

NEST ACCEPTANCE BY THE CRAB SPIDER *MISUMENA VATIA* (ARANEAE, THOMISIDAE)

Douglass H. Morse

Graduate Program in Ecology and Evolutionary Biology
Division of Biology and Medicine
Brown University
Providence, Rhode Island 02912 USA

ABSTRACT

I tested whether female crab spiders *Misumena vatia* responded differently to their own nests and to other spider nests or parts of nests. They accepted nests of conspecifics as readily as their own, although initially showing more activity on others' nests than their own. They accepted intact *M. vatia* nests more often than nest silk placed on leaves, turned-under leaves, or artificial nests; and unaltered leaves less frequently than any of the latter. They accepted nests of other spider species less frequently than conspecific nests, probably in response to the differences between these nests and conspecific nests. Some crab spiders about to lay their eggs accepted conspecific nests, but hunting adult females did not accept them more than predicted by chance.

INTRODUCTION

Parental care has recently engendered considerable interest because of its importance to theories of parental investment (Trivers 1972), parent-young conflict (Trivers 1974) and life histories (Stearns 1976, 1977). Considerably less attention has been simultaneously paid to the proximal cues used by parents to identify their young or their nest-sites. Nevertheless, these cues are crucial to the success of parental strategies and are therefore demanding of attention. In the past such cues have been the subject of considerable attention in their own right as sign stimuli or releasers (e. g., Tinbergen 1951).

Parental care ranges from guarding eggs to caring for them and the resulting offspring until they approach reproductive maturity. The extent of this commitment depends in part on the ability of parents to perform a variety of acts, ranging from site tenacity to recognizing their own nests, and their predisposition to care for eggs or young (see Trivers 1974). Sometimes it is unclear whether parental care results from site tenacity or recognition, especially among invertebrates, including ones whose behavioral patterns might help to clarify the evolution of parental care and other types of sociality (Wilson 1975). Understanding the conditions, cues, and mechanisms associated with parental care in a broad range of animals is thus particularly desirable.

Here I provide the results of studies on nest recognition by the semelparous crab spider *Misumena vatia* (Clerck) (Thomisidae). Female crab spiders lay their single egg mass in a nest that they construct from a large ovate leaf. They build this nest by bending under the distal tip of the leaf and securing it to the under side of this leaf (mid-section). Eggs are laid on silk within the cavity produced,

and the lateral sides are then drawn tight (Morse 1985). They subsequently guard this nest, often until young have emerged from the nest nearly four weeks later and sometimes until all the young have dispersed from the nest, as much as 12 days after that time (Morse 1987). Guarding behavior enhances survival of the affected offspring (Morse in press).

These spiders seldom wander far from the nests during the guarding phase, and they usually are connected to their sites by a silken line, which would facilitate return. However, they occasionally become separated from their nests. These individuals do not appear to have abandoned the sites "intentionally", for they may assume guarding positions in similar locations on nearby plants ($N = 4$).

Misumena vatia can be readily removed from their nests for weighing at any time during the guarding period and then returned, without affecting their desertion rate (Morse 1987). This result suggested that they could be transferred to other selected substrates, most obviously nests of conspecifics, in order to compare their performance with those on their own nest sites.

In this paper I present the results of experiments designed to establish whether female crab spiders respond differently to their own nests and to other nests. Also I investigated several cues that may facilitate nest recognition. Specifically, I ask: 1) can crab spiders recognize their own nests, or 2) nests of their own species? 3) If so, what characteristics are crucial in their identifications? If not, to what cues do they respond that their nests have in common with other features of the environment?

METHODS

All of the post-laying *Misumena* used in this study constructed their nests on milkweed (*Asclepias syriaca* L.) leaves in a field in Bremen, Lincoln Co., Maine (see Morse 1985). These spiders were removed from their natural nest sites within a week of laying and placed on a variety of sites for 1-hour periods, and their movements recorded during this time. Spiders were characterized as active if they moved on the nest or changed orientation five or more times per hour, or if they left the nest during this time. A random sample of spiders brooding their own eggs moved 3.3 ± 3.8 times per h ($\bar{x} \pm SD$) ($N = 34$) (Morse 1987).

Tests included spiders removed from and then returned to their own nests and ones placed on other *M. vatia* nests; as well as individuals placed on superficially similar nests of other thomisid, salticid, and theridiid spiders; on unaltered milkweed leaves; on leaves turned under by spiders or by the investigator; and on leaves with *M. vatia* nest silk placed on them. Controls were also run to determine that one-hour periods insured a representative bout of behavior. After the experiments the spiders were returned to their own nest sites. For comparison, similar transplantation experiments were run on two other groups of spiders: "broody" spiders, which had turned under leaves preliminary to egg-laying; and large, actively-feeding spiders. Both were placed on completed *Misumena* nests. All of these presentations were sequential, in keeping with the natural patterns observed in the field. Thirty spiders were used in each experiment, none of the individuals in more than one experiment.

Another group of spiders was periodically tested for recognition of their own nests over the entire period that they normally would guard nests. I removed these individuals from their nests immediately after they laid their eggs and

Table 1.—Responses and activity levels of spiders placed on different substrates. Only the first 15-16 replicates were scores for activity in Experiments 2-11. $N = 30$ in each experiment. a = All at guarding stage except for Experiments 10 and 11. b = Had turned under leaf preparatory to laying. Laid 1-5 days later ($\bar{x} \pm SD = 2.5 \pm 0.7$ days). c = Actively hunting and showing no indication of nest building. Laid 4-12 days later ($\bar{x} \pm SD = 8.2 \pm 3.9$ days).

Experiment	Treatment ^a	Remain			
		on site	Leave site	Stationary	Active
1	Monitor, remove & return				
	Before removal	30	0	25	5
	After return	30	0	22	8
2	On other nest and return				
	On other nest	29	1	12	18
	After return	30	0	20	10
3	Unaltered leaf	4	26	1	14
4	Leaf turned under by spider	14	16	4	11
5	Nest silk on leaf	15	15	6	9
6	Artificial nest	19	11	8	7
7	<i>Xysticus</i> nest	18	12	4	11
8	<i>Metaphidippus</i> nest	15	15	7	8
9	<i>Enoplognatha</i> nest	10	20	4	11
10	<i>Misumena</i> nest ^b	13	17	8	7
11	<i>Misumena</i> nest ^c	5	25	3	13

completed their nests. They were placed inside large bags of nylon tricot that covered plants similar to the ones upon which they laid and subsequently kept in these bags, except when they were run in experiments on their own nests, either once or every several days. These manipulations permitted an assessment of whether time away from the nest affected the tendency to guard a nest.

RESULTS

Experiment 1. Spiders removed from their own nest and returned.—In an initial test, several spiders were monitored for an hour to record activity, then removed from their nests, moved about their home milkweed clone in a small shell vial concealed from any possible visual cues, and returned to their sites and monitored for another hour. Only a small percentage of the individuals exhibited regular activity prior to removal (Table 1), and this number did not differ significantly from those exhibiting activity after their return ($G = 0.89$, $P > 0.3$). Thus, removal in itself does not measurably affect the behavior of these species and should not be the basis for any differences reported in Experiments 2-9 presented below. This pattern of low activity characterizes guarding spiders (see Methods).

Experiment 2. Spiders switched to other recently-occupied *Misumena vatia* nests.—Spiders laying at similar times were removed from their nests and immediately placed on each others' nests for an hour. During this period one of the 30 individuals left the nest after 5 min. It was replaced and remained the next 55 min until removed. All other individuals remained on their foster nests for the full 1-hour period. Thus, no significant difference occurred between the tendency to remain on their own nests (Experiment 1) and those of other individuals at a similar stage of development ($G = 1.40$, $df = 1$, $P > 0.2$). However, the activity

of these displaced spiders on different nests was greater than that of similarly displaced ones returned to their own nests (Experiment 1) ($G = 6.93$, $P < 0.01$). The spiders made several lines that secured the nest to nearby leaves or other structures. The spiders became less active when they were returned to their own nests after one hour, ($G = 4.34$, $P < 0.05$) (Table 1), but some activity still remained. The number of active individuals did not significantly exceed that of Experiment 1 ($G = 0.16$, $P > 0.5$).

Experiment 3. Bare milkweed leaves.—I placed spiders on leaves of similar size and location to those used for nests, which had not been manipulated by spiders. Only four of the 30 *M. vatia* placed on these leaves remained for an hour, which differs significantly from the behavior of spiders returned to their own nests ($G = 58.55$, $P < 0.001$) or put on other *M. vatia* nests ($G = 50.25$, $P < 0.001$). Clearly spiders do not respond to unmodified leaves in the way that they respond to their own nests or those of conspecifics. This experiment indicates that the spiders are active enough to leave their sites within an hour. Failure of the spiders in Experiments 1 and 2 to move from the nests is thus not a consequence of a low rate of activity.

Experiment 4. Leaves with tips turned under by other *Misumena vatia*.—One of the distinctive features of a *M. vatia* nest is that the leaf used is turned down at the tip and folded under by the parent spider (Morse 1985: fig. 1). The first step in making a nest is to turn a leaf under and secure it with strands of silk between the distal tip and the ventral side of the leaf's midrib. After performing this act spiders typically remain in the resulting shelter for 1-3 days before laying their eggs and drawing the sides of the leaf tightly together with silk to complete the nest. This position differs from the one assumed by spiders that have already laid their eggs. Several spiders were collected for experiments at the leaf-turning stage, resulting in a ready source of such leaves for this experiment. Only 14 of 30 brooding spiders placed on these leaves remained there for the full test period. This response is significantly weaker than from the response to both their own nests ($G = 78.13$, $P < 0.001$) (Experiment 1) and to the nests of other *M. vatia* ($G = 21.30$, $P < 0.001$) (Experiment 2), but significantly stronger than the response to unmodified leaves (Experiment 3) ($G = 8.29$, $P < 0.01$). Thus, turned-under leaves appear to be a stimulus for remaining at a site, although not as strong a stimulus as a completed nest.

Experiment 5. Leaves with *Misumena vatia* silk applied to their distal ends.—Another potentially important feature promoting site tenacity might be the presence of silk. *Misumena vatia* place considerable amounts of silk about their nests, noticeably stiffening the distal part of the leaf. This silk can be readily removed as a sheet from the surface of the nests. In Experiment 5, sheet-like silk was removed from other nests and placed on the distal 1 cm of both upper and lower surfaces of otherwise undisturbed leaves similar to those usually used as nest sites. Except for the silk added, these leaves were similar to the leaves used in Experiment 3.

Half of the spiders remained on these sites during the experiment. Their frequency of staying is significantly lower than that of spiders placed on the nests of other conspecifics ($G = 19.23$, $P < 0.001$) (Experiment 2) or returned to their own nests ($G = 25.89$, $P < 0.001$) (Experiment 1). This response was stronger than the response to plain leaves (Experiment 3) ($G = 9.77$, $P < 0.01$) but not the response to turned-under leaves (Experiment 4) ($G = 0.07$, $P > 0.7$). Thus, the

presence of silk also appears to play a role in determining what constitutes a nest, but it is not as strong as a completed nest.

Experiment 6. Artificial nests secured by thread.—It is possible that the results in Experiment 4 were a consequence of the distal and medial parts of the leaves being only partly apposed to themselves, rather than due to a lack of silk. To test this possibility, I sewed leaves into the form of nests with fine white thread, placing segments of dried timothy grass (*Phleum pratense* L.) inflorescences inside to approximate the shape of a nest. Spiders in this experiment could not crawl inside the nest, which distinguishes this manipulation from Experiment 4.

A majority of the spiders remained on these artificial nests for the entire period of the experiments. This result did not differ from that of Experiment 4 (leaves turned under by spiders), in which the spiders had access to leaves partially turned under by spiders ($G = 1.69$, $P > 0.1$). It was weaker than the response to the nests of other *M. vatia* (Experiments 1 and 2), however ($G = 17.74$ and 11.85 , $P < 0.001$, < 0.001). Thus, turned-under, closed leaves may provide important cues for spiders, but further experiments would be required to establish whether they differ from simple turned-under leaves.

Experiment 7. Nests of other species of crab spiders—*Xysticus emertoni*.—The brown crab spider *Xysticus emertoni* (Keyserling) sometimes places its egg sacs in positions similar to those of *M. vatia*. *Misumena vatia* placed on *X. emertoni* nests remained significantly more frequently than they did on unaltered milkweed leaves (Experiments 1 and 2) ($G = 19.67$, 14.97 , $P < 0.001$, < 0.001). However, their response did not differ from those to turned-under leaves ($G = 1.07$, $P > 0.2$), silked leaves (Experiment 5) ($G = 0.61$, $P > 0.3$) or artificial nests (Experiment 6) ($G = 0.07$, $P > 0.7$).

Experiment 8. Jumping spider nests.—The small jumping spider *Metaphidippus insignis* (Banks), abundant in the study area, builds nests on milkweed leaves that are similar in location and general characteristics to *M. vatia* nests and guarded from within. Half of the *M. vatia* placed on *M. insignis* nests remained on them for the entire hour. Thus they responded more strongly to them than they do to bare leaves (Experiment 3) ($G = 9.77$, $P < 0.01$) and more weakly than to their own nests (Experiment 1) ($G = 25.89$, $P < 0.001$). However, their response does not differ significantly from the response to the artificial nests (Experiment 6) ($G = 1.09$, $P > 0.2$).

Experiment 9. Theridiid spider nests.—A theridiid spider *Enoplognatha ovata* (Clerck) occurs in the study area in small numbers. It also builds nests by turning under leaves (Wise and Reillo 1985), often milkweed leaves, but these nests are less stiff than *M. vatia* nests, probably because *Enoplognatha ovata* do not use large amounts of sheet-like silk in construction. They also guard their nests from inside. Nests built on milkweed leaves were chosen for a set of experiments.

Only one-third of the *M. vatia* remained on *E. ovata* nests for an hour, significantly fewer than the number that remained on their own nests (Experiment 1) ($G = 38.19$, $P < 0.001$), or artificial nests (Experiment 6) ($G = 5.49$, $P < 0.02$). However, this result does not differ significantly from the number remaining on plain leaves (Experiment 3) ($G = 3.44$, $P > 0.1$) or *M. insignis* nests ($G = 1.72$, $P > 0.1$).

Experiment 10. Pre-laying *Misumena vatia* placed on nests.—Spiders that had already turned under leaves in apparent preparation for egg laying (“broody”) were placed on completed nests, as in Experiment 2. Significantly fewer

individuals remained on the nests for an hour than did post-laying individuals on other nests (Experiments 1 and 2) ($G = 30.47$ and 23.48 , $P < 0.001$, < 0.001). Although relatively active at this time, spiders did exhibit a significantly greater tendency for site tenacity prior to laying their own eggs than did post-laying individuals on a plain leaf (Experiment 3) ($G = 6.91$, $P < 0.01$).

Experiment 11. Active *Misumena vatia* placed on nests.—A group of spiders within the size range of egg-laying individuals, but which had not shown any signs of broodiness (i.e., ones that had not turned under a leaf, and were still actively hunting), were also tested. These spiders showed relatively little tendency to remain on nests, significantly fewer remaining than for the broody group (Experiment 10) ($G = 5.22$, $P < 0.05$), or individuals that had already laid (Experiments 1 and 2) ($G = 54.47$ and 46.31 , $P < 0.001$, < 0.001). These individuals did not differ from post-laying spiders that were placed on leaves randomly (Experiment 3) ($G = 0.13$, $P > 0.5$).

Experiment 12. The effect of time away from nest on response.—Individuals in Experiments 1-11 were tested within a few days of laying their eggs. The tendency to remain could thus be a consequence of whether a spider was already guarding its nest. If spiders maintain strong site tenacity, contact with the nest might suffice to retain a predisposition to guard. However, if somehow separated from its nest, the spider might sometimes reoccupy it in the process of random movement by contacting the lines of silk in the vicinity of the nest that are normally laid wherever an individual goes. In the process of this study two spiders, both of known history, that had earlier left their nests established residence at abandoned nests of other conspecifics. These observations are consistent with individuals becoming separated from their own nests, but retaining an affinity to nest cues. These two individuals had been away from their own nests only one and three days, however, which raised the question of how long they would retain this predisposition in the absence of regular contact with nests.

Spiders removed from their nests after laying and placed in nylon tricot bags on similar plants exhibited a strong correlation between time of separation from the nest and tendency to guard when returned (Fig. 1). This ranged from an 88% tendency to remain when away from the nest for 1-5 days to a 20% tendency to remain when removed from 26-30 days, roughly the period between laying and emergence of young (Morse 1987). The pattern of decrease in tendency to remain appears to be somewhat stepped, but relatively slow. The number of confined individuals remaining on their former nest sites for the 1-hour testing period was significantly lower than that of unconfined, free-living individuals at each period ($G = 4.40$, $P < 0.05$ for one five-day period to $G = 9.82$, $P < 0.01$ for the 6-10 day period), suggesting that absence from the nests affects the probability of remaining on them.

This test measures the effect of absence from the nest; however, since each period away from the nest was about 5 days, it does not directly measure true time away from nests. Each of these individual tests might represent a mere five-day absence to the spider, whether five or 30 days from the initial removal. Individuals away from the nests 15 and 30 days from the initial removal were used to compare these effects (Fig. 1). They revealed no clear difference, falling very close to the periodic removals at 11-15 days ($G = 0.03$, $P > 0.8$) and not

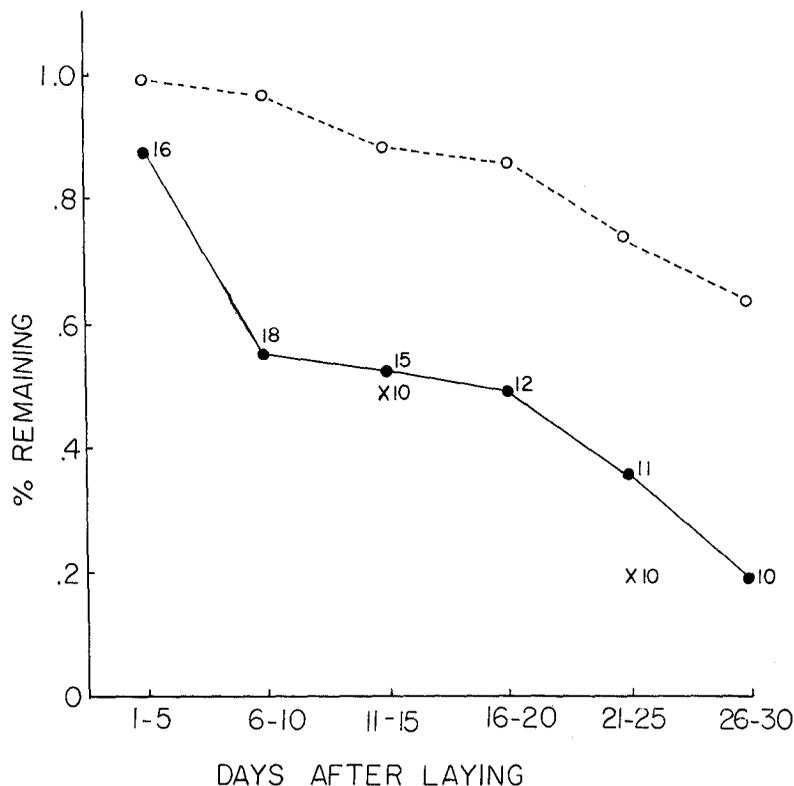


Figure 1.—Percentage of spiders remaining on their nests for one hour after being separated from these nests for five-day intervals (filled circles), percentage remaining for one hour if separated for 11-15 or 21-25 days (x's). Numbers to right of symbols are *N*'s. Percentage of 37 unscreened nesting individuals remaining on nest at the same time in the study area (open circles).

significantly different at 21-25 days, at a time that the tendency to remain at the nest was dropping rapidly ($G = 0.70$, $P > 0.3$).

Experiment 13. Tenure times of natural and cross-fostered spiders.—The cross-fostered individuals remained on their new nests for a period similar to that of undisturbed spiders ($\bar{x} \pm SD = 29.3 \pm 11.7$ vs 27.6 ± 13.3 days, $N = 40, 30$; $P > 0.5$ in a two-tailed Mann-Whitney *U*-Test). This result further supports the conclusions from Experiment 2. Thus, both Experiments 1 and 2 are probably typical of the results that would be obtained if they were to be run for more than one hour.

DISCUSSION

The response of *Misumena vatia* to these stimuli does not appear to be individual-specific, or even species-specific. It appears related to shape and tactile characteristics. The difference in activity between spiders returned to their own nest or placed on a conspecific's nest appeared to be related to the presence or absence of silken lines to adjacent leaves. Active individuals spent much of their time spinning these lines. The response of the spiders to a variety of different stimuli suggests that multiple factors play a role in nest retention. Leaves turned under by other spiders, leaves with spider nest silk affixed to them, and

artificially constructed nests (Experiments 4-6) all elicited a much more frequent response than did unaltered leaves (Experiment 3), although not as strong a response as to complete nests (Experiments 1 and 2). Resemblance of other spiders' nests to one or both cues was probably the key factor in determining how *M. vatia* responded to them (Experiments 7-9). The frequency of the response could be a consequence of either the characteristics of the silk, or of its volume. *Enoplognatha ovata* nests are extremely pliable in comparison to the other nests, especially the *M. vatia* nests, probably because members of this species apply less silk to the outside of their nests than do the others. If *M. vatia* respond primarily to tactile cues, they might perceive *E. ovata* nests as quite different from their own. Alternatively, the spiders may have responded primarily to the shape of the nests. This explanation is supported by their relatively strong response to the artificial nests.

Does the ability to reclaim a lost nest site have any selective significance, given that individuals normally occupy their nests continually, so that site tenacity itself might normally suffice to insure continuous occupation? Several factors may result in short-term disappearance, and, with the advantage that guarded nests produce more offspring than unguarded ones (Morse in press), reoccupation should be favored. I have observed several instances of temporary disappearance of *M. vatia* females from their nests in response to potential predators of either the spider or the egg mass. In 1983, several egg masses were attacked by an unknown predator. Two females that disappeared from their nest plants at this time returned to their nests within a day and resealed them tightly with silk. Spiderlings subsequently emerged from remaining uneaten eggs in both nests. Another spider was driven from its nest by ants (*Formica* sp.) shortly after completing it. It left the plant at this time, but reoccupied its nest within a day. Deer (*Odocoileus virginianus*) occasionally feed on milkweed in small amounts (Wilbur 1976), and I have had one spider nest inadvertently consumed in this way. Another nest plant was badly damaged at the same time, and the spider disappeared in the process. However, it reappeared the following day and secured its badly damaged nest in a way that protected it through the rest of the nesting period.

Individuals that have left their nests occasionally occupy other individuals' nests, thereby confirming the experimental results demonstrating that site tenacity was not confined to individuals' own nests. I have recorded two instances in which marked individuals have occupied nests earlier abandoned by other individuals. I also have one record of a displaced *M. vatia* occupying a *X. emertoni* nest.

These observations support the experiments, suggesting that displaced spiders sometimes find their way back to their nests, but that any such ability results from a general response that may produce an inappropriate relocation. Since the spiders are usually sedentary at this time and do not nest at high densities, most reoccupations are likely to occur on their own nest.

The decrease in acceptance of nests over time by the bagged individuals closely matched the disappearance of undisturbed spiders from their nests (Morse 1987). This result suggests that the removed individuals' behavioral patterns are relevant to those of undisturbed guarding spiders. The similarity in responses of individuals periodically returned to their nests and those only returned a single

time suggests that the tendency to reoccupy a nest is not related to time away from a nest, but to the actual condition of the spider.

ACKNOWLEDGMENTS

I thank J. P. Hailman, C. S. Hieber, R. A. Jackson, G. Rosenqvist, and J. K. Waage for comments on the manuscript. G. B. Edwards kindly identified the jumping spider. E. B. Noyce and the National Audubon Society generously permitted use of their properties. S. Chang, J. M. Cleaveland, K. Hayford, A. Kahn, M. Memmott, E. K. Morse, J. R. Morse, W. P. Morse, S. Schrag, and M. Spitzer assisted with the experiments. This work was supported by the National Science Foundation (BSR81-18105-AO1 and BSR85-16279).

LITERATURE CITED

- Morse, D. H. 1985. Nests and nest-site selection of the crab spider *Misumena vatia* (Araneae, Thomisidae) on milkweed. *J. Arachnol.*, 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. *J. Arachnol.*, 15:193-204.
- Morse, D. H. Nesting success of the crab spider *Misumena vatia* and its relationship to earlier patch-choice decisions. *Ecology* (in press).
- Stearns, S. C. 1976. Life history tactics: a review of the ideas. *Quart. Rev. Biol.*, 51:3-47.
- Stearns, S. C. 1977. The evolution of life-history traits: a critique of the theory and a review of the data. *Annu. Rev. Ecol. Syst.*, 8:145-171.
- Tinbergen, N. 1951. *The Study of Instinct*. Clarendon Press, Oxford.
- Trivers, R. L. 1972. Parental investment and sexual selection. Pp. 136-179, *In Sexual selection and the descent of man, 1871-1971*. (B. Campbell, ed.). Aldine, Chicago.
- Trivers, R. L. 1974. Parent-offspring conflict. *American Zool.*, 14:249-264.
- Wilbur, H. M. 1976. Life history evolution in seven milkweeds of the genus *Asclepias*. *J. Ecol.*, 64:223-240.
- Wilson, E. O. 1975. *Sociobiology*. Harvard University Press, Cambridge, MA.
- Wise, D. H. and P. R. Reillo, 1985. Frequencies of color morphs in four populations of *Enoplognatha ovata* (Araneae: Theridiidae) in eastern North America. *Psyche*, 92:135-144.

Manuscript received June 1988, revised September 1988.