproductive effort ($r_s < 0.2$ in each Spearman rank correlation, $P > 0.1$, $N = 71$).

Fifteen of the 71 (21%) remained until all the young had dispersed from the nest (Fig. 2). Those post-productive individuals dispersed or died slowly after this period, the last one being noted 13 days after the last young left. Observations were inadequate to tell whether most of these individuals died over this time; however, three were found dead. Many of the individuals thus remained during dispersal of their offspring. Spiders that stayed until their last young left the nest did not differ from the others in pre- or post-laying mass, egg mass, or reproductive effort (Table 3).

Adult mortality.—A minimum of eight spiders, 11% of the total, died before their young emerged from the nest. In most instances I could not separate deaths unambiguously from abandonments, since individuals from either category might simply disappear. The probability of finding dead individuals was low, unless they were found dead on their nest, held by a line of silk in which a limb had become entangled, or picked up directly under the nest shortly after dying. Harvestmen (*Phalangium opilio*) and ants (*Myrmica* sp.) scavenged many corpses of arthropods, including crab spiders, in the milkweed clone (Morse 1985b). Not all that disappeared died, however, since 10 (13% of the total) of these post-reproductive individuals were subsequently found at varying distances away from the nests. Thus, I have retained the distinction between the two categories.

The experiment in which 21 individuals and their nest-sites were covered with nylon tricot bags after egg-laying provided an independent basis for comparing numbers of abandoning and dying spiders. Four of these individuals died before the young were old enough to emerge, and another four individuals abandoned

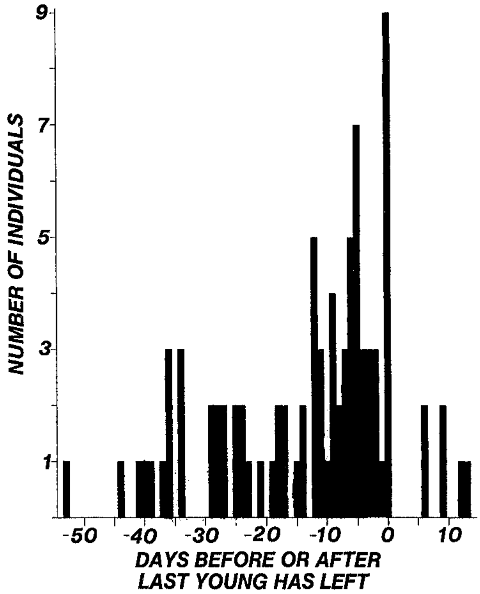

Fig. 2.—Number of adult spiders that ceased guarding their nest before and after the last spiderling left the nest. Day of last departing spiderling is 0, negative numbers on abscissa refer to adult spiders that left before all spiderlings had gone, positive numbers on abscissa refer to adults that remained after all spiderlings had gone. The peak at 0 days is partly an artifact, because several of the nests with adult spiders were collected at that point. These individuals had, however, remained until the last young had left.

their nests, subsequently occupying other parts of the plant covered by the tricot bag. The combined proportion of dead and abandoning spiders in this experiment was not significantly different from the proportion of unrestrained spiders that died or disappeared (Table 2) (G = 0.74, $P > 0.3$). Although the sample is small, this result suggests that many of the individuals placed in the "disappeared" category of Table 2 also died.

Loss of biomass and survival.—Survival time could be a consequence of body condition. Observations and experiments on individuals in the laboratory and field provide insight into this question.

At the time that they died, spiders maintained in the laboratory at ambient temperature had lost 39.8 ± 12.8% ($\bar{x}$ ± SD) of their biomass subsequent to egg-laying ($N = 16$). Some individuals in the laboratory began to approach this critical level (dashed line of Fig. 3) after as little as 15 days. Despite their high

Table 3.—Size and reproductive characteristics of spiders that remained on nests until after all young left, left before this time.

Variable	Remained until end $\bar{x}$ ± SD	*N*	Left before $\bar{x}$ ± SD	*N*	t^1 or z^2	*P*
Size before egg laying (mg)	209.1 ± 72.8	22	225.5 ± 66.6	88	1.016^1	>0.3
Size after egg laying (mg)	74.9 ± 22.0	22	75.0 ± 18.0	107	0.025	>0.9
Size of egg mass (mg)	134.2 ± 56.2	22	149.7 ± 52.4	88	1.222^1	>0.9
Reproductive effort (%)	62.3 ± 10.1	22	65.6 ± 6.3	88	0.975^2	>0.3

[1] t-tests, two tailed (df = *N*-2)
[2] Wilcoxon pairs test, two-tailed

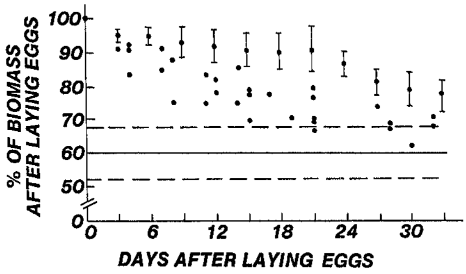

Fig. 3.—Loss in biomass subsequent to egg-laying. Solid line with error estimates is % loss in biomass of spiders monitored in the field ± 2 SE. Twenty spiders were used, N at any one of these points = 12-20. Points immediately below this line are losses in biomass of spiders kept without food or water in the laboratory. Data are from 14 different spiders; in some instances more than one point was obtained from a spider. Shaded area below the points is the mean % loss in biomass at death ± SE in the laboratory, $N = 16$.

rate of decline in biomass, most of the spiders brought into the laboratory with their egg masses survived for long periods without being fed or given moisture ($\bar{x} = 32.4 \pm 7.8$ days, $N = 31$). Survival time in the laboratory was, however, correlated with the mass of individuals after egg-laying ($r_s = 0.43$, $P < 0.05$ in a Spearman rank correlation), but not with mass immediately prior to egg laying ($r_s = 0.30$, $P > 0.2$), or reproductive effort ($r_s = -0.12$, $P > 0.5$).

Since most of the individuals (39/47) followed through the dispersal of young in the field survived until the young began to emerge (24 others disappeared), the results are not directly comparable to the laboratory data. Taking only those spiders known to have died, eight before the young emerged and two after, a significant correlation occurred between survival time and post-laying mass ($r_s < 0.63$, $P < 0.05$), but not pre-laying mass ($r_s = 0.41$, $P > 0.1$, or reproductive effort ($r_s = -0.40$, $P > 0.1$). Thus, the pattern of adult mortality in the field appeared to resemble that in the laboratory, but longevity was apparently considerably greater in the field, with the result that most spiders survived well in excess of the time that their young emerged from the nest. The disappearance of many of the spiders from their nests precludes a more sensitive analysis.

Condition of adults.—The physiological ability of the spiders to remain on nests in the field could be confounded by a tendency to leave once the young emerge. The individuals maintained in the nylon tricot bags in 1983 provided insight into the potential survival of these individuals in the field. Of the 21 individuals, 17 were still alive 27 or more days after egg-laying, the mean period to the commencement of spiderling emergence in the field. Some survived as long as 39 days, the point at which observations ceased. Although four of these individuals did die over the period, none of them lost percentages of total biomass as great as those dying in the laboratory (losses in the field ranged from 7.3% to 16.4%). The basis for death in these individuals could not be determined, but the differences in loss of mass suggest that it differed from the laboratory individuals.

Basis for changes in mass.—In general, spiders guarding their egg masses in the field lost biomass slowly (Table 2). This result could be the consequence of feeding or of differences in water balance between field and laboratory.

Capture of prey. Given the similar environmental conditions experienced by the sample of 21 spiders confined to the tricot nets in 1983 and the unconfined spiders, one can test the importance of prey in determining changes in biomass over the season. The confined spiders did not differ in change of biomass over this period from the 12 unconfined spiders measured in 1983 (F = 0.11, *df* = 1, $P > 0.7$ in a repeated measures ANOVA). Neither did the confined individuals differ in loss of biomass from the 20 unconfined spiders measured in 1982 (F = 0.01, *df* = 1, $P > 0.9$) or the 27 unconfined spiders in 1984 (F = 0.51, *df* = 1, $P > 0.4$). Thus, prey do not appear to play a significant role in the maintenance of body mass at this time.

It was possible to investigate and test this result further with observations made on prey visits to the vicinity of the spiders, kills made by the spiders, and fluctuations in patterns of loss in mass. Since most individuals laid their eggs on non-flowering milkweed stems (Morse 1985a), and those using flowering stems usually did so only after the flowers had senesced (three exceptions), these spiders seldom experienced the high densities of insects that they found prior to egg-laying. Only small numbers of insects visited the spiders' nest sites. During 95 hours of observing 27 different brooding spiders, only three insects (a treehopper (Membracidae), a big-headed fly (Pipunculidae), and a tachinid fly (Tachinidae)) visited the leaves upon which nests were placed, or other sites within 5 cm of the nest. The spiders did not attempt to capture any of these insects. During this time an additional 21 insects, also all homopterans and dipterans, alighted elsewhere on plants containing the spiders' nests. Spiders did not attempt to capture any of these insects, either.

Not surprisingly, the spiders captured few prey during this period. In only 23 of 3914 daily census records of spiders (0.6%), involving 220 individuals, was a spider observed feeding on an insect. These prey included an arctiid moth and small hemipterans, membracid homopterans, tachinid flies, halictid bees, and tortricid moths. As a group spiders capturing prey did not differ in mass from non-feeding spiders before and after egg laying, mass of eggs laid, or reproductive effort (Table 4).

Another way to identify possible captures of prey by post-reproductive spiders is to weigh them regularly and search for substantial increases in mass (here defined as greater than 2 mg, the greatest gain shown by the spiders confined with the nylon tricot bags). In the occasional instances in which I observed the spiders feeding on prey, they exhibited such increases at their next weighing, as much as 5-10 mg. However, gains of greater than 2 mg occurred at only 21 of the 354 weighings (5.9%) made every third day in the field. Put another way, these data suggest that on average a guarding spider captured a prey item providing substantial sustenance only once every 51 days (354 weighings, each done every third day = 1062 days, ÷ 21 prey), a period considerably exceeding that of any spider's tenure at a nest.

I divided into three groups spiders monitored more than 10 days: those that registered more than one gain of greater than 2 mg, those that registered one such gain, and those that did not register any gains greater than 2 mg. I then compared their mean percent biomass change per day (Table 5). Individuals of the groups that apparently caught prey did lose mass significantly more slowly than those that did not (H = 19.54, *df* = 2, $P < 0.0001$ in a Kruskal-Wallis one-way ANOVA). Of the three individuals with more than one gain exceeding 2 mg, two roughly maintained their mass over the guarding period, and the third registered a 10% gain. Thus, although spiders apparently measurably slowed their

Table 4.—Size and reproductive characteristics of spiders that captured and did not capture prey while attending their nests.

Variable	Seen with prey 1 ± times $\bar{x} \pm$ SD	*N*	Not seen with prey $\bar{x} \pm$ SD	*N*	t^1 or z^2	*P*
Size before egg laying (mg)	231.8 ± 80.9	8	222.9 ± 74.0	185	0.329	>0.7
Size after egg laying (mg)	70.9 ± 21.8	10	76.7 ± 25.0	207	0.721	>0.4
Size of egg mass (mg)	160.1 ± 61.5	8	145.8 ± 56.4	185	0.701	>0.4
Reproductive effort (%)	68.3 ± 4.2	8	64.3 ± 8.0	185	0.414^2	>0.6

[1] t-tests, two tailed (df = *N*-2)

[2] Wilcoxon pairs test, two-tailed

loss in mass if they captured prey, only one of the 47 individuals monitored for more than 10 days registered a persistent gain in mass. Overall, these results do not suggest that feeding appreciably slows loss in mass of most individuals in the field. Spiders registering large gains did not differ significantly from non-gaining spiders in mass before and after egg-laying, in mass of the eggs, or in reproductive effort (Table 6).

Effect of moisture. Another group of spiders was kept in the laboratory without food as a second control, permitting me to assess change of biomass in the absence of both food and the moisture regime normally encountered. Since netted and unnetted individuals in the field did not differ in loss of biomass, this comparison actually provides information about relative water loss. Loss by spiders in the laboratory was roughly linear subsequent to egg-laying, and averaged slightly over 1% per day (1.13 ± 0.20% per day, $N = 12$).

Individuals in the field (confined and unconfined) lost biomass at about two-thirds the rate of the ones confined to the laboratory (Table 2, Fig. 3). The regressions of biomass loss over time differed significantly between the field and laboratory groups in a test for homogeneity of slopes ($F = 29.83$, $df = 1$, $P < 0.0001$).

The ability of post-reproductive *Misumena* to absorb water can be readily observed in the laboratory. Individuals brought into the laboratory in open containers for 10 days and then placed in a sealed jar with moist paper towels for 24 hours at ambient temperature took up considerable amounts of water, a few increasing up to nearly 30% of their mass immediately previous to treatment ($\bar{x} =$ 16.8 ± 6.6%, $N = 9$). This uptake recouped most of their loss in mass over the period of their incarceration. None of the gains in the field approached this level, however.

Spiders attending their nests in the field regularly registered small (<2 mg) increases in mass (42 of 354 observations; 11.9%), many probably resulting from changes in their water content. Loss of mass was significantly lower at weighings

Table 5.—Changes in mass / day as a consequence of the number of times spiders gained more than 2 mg between weighings. Each of these spiders was monitored for 10 or more days.

Number of gains > 2 mg	*N*	% change in mass per day ± SD
0	29	−0.86 ± 0.50
1	15	−0.29 ± 0.29
2	3	−0.04 ± 0.25

Table 6.—Size and reproductive characteristics of attending spiders that registered gains of over 2 mg mass, spiders that did not register gains of this size.

Variable	Gain of > 2 mg $\bar{x} \pm$ SD	N	No gains of > 2 mg $\bar{x} \pm$ SD	N	t[1] or z[2]	P
Size before egg laying (mg)	195.0 ± 53.4	22	224.9 ± 74.8	87	1.765[1]	>0.05
Size after egg laying (mg)	67.0 ± 15.3	23	76.0 ± 21.0	91	1.925[1]	>0.05
Size of egg mass (mg)	128.3 ± 41.6	22	147.3 ± 58.0	87	1.444[1]	>0.1
Reproductive effort (%)	64.7 ± 6.5	22	64.2 ± 8.2	87	0.106[2]	>0.9

[1] t-tests, two tailed (df = N-2)

[2] Wilcoxon pairs test, two-tailed

made less than one day after a rainy or foggy period (−0.04 ± 1.2%, 145 observations) than if weighings were preceded by more than three days of dry weather (−0.7 ± 1.4%, 211 observations) ($P < 0.001$ in Wilcoxon two-sample Test). However, such differences soon disappeared, for spiders exposed to rain or fog two or three days (−0.6 ± 1.4%, 276 observations) previously did not differ significantly in mass from those that had experienced only dry weather over that period ($P > 0.1$ in Wilcoxon two-sample Test).

DISCUSSION

Spiders that disappeared from their nests did not differ from those that remained, in laying dates and reproductive variables (Table 1). The significantly higher permanent disappearance rate of individuals seen off their nests once or more (Table 1) might thus be a simple consequence of becoming lost as a result of that activity. Although the spiders habitually lay down a line if they move; which often results in a network of threads about the nest (illustrated in Morse 1985a), chances of losing contact would appear more likely as distance from the nest-site increased. Three of the four abandoning spiders that I found and returned to their nests remained on the nests for a day or more after being returned.

Spiders do not lose a large proportion of their mass before their young leave the nests, at least as judged by the presumably lethal losses of mass incurred in the laboratory. This result suggests that energy and moisture reserves of the females in the field are usually adequate for them to survive until their young emerge. The inability of most hunting individuals to increase their size substantially, in turn probably a consequence of the small number of insects visiting these locations, suggests that the spiders do not depend on food supplements for survival through this stage. The advantage obtained by guarding (Morse, submitted) thus suggests that gains come about as a result of allocating adequate reserves for survival in the first place, rather than obtaining them later. The extremely low metabolic rate of spiders (Anderson 1970) enhances this ability. However, the correlation between length of survival in the field and post-reproductive size, which parallels the pattern found in laboratory survival studies, suggests that selection may act (or has acted) positively on large body size.

The rates of loss of mass in laboratory and field suggest that the principal advantage realized by the spiders in the field is an ability to control their water balance. Spiders seldom exposed themselves on the upper side of the nests, except early in the morning when sunning themselves in relatively cold conditions. Further, their tendency to gain mass on damp days, and upon occasion to occupy the upper sides of nests on rainy days, suggests that they take in water directly (Volmer and MacMahon 1974). This conclusion is consistent with the changes in mass of those exposed to damp conditions in the laboratory. I have also observed *Misumena* apparently drinking both dew and nectar in the field (Morse, unpublished observations).

Surviving in vigorous condition over this period has clear advantages to the spiders. Nests guarded throughout the nesting period suffered lower predation on their egg masses than unguarded ones; further, large spiders, which probably have larger energy reserves at this time, experienced lower rates of predation on their egg masses than did small ones (Morse, submitted).

Differences in earlier foraging success, characterized at this stage by large female size and large egg mass, thus did not appear to affect any of the behavioral patterns observed in this study (activity about the nest, leaving the nest, hunting); that is, no behavioral trade-offs occurred. However, since large spiders suffered lower levels of egg predation from insects (ichneumonids, dipterans) (Morse, submitted), it seems likely that their ability to defend their nest differs. These size-related differences in success are not a simple consequence of predators choosing small egg masses, because predation was not related to size if spiders were removed immediately after laying their eggs and completing their nests (Morse, submitted). In order to address this factor further, it will probably be necessary to monitor nests with time-lapse photography. No data on these egg predators were obtained during the 95 hours of continually watching the nests noted above.

It is possible that the size-related survival of adults will affect the level of predation on the young as they emerge from the nests over several days after initially making small openings to the outside. Although the results suggested that most spiders could survive until their young began to emerge, the protracted departure of many young might result in a higher proportion of small females dying before all the young left; further, large females might also be more effective at minimizing predation on emerging young than are small females. Considerable predation may occur at this time. Seven times in the regular censuses I have observed jumping spiders (*Metaphidippus insignis* (Banks)) positioned on *Misumena* nests, all without guarding females, and with emerging young. These jumping spiders are abundant in the study area and readily capture second and third-instar *Misumena* presented to them (Morse unpublished).

ACKNOWLEDGMENTS

I thank M. Cheo, R. S. Fritz, R. Gillespie and M. H. Greenstone for comments on the manuscript. H. Townes identified the ichneumonid wasp, E. Fisher identified the phorid fly, and G. B. Edwards identified the salticid spider. R. Bartlett and the National Audubon Society generously permitted use of their properties. R. S. Fritz, E. K. Morse, and J. Olson assisted in the field. This work was supported by the National Science Foundation (DEB80-08502, DEB81-18105, and BSR81-18105-A01).

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Manuscript received May 1986, revised October 1986.