

Post-emergent behaviour of juvenile lycosid spiders¹

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Summary

Lycosid spiderlings spent most of their time on the female in the "settled" posture, which is probably an adaptation for maximum compactness and stability of the brood. After periods of water deprivation, in response to an undetermined stimulus, the young swarmed off the mother to drink. Under conditions of water availability, drinking by juveniles occurred as often as twice every three days. Return to the female seemed dependent on tactile cues, especially draglines that had been laid down by the spiderlings when dismounting.

When offered substitute parents, young readily settled on adult, female conspecifics carrying egg sacs. Less frequent settling occurred on unmated, adult, female conspecifics that had produced and discarded egg sacs. Adult, male conspecifics and congeners, and adult, female congeners were not settled.

After forced separation from their mother, spiderlings did not aggregate into clusters. They readily drank water and survived as well as siblings that remained on the female.

Introduction

Several weeks after construction of the egg sac, the female lycosid spider tears the equatorial seam with her fangs. She then remains inactive while the spiderlings emerge, climb onto her abdomen, and form a multi-layered mass. This intimate contact lasts until the spiderlings' yolk supply is depleted, at which time they disperse.

Eason (1964) reported a higher mortality rate in young lycosids removed from their mothers before the onset of dispersal than in those allowed to maintain their normal contact. This was not the case in Engelhardt's (1964) study. We decided to examine the question of whether survivorship of lycosid spiderlings depended on the mother's presence (in an

environment lacking predators). Also, we investigated the permanency of site selection by the young on the mother; the interactions between spiderlings and substitute parents other than those of the normal age, sex, and species; and the dismounting-remounting behaviour that is required for the drinking of water by the young.

General Methods

Species used included: *Schizocosa crassipes* (Walckenaer), *S. saltatrix* (Hentz), *Lycosa rabida* Walckenaer, and *L. punctulata* Hentz. Adult spiders were housed individually and observed in rectangular, plastic boxes (70 mm. x 125 mm. x 70 mm. high). Mealworm larvae (*Tenebrio molitor*) were used for feeding; water was available *ad libitum* from a cotton-stoppered vial. The laboratory temperature was $26 \pm 3^\circ$ (SD) and relative humidity, $54 \pm 12\%$ (SD). Carbon dioxide was used for anaesthesia, and camel hair brushes for handling the young. Although some females with egg sacs were collected in the field, most broods resulted from laboratory matings.

Behaviour of the Young with their Mother

Emergence and Site Selection

Emergence from the egg sac was observed in five broods of *L. rabida*. The female remained stationary, with her abdomen usually lifted high, so that the egg sac (attached to her spinnerets) did not touch the substratum. Sometimes pausing on the surface of the egg sac, the young then walked from the sac to the lateral, ventral, or dorsal abdominal surface. Spiderlings emerging later clung to the previous layer of young, the brood eventually covering the mother's abdomen with a multi-layered mass. Unlike the young of *L. rabida*, those of *S. crassipes* showed a tendency to settle on the dorsal surface of the abdomen first.

Postures

While on the mother, lycosid young occasionally adopted the "rest posture" but most typically maintained the "settled posture" (Fig. 1). In the rest posture the body was partly elevated and the legs extended so that each femur was raised less than 60° from the horizontal. This posture was assumed at the onset or termination of locomotion and is similar to that adopted by adult lycosid spiders.

¹Research supported in part by National Science Foundation Grant GB 35369 to J. S. Rovner.

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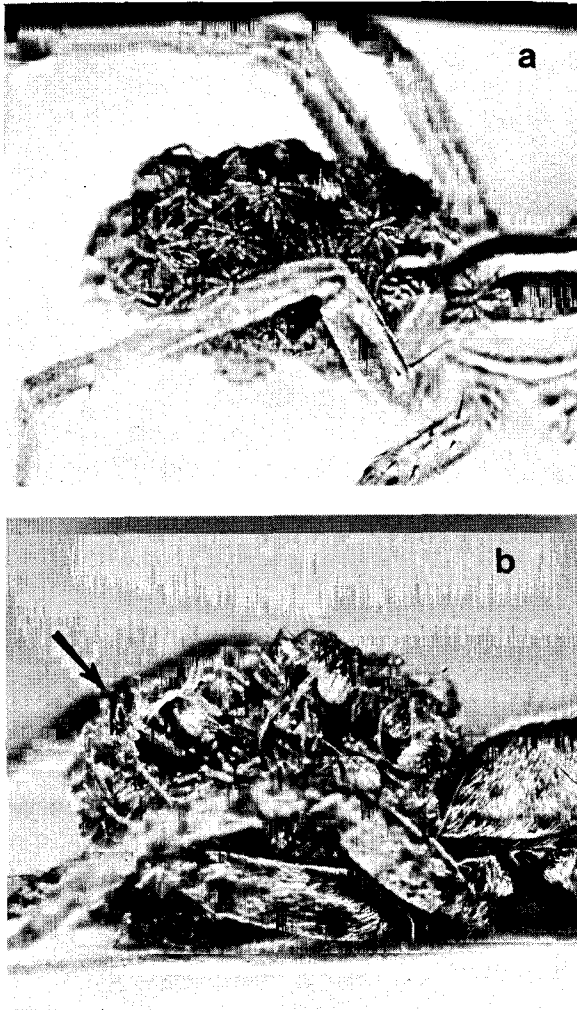


Fig. 1: (a) Brood of young *Lycosa rabida* on mother (x 3). All of the spiderlings on the abdomen are in the settled posture. (b) Brood of young *Schizocosa avida* on the mother's abdomen (x 4). One spiderling (arrow) is in the rest posture; the others are in the settled posture.

The settled posture was adopted for prolonged periods of attachment to the female (or to an inner layer of spiderlings). The spiderling's body was lowered and its legs drawn in tightly, so that the femora were almost perpendicular to the substratum. This resulted in the spiderling taking up less surface area than in the rest posture. In the outer layer, the spiderling's cephalothorax is pressed closer to the female's body, resulting in a kind of "headstand".

Changes in Site

During preliminary observations, we noted occasional shifts in location by young upon the female. Subsequently, in each of nine broods of *S. crassipes*, we tagged the abdomen of four randomly chosen individuals with non-toxic enamel and recorded daily the relative location of these spiderlings on a map of the female's abdomen. On the next few days after tagging, 27 of the 36 marked spiderlings were observed at sites other than the original ones adopted after tagging. Some individuals shifted two or more times, moving to new sites on the mother's abdomen or to a location on the inner surface of the cage. Often, the latter animals re-adopted contact with the mother.

Remounting

Three broods of *S. crassipes* and one each of *S. saltatrix* and *L. rabida* were separated from the female with a camel hair brush, all but *L. rabida* being done with the animals under anaesthesia. During remounting there was no obvious visual orientation by young to the female, nor was there any active adult behavioural assistance for remounting. Indeed, some spiderlings were flicked off when their mothers twitched the appendage contacted. The young returned to the mother's body by way of her legs or palps, or by climbing silk lines extending from her legs or body. The only oriented approaches to the female occurred when young returned via a dragline.

Drinking

Nine broods of *S. crassipes* were monitored for drinking. To establish whether the young engaged in drinking during periods when they were not being observed, spiderlings were given coloured water that later could be seen easily through the light areas of the carapace and dorsal abdomen. The solution was made of one part (by volume) food colouring and nine parts distilled water. Water colours were changed daily in the sequence of red, blue, and yellow. On the basis of abdominal colour changes, we estimated that some of the young left the female at least once every three days and some as often as twice every three days. (Exact numbers of young that drank could not be determined since we could not see individuals deep within the brood.)

Drinking of non-coloured water by spiderlings in

nine broods of *L. rabida* was observed on 18 occasions. A bout typically began when the female extended her first (and often second) pair of legs and made contact with the moist cotton stopper. As she did so, more than half of the brood swarmed over her body and climbed down to the moist cotton by way of her palps or first two pairs of legs. Spiderlings descended to drink anytime before, during, or after the female's own drinking bout, as long as the mother was still contacting (or very close to) the water source.

After a female drank, she usually groomed her palps and forelegs while standing near the water source. During this time some young would still be swarming toward the water, while others were returning to her abdomen from their visit to the water. Spiderlings often used silk lines to travel between the mother and the substratum. In some cases, when the mother began to move away from the water, young that were drinking immediately returned via silk lines to her abdomen, suggesting that increased tension in the lines provided a cue for the young to return.

The mothers of two broods of *S. crassipes* died from unknown causes. When the carcasses were placed on the water source, young readily left the abdomen, drank, and then settled again on the abdomen.

Interactions between the Young and Substitute Parents

On the second day after emergence, young *L. rabida* were brushed off their mothers, separated into groups of ten, and each group placed with a potential "parent." A minimum of five trials was run for each substitute parent category. At least five of the substitute parents in each category were fed two mealworms apiece on the day of the spiderlings' emergence. A half-hour observation of the initial interactions between the young and the substitute parents was made; thereafter, the location and posture of the spiderlings were recorded daily.

a) *Mated female conspecific with unhatched egg sac*

The typical initial behaviour of these females was either to remain quiescent and permit young to settle or to flick contacting spiderlings off those appendages serving as access routes. Some incipient prey capture behaviour occurred in two females; however, it was never carried to completion. On subsequent days

(until the completion of dispersal), a mean of 4.2 ± 1.5 (SD) young per day were observed in the settled posture on the substitute female's abdomen. From one to nine spiderlings were settled on any one female at one time. Out of a total of 198 observations of settling, 192 occurred on the dorsal or lateral abdomen and six on the ventral abdomen. Young were all dispersed after a mean of 8.8 days (range = 5-12).

b) *Unmated, adult female conspecific*

These substitute parents were adult females that had not been allowed to mate but which had produced and then discarded an infertile egg sac. They were, therefore, physiologically older than the females of category a. On the other hand, these unmated females were of a similar post-moult age ($\pm 1-3$ days) as the biological mothers of the broods, in four of the five cases. During the 9-day observation period, two of these females never had settled young, while the other three females had 2.0 ± 0.7 (SD) settled young per day on the abdomen.

c) *Adult male conspecific*

Two male *L. rabida* immediately ate all ten spiderlings presented to each. For eight other male conspecifics that were fed mealworms before young were placed in their cage, four males still devoured some of the young during the initial 30 minutes, while the other four remained quiescent. Lone spiderlings were seen on males only three times (twice on the carapace and once on the ventral abdomen) during subsequent daily checks, and always in the rest posture rather than the settled posture.

d) *Adult female of another species*

Two female *L. punctulata* remained quiescent during introduction of juvenile *L. rabida*, while the other three females ate several spiderlings each. On only one of the subsequent days were young found on the substitute parent, one spiderling on each of two females, both in the rest posture rather than the settled posture. The other young remained scattered in the cage.

e) *Adult male of another species*

One male *L. punctulata* ate several spiderlings, while another flicked off the young that touched his

legs. On subsequent days, young were never seen on any of the males, but remained scattered in the cage.

Survival of the Young without a Parent

Methods

To observe the young's drinking behaviour and tendency to aggregate in the absence of the female, we anaesthetized and separated into two equal (or nearly equal) groups the members of each of nine broods of *S. crassipes*. One group of each brood was returned to the female's cage, and the other was kept in a separate cage with water available. On subsequent days the latter groups were checked for aggregation and drinking behaviours. ("Aggregation" was defined beforehand as the formation of a group of five or more spiderlings, each of which physically contacted at least two other individuals in the clump.) In addition, groups of juvenile *L. rabida* were checked for aggregation tendencies during temporary separation from the mother and her cage.

Survivorship rates in the nine broods of *S. crassipes* were compared between the groups returned to the mother and the groups of separately caged

siblings. After a week, a brood count was taken with the young under anaesthesia. Dead spiderlings were removed daily. The accumulative number of dead spiderlings was subtracted from the total number alive at the beginning of the experiment. Spiderlings missing in counts of living and dead individuals were presumed to have been either cannibalized or scavenged after dying.

Results

Spiderlings of *S. crassipes* and *L. rabida* never formed aggregations when separated from their mother. They were often observed drinking from the water vial. There was no significant difference between survivorship of young *S. crassipes* separated from their mother and those remaining with her (Table 1). For spiderlings permitted to remain with their mother, the mean time between emergence and dispersal was 7.2 days (range = 3-12).

Discussion

Site Selection and Posture of the Young

When initially settling after emergence from the

Brood	Young with mother			Young without mother		
	N _O	N _f	% survivorship	N _O	N _f	% survivorship
1	15	9	60	19	19	100
2	13	13	100	12	12	100
3	28	17	61	28	22	79
4	22	2	9	21	17	81
5	35	32	91	35	34	97
6	22	16	73	22	18	82
7	19	16	84	18	13	72
8	36	24	67	36	29	81
9	25	12	48	25	8	32
Total	215	141		216	172	
Mean	23.9	15.7	65.9	24.0	19.1	80.4

Table 1. Survivorship compared between two groups of spiderlings, one allowed to remain with the mother and the other permanently separated from the mother, in each of nine broods of *Schizocosa crassipes*. N_O = original number of young in each group at the start of the experiment (as counted on the day after emergence from the egg sac). N_f = final number of young surviving in each group at the end of the experiment (as counted on the day before dispersal was completed by the group of young that had been allowed to remain with the mother).

When the survivorship values of young with and without the mother were tested by the Wilcoxon matched-pairs test (two-tailed), the differences were not significant ($P > 0.05$).

egg sac, young *S. crassipes* and *L. rabida* selected sites on the female's abdomen; large broods involved some settlement on the posterior carapace. In *Pardosa amentata*, Vlijm *et al.* (1963) reported that the young settled the abdomen in the order of dorsal, lateral, and ventral surfaces, and then the posterior carapace. On the other hand, in *Trochosa* spp., young settled the female's dorsal surfaces (abdomen, then carapace) before the ventral (Engelhardt, 1964). In *L. rabida* we could discern no definite temporal pattern in the initial settlement among the ventral, dorsal, or lateral surfaces of the mother's abdomen. Some of the apparent species differences might reflect the failure of some workers to use the settled posture as a criterion of site selection; i.e., young may temporarily remain at a site in the rest posture prior to moving to a more permanent attachment site. However, species differences in site selection may well relate to possible differences in the distribution of the specialized knobbed hairs that are used by the spiderlings for attachment (Rovner *et al.*, 1973).

It is unlikely that the original site selected by a spiderling is used throughout the period prior to dispersal. Marked spiderlings were noted to shift their locations within the brood. More importantly, young were observed to swarm off the female to reach a water source. (It is possible, however, that the latter may not occur in the optimum conditions of the proper microhabitat.)

During most of the period of contact with the mother, the young maintained the settled posture. Since its legs are drawn in tightly to its body, each spiderling occupies less surface area than would be used in the rest posture. Thus, each layer of young could contain more individuals. Moreover, with the body lowered (and, thereby, the centre of gravity lowered) the settled animal is probably more stable. This would be important for the innermost layer of young, which are holding on to the female's abdominal hairs and supporting the rest of the mass. The "headstand" used by members of the outer layers of large broods (noted also by Engelhardt, 1964) may be an additional means for achieving compactness and, thereby, improving the stability of the entire mass.

Dismounting, Drinking and Remounting

When the mother is near or contacting water, some

of the young move rapidly over her body and down her appendages to reach the water. Whether a cue for dismounting is provided by some postural feature or movement of the female (Eason, 1964, 1969) or whether the spiderlings are responding to the water directly via their own receptors is not known. The frequency of drinking by spiderlings determined in this study (as often as twice every three days) obviously reflects the humidity levels in the laboratory and probably would be lower in the moist microhabitat typically selected by female lycosids carrying young.

Draglines deposited during the spiderlings' descent provided a means for re-locating the mother and sometimes served as return routes to the female's body, enabling the young to bypass the female's appendages. If the mother began to move away from the site, the spiderlings' draglines may also have signalled this event by the sudden increase in tension, perhaps a cue to return.

Interactions between the Young and Substitute Parents

The phenomenon of spiderlings aggregated on the mother has stimulated experiments on the specificity of this interaction. Conspecific young were adopted by other females with broods (Fabre, 1913; Eason, 1964), and exchange of broods between lycosid females of different genera also is readily achieved (Meyer, 1928). Apparently the young are responding to mechanical cues that are general among the lycosids. Correspondingly, adult female lycosids in the brood phase tolerate on their abdomen the presence of young of other families of spiders (Meyer, 1928) and even other classes of arthropods (Engelhardt, 1964). Indeed, there is no need for specificity, since the spiderlings move immediately from the egg sac (attached to the mother's spinnerets) to the female's body.

The female's tolerance of young and inhibition of prey capture can be triggered during the egg sac-bearing phase, i.e., prior to the time of emergence (Meyer, 1928; Eason, 1964). (As shown by Engelhardt, 1964, the mechanical stimulation caused by spiderlings climbing about on the female inhibits her feeding activity.) Our data on *L. rabida* agree with those of earlier workers; spiderlings readily settled upon females with egg sacs.

What is known about the activity cycle of female lycosids correlates nicely with such observations. Vlijm and Richter (1966) described the activity fluctuations of *Pardosa lugubris* during the breeding season. Recently moulted females were restless and ate well, but both of these parameters decreased a few days before the sac was constructed and remained depressed thereafter. During the young's emergence, the female's activity was at its lowest. Apparently, then, only females with egg sacs or broods (or unmated females of equivalent physiological ages) are quiescent and tolerant enough for young to mount.

When provided with unmated, conspecific, adult females of post-moult ages similar to those with egg sacs in group a, few or no young settled. Spiderlings were sometimes preyed upon or were not able to climb a female due to her restless activity. Having discarded infertile egg sacs, such females may have shifted back to a pre-egg sac state of higher activity. Equally possible, they may have jumped ahead physiologically to a post-dispersal state. (Vlijm and Richter (1966) report higher activity levels in females of the post-dispersal period compared with those having egg sacs or broods.) In any event, it is clear that one must distinguish between chronological age and physiological age in examining the behaviour of these animals.

Engelhardt (1964) found that male *Trochosa* spp. preyed upon young of their own species. We found the same in *L. rabida*. In the few cases in which spiderlings managed to climb upon a male, they did not adopt the settled posture. Perhaps the latter behaviour requires the presence of knobbed hairs (Rovner *et al.*, 1973), which are lacking in males (Graefe, 1964).

L. punctulata was chosen for interspecific adoption experiments because members of this species are morphologically similar to *L. rabida*, are found in the same habitat, and have overlapping life cycles (Eason & Whitcomb, 1965). (*L. punctulata* is present in the penultimate instar and as the young adult during the time that female *L. rabida* are carrying young.) In our experiment, young *L. rabida* were eaten or were not allowed to mount young adult female *L. punctulata*. As discussed above, females do not become tolerant until the time of egg laying is near. Had we "slowed down" the pre- or post-

emergence development of the young *L. rabida* (by holding them in a cool environment for 2-3 weeks), we could have presented them with female *L. punctulata* that would have been advanced enough physiologically to be in the egg sac or brood-carrying phase. Based on the findings of previous workers such as Meyer (1928), interspecific adoption would be expected to occur under such conditions, i.e., where exchange involves physiologically similar mothers. (Of course, Meyer simply used species having near synchrony in breeding seasons.)

Behaviour and Survival of the Young without a Parent

Engelhardt (1964) reported clustering in juvenile *Trochosa* spp. (1-4 days post-emergence) separated from the female. He suggested that this tendency contributed to the maintenance of brood aggregation on the female. The clustering behaviour decreased with time, lasting only as long as the normal length of time that the young spent with the female. The amount of space available seemed important, since young that were brushed off into an area larger than the burrow ($> 2 \text{ cm}^2$) did not cluster. In our study, young of *S. crassipes* and *L. rabida* of ages comparable to those of Engelhardt's study dispersed instead of aggregating when separated from the mother. The area of our containers (87.5 cm^2) corresponded to a "larger area" as in Engelhardt's study. Observations by Eason (1969) and Enders (1972) indicated that humidity plays a role in the aggregation behaviour of juvenile lycosids. Young cluster in a low humidity environment and disperse when in high humidity. Clustering of newly emerged juveniles is well-known among various spider families, e.g. araneids (McCook, 1889), and deserves future study as to whether it functions to reduce water loss, as suggested by the observations on lycosids. Additionally, one wonders whether the lycosid condition arose as a post-emergence cluster which, as in other families, uses a site near the egg sac, that in this case happens to be mobile — the mother's body.

Eason (1964) claimed higher mortality in groups of young separated from the female than in those maintaining normal contact. She suggested that the mother's forelegs provide directional cues and that they were withdrawn from the water only after the last spiderling had drunk. Eason also mentioned an

instance where young on a dead female would not leave her body to drink. Those removed from the mother by the experimenter did drink, but those remaining on the carcass eventually died, Eason presumed, of thirst.

In our study, two broods of *S. crassipes* whose mothers died (from unknown causes) did leave the carcass, drank, and returned. Moreover, individuals in nine groups separated from their mothers readily drank on their own and survived as well as their siblings, which were on the female. Furthermore, Engelhardt (1964) successfully raised isolated first and second instar lycosids to maturity. Obviously newly emerged juvenile lycosids will initiate drinking behaviour in the absence of their mother. The question remains, however, whether under normal conditions (with the brood on the female's abdomen) the female's drinking behaviour triggers the swarming of the young to water, as hypothesized by Eason (1964, 1969).

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