HOMING BY CRAB SPIDERS *MISUMENA VATIA* (ARANEAE, THOMISIDAE) SEPARATED FROM THEIR NESTS

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Abstract. Nest-guarding female crab spiders *Misumena vatia* sometimes become displaced from their nests on milkweed leaves. Experimentally displaced individuals usually found their way back to their nests if put at the bottom of the stem containing their nest, even though they had no silken lines to guide them. In repeat runs they performed similarly, although returning more rapidly than in the initial runs. Spiders displaced several cm from their nests recruited to them much less successfully than spiders at the base of the stem. Finding lost nests may be important because more offspring survive in guarded nests than in unguarded ones.

The advent of parental care presents the parents with a number of problems. One is to provide for their own young, because an individual typically negates its fitness by tending unrelated offspring. Solutions to this problem might either be direct, as in identifying one's own young, or indirect, as in locating a rearing site, such as a nest (Beer 1970; White 1971). If the parents provide extended care, they may have to forage for themselves or for their young. Hunting for food may present another problem, returning to the site at which offspring have been left. Many of the classic homing experiments test returns to nest sites, and both olfactory and visual cues have been implicated (e.g., Tinbergen 1951; von Frisch 1967). As an alternative to recognition of young or site, parents may remain in contact with offspring throughout the period of care. In the latter instance, parents may not have a well-developed recognition of either their site or offspring (Morse 1989). If such animals become accidentally displaced they may have only a limited ability to relocate their sites, which may have serious consequences for their offsprings' success.

Crab spiders *Misumena vatia* (Clerck) provide an opportunity to explore and test the responses of displaced individuals that normally do not stray from their nest site. They lay a single clutch of eggs (Gertsch 1939; Morse 1988), which they guard, often until the young emerge from the egg masses nearly a month later (Morse 1987). However, some individuals disappear from the nest sites before their young emerge. Probably about half of these adults die of senescence, and the other half leave, or, occasionally, are preyed upon at the nests (Morse 1987). Some of the spiders that leave appear to become accidentally separated from their nest sites (Morse 1989). Displacement might occur if they are attacked or otherwise disturbed and drop from the nest without laying down silken lines as they do at other times. Occasionally the spiders resort to this behavior when handled by humans, and under natural circumstances ants may cause the spiders to give this reaction (Morse 1989), although they usually do not nest in the presence of aggressive ants. As a result, the spiders contact the ground stratum without a line to retrace to their previous site. Without a line, their ability to find their nest may be compromised. These matters are important to the spiders, because guarded nests are more successful than unguarded ones (Morse 1987, 1988, in prep.). The present study tests the ability of individuals separated from their nests to return to them, both with and without previously deposited silken drag-lines.

METHODS

I carried out these studies in a field in Bremen, Lincoln Co., Maine. I have described this area in detail elsewhere (Morse 1979, 1981). During the summers of 1988 and 1990 I tested the ability of post-reproductive brooding spiders to find nest sites from which I had displaced them. Since nest sites on nonflowering common milkweeds *As-*

Table 1.—Performance of nest-guarding spiders placed at various sites. a = Results in 1988 and 1990 did not differ significantly, so data pooled. b = This individual did not return to nest on either first or second run. c = Does not include one individual that did not return. d = Data from 1990 only. e = Does not include 10 individuals that did not return.

Manipulation	N	Return to nest	Did not return to nest	Time to return	
				N	S ± SD
Placed at bottom of nest stem[a]	30	26	4	14	40.0 ± 32.4
Placed at bottom of nest stem a second time[d]	15	14	1[b]	14	27.6 ± 23.6[c]
Placed on substrate[a]	30	12	18	5	75.8 ± 42.3[d,e]

clepias syriaca L., the most commonly used locations in the study area, averaged over 50 cm above the ground, and nests on flowering milkweeks over 80 cm (Morse 1985), cues to the presence of their nests may be obscure or nonexistent from the substrate below.

I placed spiders that were about to lay (Morse 1988) on the upper leaves of nonflowering milkweed plants and then put cages (50 cm × 50 cm × 150 cm) of 0.2 cm × 0.2 cm metal screening over these plants. The spiders always lay at night, usually one to three days after being placed on those sites (Morse 1985). In this set of experiments I only used spiders that laid on the night following placement in the cages, thereby minimizing the probability that they would produce a silken thread between the substrate and the nest. In observations made in this and other studies, spiders that laid on the night following release invariably remained on the leaves of the upper parts of the plants, and all observed shifts in site took place at that height. Several individuals began to manipulate their nest leaf within a few hours (see Morse 1985) and subsequently confined their activity to that leaf. Individuals that moved to the substrate or the screening of the cage laid on a subsequent night and were thus not included.

I removed post-reproductive individuals (not over four days after laying) from their nests and released them in two different places: 1) at the base of the stems on which their nests were placed, and 2) one (1988) or two (1990) days later, in the grassy substrate underneath these plants at the outer edge of the area covered by the nest-stem's leaves. Distances of releases from the stems of the spiders' nest plants using the latter criterion (lengths of longest leaves) averaged 12.1 ± 1.5 cm (measured only in 1990). Individuals placed on the stems in 1990 were run on the

stems in the same way a second time one day later. This manipulation provided a comparison with the initial run, the difference being the presence of a silken thread on the stem. All of the 1990 spiders were placed in the substrate one day after the second run on the stems to test their ability at finding the stem of their nest plant.

In testing responses of spiders put at the bottom of their nest plants, I assumed a 50:50 probability that they would move up the stems toward their nests by chance. This was a reasonable assumption, given that they were placed in contact with the stem, and that approximately half of the path directions available to them if they moved forward would subtend the stem immediately in front of them.

RESULTS

Brooding spiders displaced to the base of the stem of their nest plant returned to their nests more frequently than predicted by chance over a two-hour period, assuming a 50:50 predicted level of choice, as above (Table 1: $Z = 3.83$, $P < 0.001$ in a one-tailed binomial test). Individuals run a second time on the following day performed equally accurately (Table 1). Further, they returned to their nests significantly more rapidly on the second day than the first (Table 1: $T = 16\frac{1}{2}$, $Z = 2.027$, $P < 0.02$ in a one-tailed Wilcoxon signed ranks, matched pairs test). This difference could have been a response to the threads that the spiders laid down on the stems during the previous day's ascent. Since I initially placed these individuals on the plants shortly before they deposited their egg mass, they were very unlikely to have had access to a line on their first run.

These spiders were then placed on the substrate under the outer extremity of the leaves of the nest plant, but nearer to its stem than to any

other milkweed stem. They returned to their nest significantly less frequently from here than from the base of the stem (Table 1: $G = 14.92$, $df = 1$, $P < 0.001$ in a G-test). Further, the four individuals that failed to find their nests from the bottom of the stem in the first test (Table 1) also failed to find their way to the stem in this test.

DISCUSSION

These spiders clearly have well-developed abilities to respond to displacement on the nest plant. Simply moving upward on the stems would suffice if they drop to the base of the stem, because they will soon reach nest height, where parent spiders almost invariably lay down lines among the nest leaf, adjacent leaves, and stem proper (Morse 1985). This architecture results from the periodic movements that the spiders make in the immediate vicinity of their nest site, laying down lines in the process, as a result securing the nest tightly to the surrounding vegetation. In many instances a line would naturally extend from the bottom of the stem to near the top, a result of the spider's initial recruitment onto the plant. However, if they moved from the leaf of an adjacent plant, no such line would exist. The present experiments attempted to eliminate the question of initially using lines by placing the spiders onto the sites just before they built their nest. The shorter recruitment time on the second runs suggested that a line, when present, hastened movement to their nest, although it did not eliminate the possibility of experience playing a role.

The spiders responded significantly more poorly to greater displacement, suggesting that falling off a plant without using a line is a drastic action. Spiders do not appear to take this option frequently. Under natural conditions, aggressive ants may prompt this response most often. The only ants observed to attack the spiders (*Formica* sp. L.) have a patchy distribution in the study area, and the spiders do not appear to build their nests at sites frequented by them. However, nesting spiders may not always be able to avoid ants, because if aphids recruit to plants after the spiders choose their nest sites, ants may recruit in turn in response to the aphids.

Although some of the spiders displaced in the substrate might eventually have found their nests, occasional observations of individuals naturally displaced from their sites shortly after laying, and showing no signs of hunting, suggest that these spiders may frequently be unable to relocate their nests. Four such individuals located on vegetation 30–100 cm from their nests for either two or three days were placed back on their nests, and three of them remained there for one day or more, strongly suggesting that although the propensity to guard remained, they did not have the ability to relocate their nests (Morse 1987). Given the demonstrated importance of guarding (Morse 1988), even moderate periods of absence from these nests may appreciably increase the chance of failure.

The performance of these post-reproductive spiders is profitably compared with results from analogous experiments run on pre-reproductive adult female spiders searching for hunting sites on flowering milkweed stems (Morse in progress). In contrast to the 26 of 30 post-reproductive spiders finding their nest sites (Table 1), only 16 of 32 pre-reproductive individuals selected flowering stems when they were placed on the base of them ($G = 10.05$, $df = 1$, $P < 0.01$ in a G-test). These results suggest that the parents' success in relocating their nest sites involved traits missing or poorly developed in the pre-reproductive individuals. In contrast, post-reproductive individuals placed on the substrate did not differ in nest-finding success from pre-reproductive individuals finding stems with satisfactory hunting sites on the flowering plants [12 of 30 post-reproductive individuals successful (Table 1), vs. 34 of 76 pre-reproductive spiders: $G = 0.20$, $df = 1$, $P > 0.5$ in a G-test].

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