

Do adult female lycosids feed during the period of maternal care?

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Summary

It has been stated in some literature reports that in the highly cannibalistic wolf spiders (Lycosidae) the adult females do not feed while engaged in maternal care (i.e. their predatory behaviour is inhibited), whereas other reports based on laboratory studies indicate that maternal females resume feeding. During a two-year field study on the feeding habits of the wolf spiders *Pardosa agrestis*, *P. palustris* and *P. amentata*, I had the opportunity to investigate the question whether in these species maternal females do feed (or not). Overall, 25 instances of wolf spider mothers feeding during the period of maternal care are reported. Eighteen cases refer to egg sac-carrying females, 7 cases to pulli-carrying females. It must be stated, however, that the feeding rate of maternal females was significantly lower than that of non-maternal females, which is in agreement with the findings of other researchers obtained in the laboratory. It is hypothesised that there may be genus-specific behavioural differences between free-moving and burrowing wolf spider species which may (at least in part) explain the apparent discrepancies between the reports of various authors.

Introduction

Wolf spiders (Lycosidae) are vagrant hunters that forage on the soil surface and in the leaf litter of a wide variety of terrestrial habitats (Gertsch, 1979; Wise, 1993; Nyffeler *et al.*, 1994). Often they are the dominant invertebrate predators in terms of biomass, energy flow, and nutrient transfers (see Van Hook, 1971; Moulder & Reichle, 1972; Schaefer, 1974). They feed primarily on insect prey and to a lesser degree on other spiders (Nyffeler, 1999).

Though highly cannibalistic (see Hallander, 1970; Schaefer, 1974), the wolf spiders are known for their maternal care (Gertsch, 1979; Foelix, 1996). After oviposition has occurred, the spherical egg sac attached to the mother's spinnerets is carried around for several weeks. In some lycosids, which dig burrows in the ground, the female guards its egg sac there. Thereafter the mother bites open the sac at the seam. Immediately after hatching, the 40–100 pulli climb up the mother's legs on to her back where they hold fast to her abdominal hairs. They are carried by her for about one week until the second moult, by which time they are ready to disperse. While riding on the mother's abdomen, the pulli live exclusively on their yolk supply. It has been stated in the literature that adult female wolf spiders do not feed during the period of maternal care (i.e. their predatory behaviour is inhibited, thereby reducing the risk of cannibalism on conspecific spiderlings) (e.g. Engelhardt, 1964; Higashi & Rovner, 1975; Foelix, 1996). In contrast to this, Gertsch (1979) wrote: "During the time of carrying the young, the mother engages in normal hunting activities ...". Thus, the published

reports on the feeding status of maternal females differ. In the course of a comprehensive study on the feeding habits of three species of *Pardosa* wolf spiders, I gathered a large set of data on the activities of females in various stages of their adult life, which allowed an investigation of the question whether maternal females stop or resume feeding.

Material and methods

This study was conducted during two consecutive years in cereal fields belonging to the Swiss Federal Research Station for Agroecology and Agriculture near Zurich. During 104.5 h (from mid-May to mid-August in the first year and from mid-May to mid-July in the second year), the soil surface of the fields was thoroughly searched for wolf spiders. Each time a spider was encountered, it was recorded whether it was in possession of prey or not. Spiders were caught by hand with a transparent plastic cup of 7 cm upper diameter, killed, preserved in 70% ethanol and later identified (along with their prey) in the laboratory under a dissecting microscope (see Schaefer, 1974; Nyffeler & Benz, 1988). The study was conducted during the daytime hours (between 09.00 and 19.00) only, as spiders of the genus *Pardosa* are known to be exclusively diurnal, at least in the temperate and northern zones of Europe (see Nyffeler & Breene, 1990). Air temperatures ranged from c. 17–23°C (half-monthly means at 13.00 h) according to data of the Swiss Meteorological Institute in Zurich.

In this way, a total of 1,624 adult female wolf spiders — representing the three species *Pardosa agrestis* (Westring), *P. palustris* (Linnaeus), and *P. amentata* (Clerck) — were collected (Table 1). These spiders are stenochronous species reproducing in spring and summer (Schaefer, 1976). The data refer to 996 females involved in maternal care and 628 females not involved in maternal care (Table 1). Egg sac-carrying females were found from May to August, and those with pulli on their abdomen from June to August. The data were pooled as *Pardosa* spp., because the number of observed events was too low for meaningful between-species statistical analyses. A chi-square test of independence was used to examine whether the frequency of feeding (= number of spiders with prey/total number of spiders) differed significantly between wolf spider females involved in maternal care versus those not involved in maternal care. The chi-square was computed by means of the uncorrected formula (without Yates's adjustment, because of large enough samples) (Sokal & Rohlf, 1995).

Results and discussion

Direct observations in the field

Overall, it was found in 25 instances that wolf spider mothers fed during the period of maternal care (Table 1). Eighteen of these cases referred to egg sac-carrying females, and 7 cases to pulli-carrying females (Table 1). In females involved in maternal care, feeding was detected from June to July. These mothers

preyed upon small dipterans, aphids or unidentified arthropods (possibly collembolans chewed down by the chelicerae to a meat ball). No pulli were detected in the diet of these mothers (at least among the identifiable prey items). Feeding by mothers during the period of maternal care was detected in all three wolf spider species investigated (*P. agrestis*, *P. palustris* and *P. amentata*). These results are in agreement with Gertsch's (1979) statement that during the period of maternal care wolf spider mothers engage in normal hunting activities. It must be stated, however, that the frequency of feeding of wolf spider females involved in maternal care is distinctly lower than that of non-maternal females (Table 1). This difference is statistically significant ($\chi^2=34.64$; $df=1$; $p<0.01$) (combined data of both years).

Comparison with data of other researchers

In general, wolf spiders feed infrequently in the field (see Schaefer, 1974; Nyffeler & Benz, 1988; Nyffeler & Breene, 1990). To investigate their feeding behaviour under such circumstances is difficult and time-consuming. Therefore, most investigations on the feeding activities of wolf spiders have been carried out in the laboratory. In such laboratory studies conducted on *Pardosa astrigera* L. Koch [= *Lycosa T-insignita* Bös. & Str.], *P. pseudoannulata* (Bös. & Str.), and *P. lugubris* (Walckenaer), it was shown that adult females fed while carrying egg sacs or pulli (see Miyashita, 1968a,b; Edgar, 1971a). In addition to this, field samples taken by Edgar (1971b) indicated that during the egg sac-carrying period the weight of the female of *P. lugubris* remains relatively constant (≈ 20 – 25 mg), which implies that

the females must be feeding during this time period; otherwise they would lose weight.

However, in these studies the maternal females fed at a reduced rate compared with non-maternal females (Miyashita, 1968a,b; Edgar, 1971a). This is in good agreement with my own observations in the field, where the feeding rate was significantly lower during the period of maternal care (Table 1). How can this decrease in the feeding rate be explained? The weight of egg sac-carrying (or pulli-carrying) females is almost 50% less than that just before egg sac production (see Edgar, 1971b). Thus, adult females involved in maternal care have much lower energy requirements, which may (at least in part) explain the reduced feeding rates (see Edgar, 1971a).

As wolf spiders are highly cannibalistic (Hallander, 1970; Schaefer, 1974; Samu *et al.*, 1999), it has been suggested by some authors that the predatory behaviour of adult females is inhibited during the period of maternal care to avoid the pulli (mistaken as prey) being eaten by their mother (e.g. Palmgren, 1945; Engelhardt, 1964). This problem was investigated by Meier (1967) in a simple laboratory experiment. He removed the pulli from a wolf spider mother and then exposed them to her along with several small dipterans and collembolans. The mother picked out the dipterans and collembolans from the "mixed group", grasping them with her chelicerae, whereas the pulli remained untouched. The latter were permitted to re-mount the mother's abdomen. Evidently the mother can discriminate between her own young and similar-sized insects. This implies that predation is inhibited as far as the behaviour of wolf spider mothers towards the pulli is concerned (see Palmgren, 1945; Meier, 1967; Hallander, 1970; Wagner, 1995). Small insects, on the other hand,

	Total spiders	No. spiders with prey	% spiders with prey
First year:			
<i>Pardosa agrestis</i> + <i>Pardosa palustris</i>			
Females not involved in maternal care	420	27	6.4
Females with egg sac	511	9	1.8
Females with pulli	38	5	(13.2)
Second year:			
<i>Pardosa agrestis</i>			
Females not involved in maternal care	162	17	10.5
Females with egg sac	299	5	1.7
Females with pulli	58	2	3.4
<i>Pardosa palustris</i>			
Females not involved in maternal care	10	4	(40.0)
Females with egg sac	12	3	(25.0)
Females with pulli	2	0	(0)
<i>Pardosa amentata</i>			
Females not involved in maternal care	36	9	(25.0)
Females with egg sac	68	1	1.5
Females with pulli	8	0	(0)
Pooled data from all spiders:			
Females not involved in maternal care	628	57	9.1
Females involved in maternal care	996	25	2.5

Table 1: Proportion of wolf spider females with prey in cereal fields in eastern Switzerland (two-year study). Percentages based on small sample size in parentheses.

were eaten by the pulli-carrying mothers in Meier's experiments, which is supported by my own observations in the field (Table 1). Nevertheless, it cannot be ruled out with absolute certainty that the much lower feeding rate recorded in adult females during the period of maternal care may be caused to some extent by a partial inhibition of their predatory behaviour.

We have to be careful with generalisations. There may be genus-specific behavioural differences. Burrowing species (e.g. from the genus *Trochosa*), which do not leave their burrow during the entire egg sac-guarding period (resulting in extremely low prey encounter rates), may indeed eat nothing during this time period as reported by Engelhardt (1964). Spiders which remain inactive have low energy requirements. During times of starvation they can reduce their metabolic rate (see Anderson, 1974). Free-moving species (e.g. genus *Pardosa*) that exhibit high locomotor activity, on the other hand, probably have higher energy requirements (which is reflected in the need to feed during the period of maternal care) than the burrow-dwelling species; this obviously is the case in the three *Pardosa* spp. described in the present study (Table 1).

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