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EGG SAC RECOGNITION BY FEMALE *MIAGRAMMOPES ANIMOTUS* (ARANEAE, ULOBORIDAE)

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ABSTRACT. After producing a cylindrical egg sac, a female *Miagrammopes animotus* holds it until spiderlings emerge and disperse. When sacs were taken from females, these females exhibited a putative searching behavior and, upon contacting either their sacs or those of conspecifics, exhibited a putative recognition behavior. These responses would cause a female to search for and reclaim her sac if it were temporarily abandoned during feeding or web construction. Females with sacs did not respond positively to sacs from which spiderlings had emerged. Females that did not have sacs did not respond positively to viable sacs. Females separated from their sacs for increasing time periods exhibited a decline in positive responses to their sacs. Thus, contact with the sac appears necessary to maintain an affinity for the sac during the development of spiderlings.

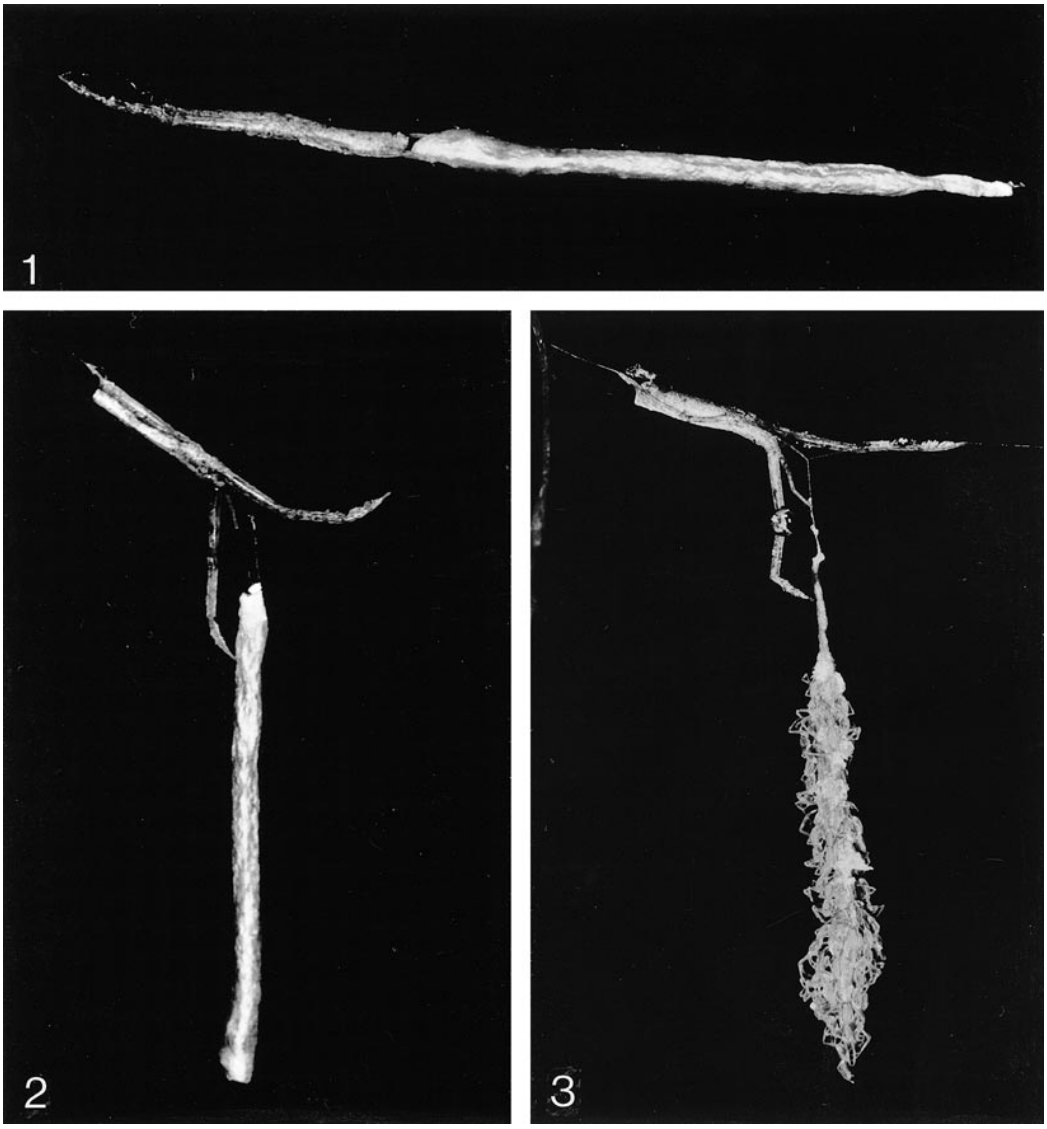
Keywords: Maternal care, spider

Females of the simple-web species *Miagrammopes animotus* Chickering 1968 produce cylindrical egg sacs consisting of two columns of eggs surrounded by two thin layers of silk (Lubin et al. 1978; Opell 1984). During the day, a female attaches her egg sac along one of the web's non-sticky lines and aligns herself with the egg sac, her abdomen touching the egg sac, her legs I and II extending directly anteriorly, and her legs III and IV extending directly posteriorly (Fig. 1; Lubin et al. 1978; Opell 1989a). This posture enhances the twig-like appearance of both the female and her egg sac. *Miagrammopes animotus* females range in color from light tan to dark, reddish-brown and produce egg sacs whose wrapping silk is similar in color to their bodies (Opell 1989a). This makes it even more difficult to distinguish a spider and her egg sac and further enhances the cryptic appearance of each.

At dusk a female detaches her egg sac from the line and holds the sac with her first leg as she monitors her web (Fig. 2; Lubin et al. 1978; Opell unpubl. obs.). This suggests that her linear, day-time posture is a defense against visually hunting predators like insects and birds. When spiderlings emerge from an egg sac as second instars, they lack functional cribella and cling to the egg sac for several days until they molt to the third instar (Lubin et al. 1978; Opell 1989b), at which time they disperse and begin constructing capture webs. Females continue to tend their egg sacs until spiderlings leave (Fig. 3).

While collecting *M. animotus* in conjunction with studies of their cribellar threads and cribella, I routinely collected females with egg sacs. When I attempted to remove a female's egg sac so that I could weigh and measure her, she held tenaciously to her egg sac. Unless all of her legs were removed from the egg sac, she quickly regained her firm grasp. After I separated a female from her egg sac and placed her on a horizontal surface, she walked rapidly and made broad, rapid sweeping movements with her first legs. When she contacted her egg sac, she held it tightly with her first two pairs of legs, immediately pressed her chelicerae to its surface for a few seconds (although I could not determine if she bit the egg sac's silk covering), and then immediately firmly grasped the egg sac with her first and second legs. When a female with an egg sac was placed on a horizontal surface, she often attached a dragline to her egg sac and walked away, possibly searching for a secure site to climb. When either the egg sac or dragline was touched, the female ran quickly to her egg sac, pressed her chelicerae to its surface and then grasped the egg sac.

I interpreted this rapid walking and leg waving behavior as searching behavior, the cheliceral contact as egg sac evaluation be-



Figures 1–3.—*Miagrammopes animotus* females tending egg sacs during the day (1), at night (2), and after spiderlings have emerged (3).

havior, and the subsequent grasping of the egg sac as positive egg sac recognition. To better understand this behavior, I evaluated the responses of females that had no egg sacs, investigated the specificity of egg sac recognition, and determined if this behavior was expressed after a female had been separated from her egg sac for different lengths of time.

METHODS

Spiders and egg sacs were collected at the Center for Energy and Environment Research's El Verde, Puerto Rico field station. Voucher specimens are deposited in Harvard University's Museum of Comparative Zoology. All observations were made in a windowless laboratory that was illuminated by fluorescent lights and had a temperature of 20–24 °C and a relative humidity of 60–63%.

After removing a female's egg sac, I placed each in a separate, clean glass vial stoppered with a cotton plug. A small piece of moist cotton was placed with each spider. Vials were numbered so that I could identify each spi-

der's egg sac, though only by referring to a record book. Observations were conducted by placing a female in a clean, 40 mm diameter aluminum weighing pan and observing her response to an object or an egg sac. I define a positive response to an object or an egg sac as the female clinging tightly to the object after contacting it with her chelicerae so that she could not be easily dislodged by repeated prodding with a small artist's brush. Occasionally, a female rested momentarily on an egg sac or object, but did not bring her chelicerae to its surface. In these cases a light prod with a brush caused her to leave the object and continue walking and I scored this as a negative response.

I examined the duration of egg sac recognition in 82 females that were collected with egg sacs. After removing their egg sacs, I kept these spiders for periods of 5–25 h. At the end of each of these 21 periods the responses of 2–10 females to their own egg sacs were observed. Thirty-four of the females that responded positively to their egg sacs were used for a second trial after each was kept in a vial with her egg sac for 12–24 h to permit prolonged contact with her sac.

RESULTS

Eleven mature females that had no egg sacs, including five whose abdomens were clearly swollen with eggs, did not cling to egg sacs or press their chelicerae to their surfaces when each was presented with 7–10 egg sacs of conspecifics, nor did they cling tightly to pieces of grass or cotton that I placed in their collecting vials. In contrast, 26 of 32 females whose egg sacs were removed 5–6 h earlier responded positively to their reintroduced egg sacs. The response of each group differed from a null model in which 50% of the individuals responded positively to egg sacs (χ^2 = 11.0 and 12.5, respectively, $P < 0.001$).

Two females that responded positively to their own egg sacs also responded positively to egg sacs produced by nine other females. Seven females that responded positively to their own egg sacs also responded positively to an egg sac of the closely related species *M. pinopus* Chickering 1968 from St. John, U.S. Virgin Islands. However, they did not respond positively to a piece of cotton, a section of wooden applicator stick similar in size to an egg sac, or to an egg sac of *Uloborus glomosus* (Walckenaer 1841) from Blacksburg, Virginia. Another five females that responded positively to egg sacs that contained eggs responded negatively to egg sacs from which spiderlings had emerged, walking over these egg sacs and continuing to exhibit searching behavior.

Figure 4 shows the percentages of females that responded positively to their egg sacs after times of increasing separation. In each of the first six time intervals, the responses of females used in a second trial did not differ from that of females that were used in only one trial ($\chi^2 < 0.425$, 1 *df*, $P > 0.50$). However, in the last interval (23–25 h) five of the six females used in a second trial responded positively to their egg sacs, a greater number than predicted by the responses of females used in only one trial ($\chi^2 = 16.000$, 1 *df*, $P < 0.001$). The median time of these seven periods regresses against the percent positive response ($Y = -2.06X + 92.92$; $F = 8.20$, $P = 0.035$, $R^2 = 0.62$), indicating that a female's ability to identify and respond to her egg sac decays with increasing separation. Additional support for this decay comes from a comparison of the responses when grouped into short, intermediate, and long periods of egg sac separation (5–9 h, $n = 35$; 10–20 h, $n = 48$; and 21–25 h, $n = 33$; respectively). For this comparison, I determined the mean positive response for each of the 21 hourly trials and then compared the grand means of responses in the three periods. A Kruskal-Wallis test showed that the values of these periods (X ± 1 SD: 78.7% ± 19.7, 66.0% ± 27.4, and 38.9% ± 7.9, respectively) differed ($\chi^2 = 6.47$, $P = 0.039$).

DISCUSSION

These observations indicate that sensory stimuli from one or several sources unique to oviposition or egg sac construction cause persistent but reversible changes in a spider's physiology that alter its response to egg sacs. Possible sources of these stimuli include the pressure exerted on the oviducts as eggs pass through them and the activation of tubuliform silk glands and spigots that, in uloborids, appear to be used only for egg sac production (Kovoor 1977; Foelix 1996; Opell 1984). Copulation is an unlikely source of stimuli, as females store sperm and mating may occur long before eggs are fertilized and deposited.

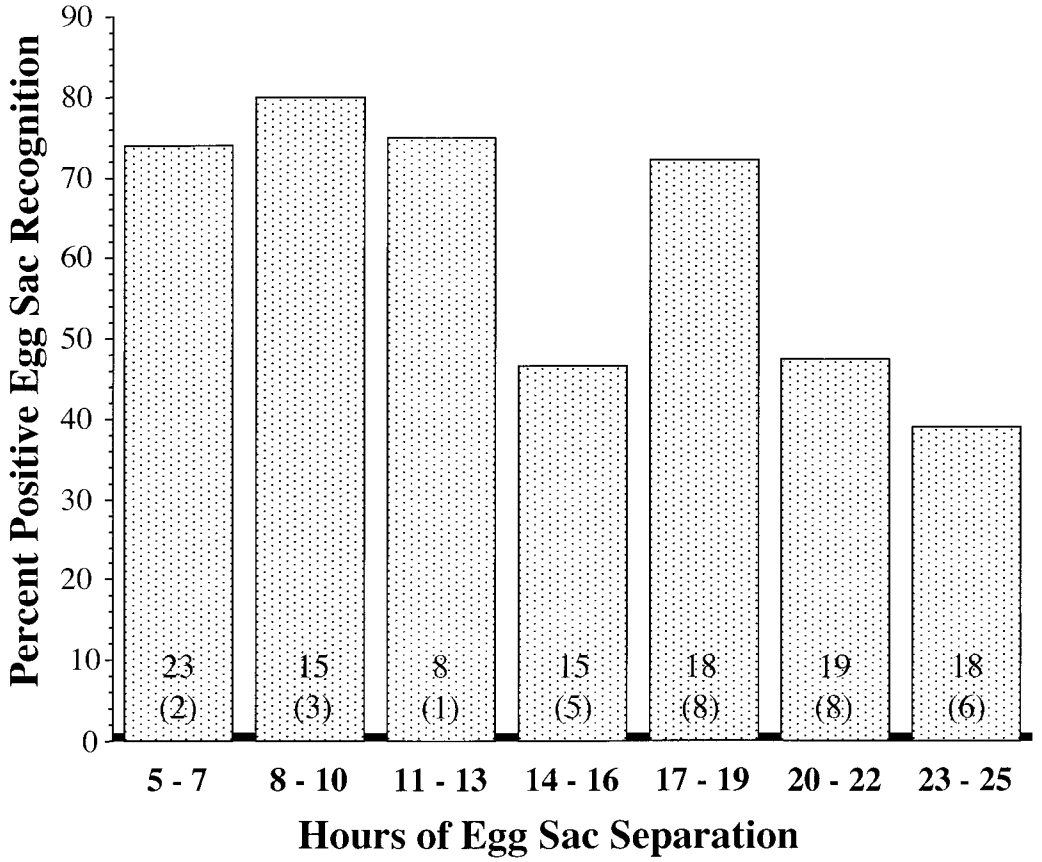


Figure 4.—Positive egg sac recognition following periods of increasing separation of a female and her egg sac. Bars represent the means of the three-hour periods. The sample size is given within each bar. The number of females used in a second trial is given in parentheses.

Once a positive response to an egg sac has been established it appears to be general and does not permit a female to distinguish her egg sac from those of conspecifics. However, unlike wolf and fishing spiders, *M. animotus* females can not be tricked into accepting substitute objects (Gertsch 1979; Foelix 1996). Egg sac recognition persists for varying periods of time, but lasts long enough to cause a female to search thoroughly for her egg sac if she left it. The regression formula for the decay of positive responses to egg sacs suggests that egg sac recognition disappears in all females after they are separated from their egg sacs for about 45 h. Continual or frequent contact with an egg sac appears to be necessary to maintain a female's positive response to her egg sac during the approximately 20 days required for the eggs to develop and the spiderlings to emerge from the egg sac (Opell 1979, 1982; Peaslee & Peck 1983).

Unlike members of other uloborid genera, *Miagrammopes* females have no permanent attachment site for their egg sacs. At night females probably temporarily attach the egg sac to a line while renewing their capture webs and feeding. This behavior has not been observed in *M. animotus*; but Lubin et al. (1978) report that females of an unidentified *Miagrammopes* species hung their egg sacs from threads at night and resumed prey capture activity until dawn, at which time they again tended their egg sacs. Egg sac recognition would cause a female to search for her egg sac if she were forced to abandon it during the day or to anchor it while building or repairing her capture web at night.

I did not investigate cues that might permit

females to distinguish viable egg sacs from those that the young have abandoned. The masses of viable and empty egg sacs differ; but, in my laboratory observations, females did not appear to lift egg sacs to assess their masses. Second instar spiderlings may deposit silk on the egg sac's outer surface and this may mask the egg sac silk that allows a female to identify an egg sac. Alternatively, the female may identify and respond negatively to the silk of these spiderlings.

The loss of egg sac recognition has advantages for *M. animotus* females that appear to produce several egg sacs during a lifetime and often reach high densities. A female's negative response to an egg sac from which spiderlings have emerged and dispersed allows her to shift her activity from egg sac tending to web building and foraging so that another egg sac can be produced. This negative response may also reduce intraspecific conflict. At El Verde, I often observed 3–5 mature females on a single under-story plant or cluster of vegetation occupying a space of about 1 m^3. Under these high densities, the loss of egg sac recognition would eliminate contests between females that were tending egg sacs and those from whose egg sacs spiderlings had recently dispersed. In the absence of individual-specific egg sac recognition, the failure of females to respond to old egg sacs also assures that they will not mistakenly abandon viable egg sacs for these discarded egg sacs that sometimes remain suspended from vegetation.

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