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The effects of maternal nest guarding behaviour by *Eremobates marathoni* Muma & Brookhart on the survivorship of offspring (Solifugae, Eremobatidae)

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Summary

Observations on the depression burrows (nests) of *Eremobates marathoni* that contained eggs indicated that the clutch size ranged from 18–69 (mean 36.5 ± 5.8). The number of first-instar nymphs per nest ranged from 9–41 (mean 22.0 ± 7.7 , S.D.). Field studies were also conducted to assess the effect of maternal guarding of the nest against a naturally occurring predator, *Schizocosa avida* (Lycosidae), on the survivorship of first-instar solifuge nymphs. The presence of a maternal parent within the nest resulted in a significant increase in survivorship of offspring in this solifuge. Twelve of 15 adult female *Schizocosa avida* spiders (80%) introduced into nests containing an adult female solifuge were killed and eaten by the maternal parent. Mortality of solifuge nymphs resulting from spider predation was observed at a low frequency (5.9–15%) in only three of these 15 nests. In no case did a spider kill an adult solifuge. In unguarded nests, mortality of solifuge nymphs was significantly higher, ranging from 45–100%. Mortality was higher than 60% in 10 out of 15 unguarded nests. The results of this study indicate that nest guarding behaviour contributes in a significant way to offspring survivorship and hence to the overall fitness of *E. marathoni*.

Introduction

It is generally assumed that the guarding of a nest by a maternal or paternal parent will contribute in a positive way to the survivorship of their young (Reznick, 1985; Clutton-Brock, 1988). When some degree of parental care is exhibited by lower vertebrates (fish, reptiles) or arthropods it is usually confined to one parent only (Dawkins & Carlisle, 1976; Smith, 1980).

Many female spiders are known to provide assistance and protection to their brood. Lycosid females carry their egg sacs (usually attached to the abdomen) with them as they move from one location to another and will frequently assist their offspring during hatching by using their chelicerae to tear open the cocoon (Fujii, 1978). The emerging spiderlings then climb on to their mother's back and remain there for several days. Pisaurid females carry their egg sacs in their chelicerae (Foelix, 1996). In a few species of theridiid, agelenid and eresid spiders,

females provide food for their young by leaving captured prey near the spiderlings, feeding them liquified food, or laying an additional batch of smaller eggs as a food source (Gundermann *et al.*, 1988, 1991; Tahiri *et al.*, 1989). Maternal guarding of the nest has also been shown to enhance the subsequent survival of juvenile scorpions (*Euscorpis flavicaudis* (De Geer)) (Benton, 1991), and spiderlings of the thomisid *Misumena vatia* (Clerck) (Morse, 1992).

Eremobates marathoni Muma & Brookhart is a common representative of the solifuge fauna of the Big Bend region of Trans Pecos Texas which lies in the northern region of the Chihuahuan Desert (Punzo, 1997a). Individuals of both sexes frequently construct a bowl-shaped depression burrow under a rock (personal observation). Females utilise these depression burrows as nests in which they lay their eggs. Females will remain in the nest and guard their eggs, as well as hatchling nymphs. First-instar nymphs remain with their mother in the nest. After moulting, the second-instar nymphs leave the nest and disperse.

During the course of field studies on several species of solifuges, including *E. marathoni*, found in this area, I have frequently observed the wolf spider, *Schizocosa avida* (Walckenaer) feeding on unguarded solifuge nymphs in their burrows (personal observation). Other than mortality resulting from cannibalism by other nymphs, this is the only predator that I have observed capturing and feeding on solifuge nymphs at this study site. In the present field study, I examined the effect of maternal nest guarding by *E. marathoni* on the subsequent survivorship of offspring. To my knowledge, no previous studies exist on the possible adaptive significance of this behaviour in solifuges.

Methods

All field experiments were conducted on solifuges found within a 3 km radius of Marathon, Texas (Brewster County), during late July and August 1995. The general topography and dominant vegetational zones have been described in detail elsewhere (Tinkam, 1948; Punzo, 1997b). I located burrows (nests) occupied by adult solifuges by turning over rocks located on the desert floodplain. Burrows containing females with first-instar nymphs ($n=86$) were identified and given a number which was placed on a small wooden marker driven into the ground next to each burrow. Females

were also marked with fluorescent paint using a three-dot combination code so that individuals could be identified and burrow site fidelity confirmed. For data analysis, I used the observations recorded from two randomly-assigned groups. One group consisted of 15 females with first-instar nymphs. The second group (controls) consisted of 15 nests containing first-instar nymphs from which the adult female had been removed (unguarded). The adult females were all of similar size (measurements represent means \pm S.D.): body weight 3.7 ± 0.11 g; propeltidium width 4.8 ± 0.07 mm.

I carefully lifted the rock covering the burrow and removed each gravid female from its nest. The solifuge was then placed in a plastic vial. Following this, I thoroughly searched the area within a 40 cm radius around each burrow and removed all of the arthropods and lizards (potential predators and prey) that were found on the surface of the ground and vegetation as well as beneath rocks. The first-instar solifuge nymphs made no attempt to leave the depression burrow even when exposed in this fashion. Following the removal of these animals, the rock formerly covering each burrow was carefully replaced, and each female in the "guarded" group was returned to the entrance of her burrow and retreated into it within a period of 10–30 s. Each burrow was then covered with a dome-shaped hemispherical structure, 20 cm in height and 40 cm in diameter, constructed of fine-mesh aluminium window screening and provided with a gated aperture on top into which a plastic vial containing predators or prey could be inserted. The dome was positioned so that the entrance to the burrow was located in the centre of the dome. The dome ensured that no other animals could move into the area around the burrow during experimental trials.

I also collected adult female *S. avida* spiders (mean body weight 1.1 ± 0.03 g (S.D.); mean body length 13.2 ± 1.1 mm) from the same general study area and maintained them individually in plastic containers until the start of encounter experiments. They were fed twice per week on grasshopper nymphs (Tettigoniidae) from the study area and provided with water ad libitum. No spider was kept in captivity for more than one week before testing. Spiders were deprived of food for 72 h before each encounter experiment.

All encounters were staged between 2100 and 2300 Central Standard Time. Previous observations had indicated that solifuges and spiders were most active during this time period (unpublished data). Encounters were observed under infrared lighting to minimise disturbance to the animals. To initiate an encounter experiment, I introduced one adult *S. avida* female into each dome-covered burrow site (enclosure) through the opening at the top of the dome. An encounter experiment was conducted once on each burrow for both groups. The spider was allowed to remain within the enclosure until it fed on solifuge nymphs, or until it was captured and killed by a female solifuge. No encounter trial was allowed to proceed for longer than 24 h. Thus I was able to determine the effect of maternal nest guarding behaviour on the survivorship of solifuge offspring.

All statistical analyses used in this study followed procedures outlined by Sokal & Rohlf (1981).

Results and discussion

Observations on the nests of *E. marathoni* containing eggs (unpublished data) showed that the clutch size ranged from 18–69 (mean 36.5 ± 5.8). Previous data on *Eremobates mormonus* from several different locations in Trans Pecos Texas reported mean clutch sizes ranging from 37.1 to 53.2 (Punzo, 1995). Clutch sizes ranging from 20–192 have been reported for solifuges from other areas of the southwestern United States and Africa (Lawrence, 1947; Cloudsley-Thompson, 1961; Muma, 1966; Wharton, 1987). The number of first-instar nymphs per nest for *E. marathoni* females at this study site ranged from 9–41 (mean 22.0 ± 7.7 , S.D.) (Table 1).

The presence of the maternal parent resulted in a significant increase in the survivorship of offspring in this species ($G=39.7$, $p<0.001$) (Table 1). Only three of 15 nests (20%) guarded by a female solifuge experienced any predation by *S. avida* and even then only a small percentage of solifuge nymphs were killed and eaten (5.9–15%). Twelve of the fifteen spiders (80%) introduced into enclosures containing an adult female solifuge were killed and eaten by the maternal parent. In the three other cases the spider was found clinging to the screen enclosure after a 24 h period. In most cases, a spider would approach the entrance to the burrow and either be grasped by the female solifuge at that site, or the solifuge would emerge from the nest and chase the spider for a short distance (<10 cm), before capturing and eating it. Female solifuges did not leave their nests until a spider moved into or very close (<0.75 cm) to the entrance of the burrow. It is interesting to note that these wolf spiders were apparently not deterred from approaching and entering the entrance of the burrow even when a female solifuge was present. In no case did a spider kill an adult female solifuge.

Burrow	Guarded by a female		Unguarded nests		
	Number of nymphs	Number consumed	Number of nymphs	Number consumed	Percent consumed
1	23	0	17	14	82.3
2	14	0	23	16	69.5
3	35	0	21	15	71.4
4	27	2	13	13	100
5	16	0	25	15	60.0
6	21	0	34	19	55.8
7	41	0	21	13	61.9
8	22	0	30	16	53.3
9	17	1	11	10	90.9
10	24	0	17	12	70.5
11	31	0	25	16	64.0
12	20	3	22	13	59.1
13	13	0	12	12	100
14	21	0	31	14	45.2
15	26	0	9	9	100

Table 1: Predation rates on first-instar nymphs of *Eremobates marathoni* by the wolf spider *Schizocosa avida*, at burrows (nests) guarded by a maternal parent and at unguarded nests.

In unguarded nests, mortality of solifuge nymphs ranged from 45.2–100% (Table 1). Mortality was higher than 60% in 10 out of 15 nests. Clearly, *S. avida* can have a significant impact on solifuge survivorship. In these experiments, encounter trials were terminated after 24 h. However, if *S. avida* had been allowed to remain in unguarded enclosures for longer periods of time, I have no doubt that mortality rates may have approached 100% for all nests. Typically, a spider would approach the entrance to an unguarded burrow and enter the nest. The spiders were observed feeding on solifuge nymphs within 30 s after entering the nest (observed by removing the rock covering the depression burrow). The mortality of solifuge nymphs observed in unguarded nests in this study is considerably higher than that reported by Morse (1992) for unguarded nests of the crab spider *Misumena vatia* (5–10%). In no case was a live predator (*Metaphidippus insignis* (Banks), Salticidae) ever found on a nest guarded by the maternal parent. The results from the present study indicate that nest guarding behaviour contributes in a significant way to offspring survivorship and hence to the overall fitness of *E. marathoni*.

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