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MOTHER-OFFSPRING FOOD TRANSFER IN *COELOTES TERRESTRIS* (ARANEAE, AGELENIDAE)

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Abstract. Three different modes of maternal food supply have been reported in the subsocial agelenid species *Coelotes terrestris*: prey provisioning, consumption of the mother's body, and regurgitation of nutritive fluids. Although the first two modes are well documented, the latter is not fully assessed.

By comparing—in the absence of any prey—the weight variations in spiderlings either left with their mother or isolated, and by simultaneously comparing the weight variations of mothers, either isolated or left within the group of spiderlings, it was possible to see evidence of a significant and long-lasting food transfer from the mother to her progeny. This food transfer probably explains the high level of survivorship and reduction of cannibalism showed by broods left with their mothers.

Close observation provided no direct evidence of mouth to mouth transfer. Rather, the food transfer appears to involve the production and emission of miniature eggs by the mother when in presence of spiderlings, a phenomenon which to date seems not to have been noted among spiders.

Providing offspring with food is one of the most important features of parental care, in that it spares the young the many risks related to food supply (Wilson 1971). In spiders, food may be provided by the mother in various forms. The yolk contained in the egg ensures the beginning of the spiderling's development during its life inside the egg sac and the few days following its emergence (Foelix 1982). This supply can be supplemented, in several species, by oophagy of non-hatched eggs inside the egg sac (Schick 1972; Valerio 1974). In a certain number of species, the mother provides food to a greater extent. Her body may be a usual, or occasional, resource for her progeny (Bristowe 1958; Cloudsley-Thompson 1955; Kullmann 1972; Seibt & Wickler 1987; Tahiri et al. 1989). Provisioning has also been reported, either in the form of prey items subdued by the mother and carried to the brood (Brach 1976; Hirschberg 1969; Gundermann et al. 1988; Tretzel 1961) or of fluids regurgitated to the spiderlings (Locket 1926; Kullmann & Zimmermann 1974). These fluids may be the result of the partial digestion of the prey, or sometimes, a production of the mother's digestive tract (Nawabi, cited by Collatz 1987).

We are currently studying the mother–young interactions related to food in a European subsocial species *Coelotes terrestris* (Wider) (Krafft et al. 1986), in particular the three modes of food supply previously reported by Tretzel (1961): prey provisioning (Gundermann et al. 1988), mother's consumption (Gundermann 1989) and regurgitation. This last mode is poorly documented. Tretzel (1961) referred, for this species, to only one definite observation, and our own observations are rare and dubious. Such a situation could be explained, either by the actual scarcity of the phenomenon—which would then lead to question its functional significance—or by its localization during the nocturnal phase making the observations difficult. Thus, the very first step of the study, as exposed in the present paper, was to demonstrate the existence of a significant food transfer from the mother to her offspring, and to try and find out its nature.

MATERIALS AND METHODS

The funnel-web agelenid *Coelotes terrestris* is a terricolous spider common in European woodlands. The female weaves a silken tube under stones, bark of dead logs, etc. From a lenticular egg sac, 40 to 60 spiderlings emerge, stay in a group inside the tube with their mother for about one month, and then disperse and lead a solitary life (Tretzel 1961; Gundermann 1989).

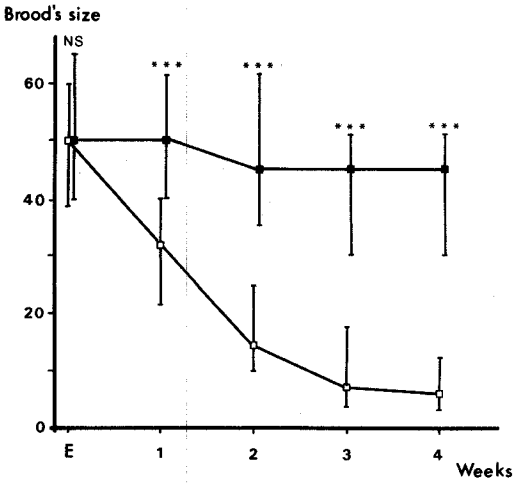

Figure 1.—Weekly variations of the broods' sizes (median, quartiles). Open squares = treatment A (N = 17): orphaned brood; solid squares = treatment B (N = 17): brood left with mother. E.: Emergence day. Mann-Whitney U-test: ns, non significant; *** $P < 0.001$.

In the present study, field inseminated females were collected, then reared in the laboratory in plastic boxes (15 × 9 × 7.5 cm) with transparent sides and a bottom covered with a mixture of sand and peat which was regularly moistened. The rearing boxes were kept in a closed room, at a temperature of 21 °C (±2 °), fluorescent lights providing a light of about 100 lux (12 L/12 D).

Two experiments were designed:

1—In the first experiment, it was hypothesized that if a food transfer did exist from the mother to her young, spiderlings left with their mother should present higher weights than orphaned spiderlings, while mothers left with their young should present lower weights than isolated mothers.

The experiment started from the broods' emergence (most of them occurred within 2 weeks) and lasted 4 weeks. Throughout that time, all the spiders were deprived of prey. Egg sacs were randomly assigned to one of two treatments:

—Treatment A (N = 17): mothers and young separated;

—Treatment B (N = 17): mothers left with their young.

Mothers and broods were weighed, first just after emergence, then at the end of each week. In order to minimize disturbance of the brood, each weighing was limited to a sample of 10 spiderlings collected, as randomly as possible, by aspiration using a pipette. The brood's weight was estimated by multiplying the individual mean weight (given by the sampling) by the number of spiderlings still alive. At the end of the experiment some broods' sizes fell below 10 individuals; in this case, of course, the totality of the brood was weighed.

2—The second experiment was designed to get further information by trying to enhance mother–young interactions. Ten groups of three day old spiderlings were separated from their mothers for 24 h without any food. The subsequent reunion of the mother with their young were thoroughly observed and videorecorded.

RESULTS

Survivorship.—Orphaned broods (treatment A) showed a very poor survivorship: at the end of the experiment, the median rate of survivorship (number of spiderlings still alive/initial size of the brood × 100) fell to 12.5% (quartiles: 6.3–25.5). In contrast, survivorship stayed high in treatment B (median rate: 81.8%, quartiles: 76.6–88.5). Actually the difference between the broods' sizes of the two treatments was significant from the end of week 1 on (Fig. 1) (Mann-Whitney U-test, $P < 0.001$). Direct observations and the fact that no dead bodies could be found in the vials lead to attribute this differential mortality to a high incidence of cannibalism within orphaned broods.

Weights' variations.—Statistical analysis showed no significant difference between treatments A and B, on emergence day, for either the broods' as well as the mothers' weight (Mann-Whitney U-test, ns).

From the end of week 1 on, the estimated weights of the broods left with their mothers were significantly higher than those of the orphaned broods (Fig. 2a). The analysis of weights' weekly variations within each treatment (Table 1) shows that, while orphaned broods' weights (treatment A) decreased (Wilcoxon matched-pairs signed-rank test: $P < 0.002$ for weeks 2 and 3; $P < 0.001$ for week 4), weights of broods left with their mothers (treatment B) varied in the opposite direction (Wilcoxon test: $P < 0.002$ for weeks 1 and 2, ns for week 3, $P < 0.02$ for week 4).

The decrease in weight observed in treatment A can be accounted for by basal metabolism and, probably, by losses of material and energy brought about by high intrabrood cannibalism. On the

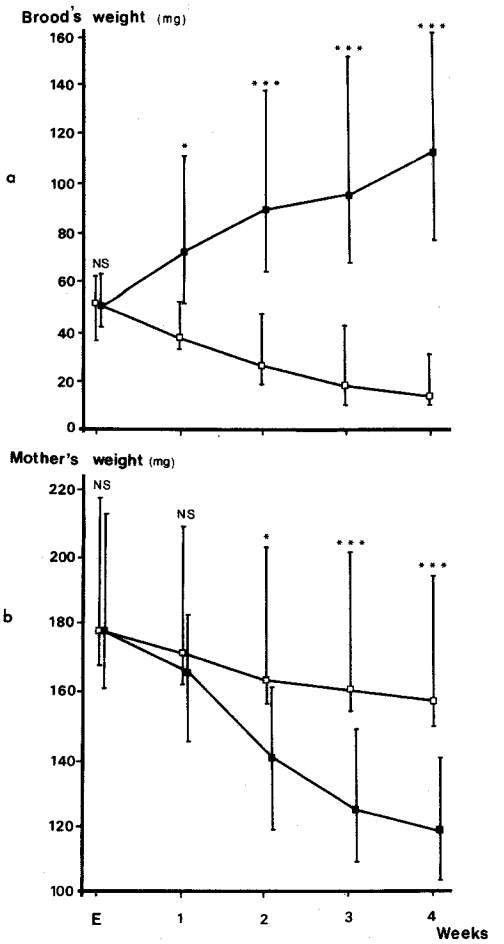

Figure 2.—Weekly weight variations in mg (median, quartiles). Open squares = treatment A (N = 17): orphaned brood; solid squares = treatment B (N = 17): brood left with mother. E.: Emergence day. Mann-Whitney U-test: * $P < 0.01$; *** $P < 0.001$. a = Brood's weight variations; b = Mother's weight variations.

other hand the low level of cannibalism in treatment B cannot explain the increase in weight observed in this treatment. Rather, the increase suggests that some sort of food is provided to the young by their mother.

This is confirmed by the study of the mothers' weight variations (Fig. 2b). From the end of week 2, treatment B mothers were significantly lighter than treatment A mothers. Furthermore, the comparison of the weekly losses in weight between treatment A and treatment B (Table 2) shows that, when left with their broods, the mothers suffered significantly more severe weight decrease than when isolated.

Modes of mother-young food transfer.—The maintenance of weight gain in broods left with their mothers over four weeks strongly suggested that the foods transfer should be a relatively long-lasting phenomenon. It was, thus, very unlikely to consist of mere regurgitation of fluids extracted from the prey eaten by the mother before the beginning of the experiment. The transferred food should, then, be produced by the mother herself.

Close examination of rearing boxes, using a stereomicroscope, showed, at times, spiderlings eating substances deposited on the web. These substances consisted of either clear yellow drops of liquid, or brownish compact clusters of more or less discernible eggs. The egg sizes varied greatly, but were always smaller (0.3–0.5 mm) than the normal ones (0.7–1 mm). Some of the egg-clusters were covered with a thin layer of silk, similar to the internal layer of the egg sacs.

The second experiment was aimed at directly observing the possible mother–young food transfer. Actually, the reunion of the mothers with their young after a 24-h separation did not induce any special reactions other than an intensive weaving activity of the mothers, except in one group in which the young, unlike the others, dis-

Table 1.—Variations of the broods' median weights per week, in mg (range), within each treatment. Treatment A (N = 17): orphaned brood; treatment B (N = 17): brood left with mother. Wilcoxon matched-pairs signed-rank test.

Treatment	Week 1	Week 2	Week 3	Week 4
Treatment A	−2.2	−11.9	−8.6	−2.8
Mothers isolated	(−47.3; +21.9)	(−32.7; +12.3)	(−29.2; +3.5)	(−23.4; +1.0)
P value 2-tailed	ns	<0.002	<0.002	<0.001
Treatment B	+19.2	+18.9	+7.0	+5.3
Mothers with broods	(−6.7; +71.9)	(−4.3; +72.1)	(−25.4; +38.3)	(−9.6; +31.6)
P value 2-tailed	<0.002	<0.002	ns	(0.02)

Table 2.—Mothers' median weight losses per week, in mg (range). Treatment A ($N = 17$): mother separated from brood; treatment B ($N = 17$): mother left with brood. Comparison treatment A vs. treatment B for each week: Mann-Whitney U-test.

Treatment	Week 1	Week 2	Week 3	Week 4
Treatment A	−6.8	−4.7	−1.8	−2.5
Mothers isolated	(−3.4; −10.6)	(0.9; −8.3)	(−0.3; −4.5)	(−1.4; −8.2)
Treatment B	−21.3	−24.1	−11.5	−6.0
Mothers with broods	(−5.9; −36.8)	(−15.0; −26.6)	(−7.0; −18.2)	(−3.7; −10.1)
P value 2-tailed	<0.02	<0.001	<0.001	<0.05

played a high level of activity and interacted frequently with their mother.

In this group, from the beginning, a few spiderlings followed their mother in her numerous movements and made attempts to come into contact with her, mainly in the direction of her hind-legs and opisthosoma (one of them was even observed hanging from a spinneret). About 2 h 30 min after the reunion, the first emission of substances took place with two more emissions being recorded within the following 10 min. As soon as the drops of substance were deposited on the substratum they immediately attracted groups of two or three spiderlings. During the last emission the orientation of the mother's opisthosoma made it possible to clearly observe the progressive exuding of substance from the vaginal opening. A spiderling, which had succeeded in climbing on to the opisthosoma, came to the vaginal opening, seized the small ball of substance and eventually took it away.

CONCLUSION

In *Coelotes terrestris* food is actually transferred from the mother to her young. This transfer occurs when no prey are available, even for several weeks, thus indicating that food is produced by the mother herself. Even though the digestive tract can not be definitely ruled out as a site of production, the ovaries appear to be playing a major role by producing miniature trophic eggs. Observations showed that these eggs are particularly attractive to the young and rapidly eaten. This might explain why they had not been noticed before.

Such a transfer of food is likely to enhance survivorship of young during food shortage in field conditions, at the expense of the mother's own survivorship. But the adaptive significance of this phenomenon remains to be more precisely assessed; some incidental observations suggest that food transfer could also occur in normally fed groups.

Further investigations are also required to find out the mechanisms involved in the process. To what extent is ovarian production continuous? Is ovarian physiology influenced by the presence of the brood? Does tactile (or other) stimulation of the mother by the spiderlings release the emission of ovarian substance, as suggested by our observations?

As far as we know, this mode of maternal feeding has never been previously reported in spiders, but can be related to a somewhat similar phenomenon described in the cricket *Anurogryllus muticus* (West & Alexander 1963). In this sub-social insect, after interactions between the nymphs and their mother (recalling those observed in *Coelotes terrestris*), the nymphs are provided with miniature eggs, that the authors liken to the trophic eggs of ants (Brian 1953; Wilson 1971). Actually, another mode of maternal feeding, not unlike what is here reported in *Coelotes terrestris,* has recently been observed in our laboratory (Tahiri et al. 1989). In two species of the genus *Amaurobius, A. ferox* and *A. fenestralis,* about 3 days after the emergence of the offsprings, the mother lays an egg mass deprived of any silken envelope which is immediately eaten by the spiderlings. This egg-laying appears to be systematic and to represent the only source of food for the young during the first ten post-emergence days. These findings, together with those of spiderlings feeding on eggs inside the egg sac (Schick 1972; Valerio 1974), suggest that egg cannibalism could play a significant role in the reproductive strategies of many spider species (see Polis 1981).

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