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SHORT COMMUNICATION

MATRIPHAGY IN THE NEOTROPICAL PSEUDOSCORPION *PARATEMNOIDES NIDIFICATOR* (BALZAN 1888) (ATEMNIDAE)

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ABSTRACT. We studied the natural history and social behavior of *Paratemnoides nidificator* (Balzan 1888) in a tropical savanna system. Females were responsible for all nymphal care. We observed, for the first time in pseudoscorpions, the occurrence of matriphagy behavior by the offspring. During conditions of food deprivation, the mother went out of the nest and passively awaited the protonymphs' attack, not reacting to the capture nor to the nymphs feeding on her body. We suggest that this extreme form of parental care, matriphagy, can reduce cannibalism among protonymphs and facilitate the evolution of social behavior in pseudoscorpions.

RESUMO. Nós estudamos a história natural e o comportamento social de *Paratemnoides nidificator* (Balzan 1888) na região dos cerrados. As fêmeas foram responsáveis por todo o cuidado às ninfas. Nós observamos, pela primeira vez em pseudoescorpiões, a ocorrência de matrifagia pela prole. Em condições de fome, a mãe deixa o ninho e passivamente espera que as protoninfas a ataquem, não reagindo nem à captura, nem à alimentação das ninfas sobre seu corpo. Nós sugerimos que esta forma extrema de cuidado parental, matrifagia, possa reduzir o canibalismo entre as protoninfas e assim facilitar a evolução de comportamento social em pseudoescorpiões.

Keywords: Social behavior, maternal care, Arachnida, cannibalism, tropical savanna

The order Pseudoscorpiones is highly diversified with more than 3,239 described species in 425 genera and 24 families, representing around 3.3% of all arachnids (Harvey 1991, 2002). In general, pseudoscorpions are small (2–8 mm) and are non-social animals that behave aggressively in intraspecific contacts (Weygoldt 1969; Zeh 1987). Zeh (1987) reported fights between males of a Chernetidae species during contests for food or females, resulting in cannibalism. Some Atemnidae species, however, show a high level of sociality, living in groups, sharing food and hunting cooperatively (Brach 1978; Zeh & Zeh 1990).

All pseudoscorpion species present some level of parental care. Indeed, females of all species take care of embryos that are maintained inside a brood sac attached to her genital opening (Levi 1953; Gabutt 1970b; Weygoldt 1969). Females can also build silk chambers in which they rest with the brood sac until the emergence of the protonymphs (Brach 1978; Gabbutt 1962, 1966, 1970a; Levi 1948, 1953; Harvey 1986; Zeh & Zeh 2001). In *Neobisium maritimum* (Leach 1812) the silk chamber is built and occupied by one individual, and several chambers may occur in the same rock fissure (Gabbutt 1962, 1966). Females of *Neobisium muscorum* (Leach 1817) can have chambers placed side by side (Weygoldt 1969). In *Paratemnoides elongatus* (Banks 1895) and *P. minor* (Balzan 1892), both species that occur beneath tree bark, nymphs can build molt chambers cooperatively and adult females bearing a brood sac can use molt chambers for brood care as well (Brach 1978; Hahn & Matthiesen 1993b). This cooperative building of nests saves time and silk, maintains appropriate humidity conditions and protects the brood from predators (Brach 1978). In both those *Paratemnoides* species females in the nest remove the brood sac from the genital opening after secreting the nutritive fluid to the embryos (Brach 1978; Hahn & Matthiesen 1993a). Protonymphs of *Pselaphochernes scorpioides* (Herman 1804) remain 2–3 days inside the nest receiving care until they disperse (Weygoldt 1969).

Pseudoscorpions are widespread. For instance, in Central Amazon, Adis & Mahnert (1985) recorded 60 species belonging to 25 genera in 10 families. The Brazilian cerrado savanna originally covered approximately 25% of the country and is currently

Table 1.—Composition of all colonies (by sex and age classes) of *Paratemnoides nidificator* (Atemnidae) studied.

Colony	Males	Females	Tritonymphs	Deutonymphs	Protonymphs	Total
1	3	4	8	—	—	15
2	4	5	16	14	3	42
3	8	12	15	5	—	40
4	7	5	4	12	21	49
5	9	10	4	—	—	23
6	4	7	1	28	30	70
7	12	11	7	3	—	33
X ± SD	6.71 ± 3.25	7.71 ± 3.25	7.85 ± 5.7	8.86 ± 10.08	7.71 ± 12.47	38.86 ± 17.98

one of the most endangered tropical ecosystems (Oliveira & Marquis 2002). To our knowledge there is no study about pseudoscopions in the cerrado. Here, we studied the biology and natural history of *Paratemnoides nidificator* (Balzan 1888) an atemnid species that occurs under the bark of living trees of *Caesalpinia pelthophoroides* (Caesalpiniaceae), a tree found throughout the cerrado domain.

Observations for this study were conducted from October 2001 to December 2003 in Uberlândia, Brazil (18° 53′S, 48° 15′W; 863 m el.), in the southeastern limit of the cerrado distribution. Seven colonies of pseudoscorpions (Table 1) were collected from the field and maintained in captivity during all the study. Each colony was kept in a glass bottom culture dish (12 cm of diameter) having the original piece of tree bark and was fed twice a week with live termites (*Armithermes* sp.) and beetles (*Acanthocelides obtectus*, Bruchidae). Moisture was provided by a small piece of water-soaked cotton. Behavioral observations were made using the ''all occurrence samples'' method (Altmann 1974). Using this method, everything that a group or individual does during an observation session is recorded *ad libitum.* This method is particularly useful to begin a study or to observe rare or fortuitous behaviors (see also Martin & Bateson 1993; Del-Claro 2004). Individual observation sessions lasted 30–40 min and were made during the day (mainly between 09:00h and 15:00h) using natural light. As colonies are built under the bark of trees, during the observation sessions the petri dishes with the colonies were put on a wire stand with a mirror below that enable the observations without be disturbing the animals. In the present paper we describe the social and reproductive behavior of *P. nidificator* based on 50 observation sessions (34 hours total observations). Voucher specimens have been lodged with the Museu de Zoologia de São Paulo (MZUSP).

We observed that females wove the reproductive nest alone. Inside the chambers, the female provided parental care continuously to embryos and nymphs by feeding and grooming them. This lasted until the nymphs were adults or were forced from the nest. The female also guarded the nest entrance against enemies. In some cases, the female produced an additional brood and then forced nymphs from the first brood out of the chamber by touching them with her pedipalps. After chasing the original brood, the female sealed the exit with new silk and produced the new brood sac. The ''displaced'' nymphs then cooperatively built another chamber in which they molted. The reproductive and the molting chambers were built side by side sharing the vertical walls. This behavior has also been observed in *P. elongatus* (Banks 1895) and *P. minor* (Balzan 1892) (Brach 1978; Hahn & Matthiesen 1993a). In the field, we found colonies of *P. nidificator* with nests composed of 3–20 chambers.

We identified 95 distinct behavioral acts, of which 16 were related to reproductive behavior, mainly parental care (Table 2). Parental behaviors comprised 10.13% of the behaviors seen in this species. However, the acts in this category are performed only by adult females, so more than 75% of adult female behaviors are related to taking care of embryos and young. Other important behavioral acts of females were self-grooming and feeding. Males directly cooperated in parental care by catching and offering prey to all members of the colony (94 records during 50 observation sessions). However, nymphs in general were fed by the mother. Our data revealed that females left the nest to hunt prior to feeding the brood (56%, or in 42 out of 75 times that we observed females leaving the nest during the observations). The mother ate the rest of the carrion left by the nymphs. Tritonymphs hunted cooperatively with the mother (3 in 42 observations of the mother hunting), or without the mother (n = 14 records during 50 observation sessions).

At the end of our observations we recorded colony behavior under food deprivation by depriving the colony food for one week. On the seventh day we observed matriphagy behavior in three of the seven colonies. The mother exited the nest, raised her pedipalps and passively waited for her nymphs to attack. Nymphs (9 ± 3 protonymphs, X ± SD,

Table 2.—Behavioral acts of *Paratemnoides nidificator* (Atemnidae) associated with ''Parental Care''. Data recorded from a clutch of 90 individuals (33 adults and 57 nymphs) reared in captivity (n = 34 hours of observations).

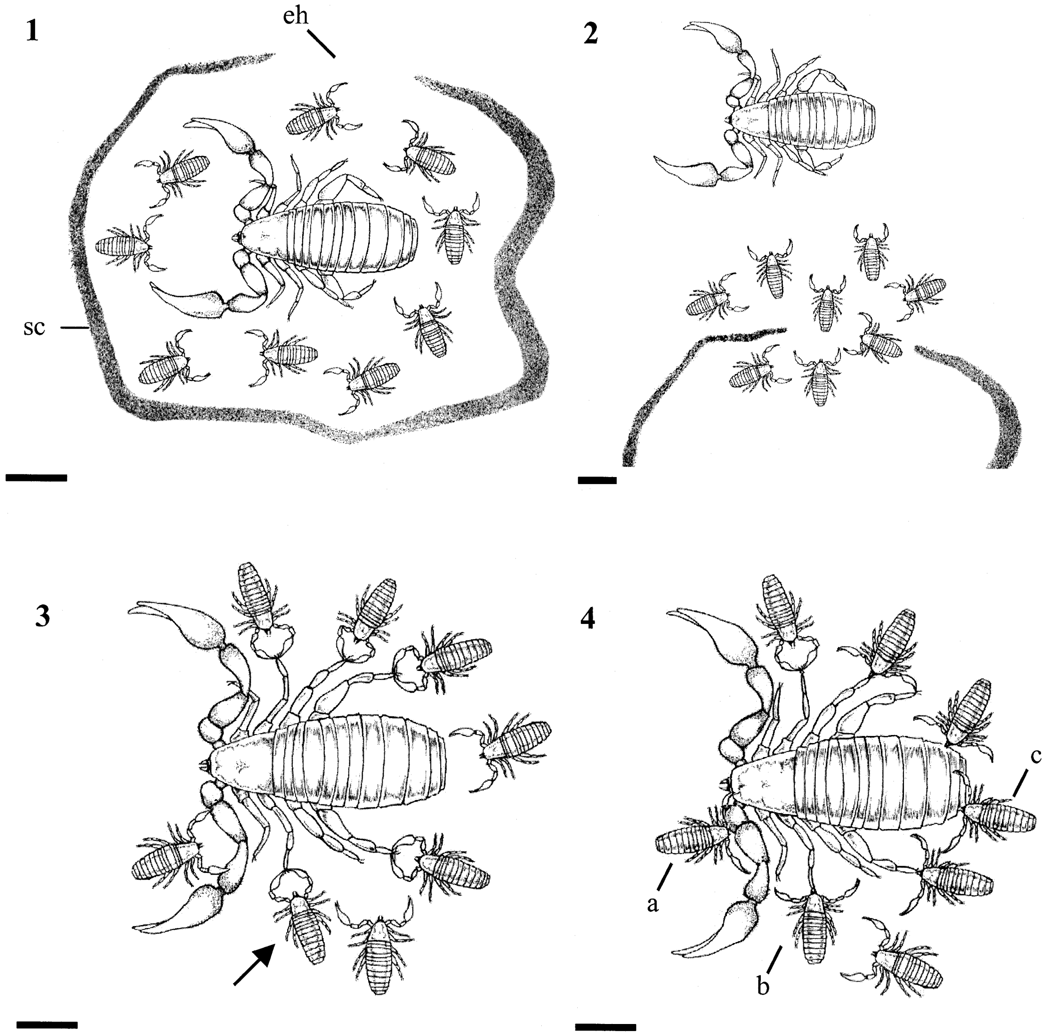
Behavioral act	Number of observations	Percent frequency of the behavioral act (total 453 acts)
1-Female weaving chamber.	179	30.4
2-Female occupying a woven chamber previously built by another individual.	5	0.85
3-Female excluding conspecifics from chamber.	4	0.68
4-Female resting in the nest.	76	12.9
5-Female moving in the nest.	19	3.23
6-Female touching the nest wall with pedipalps.	10	1.7
7-Female touching the embryos with pedipalps.	84	14.3
8-Female touching the protonymphs with pedipalps.	29	4.92
9-Female transporting wood pieces inside the nest.	4	0.68
10-Female inserting fragments of wood in the nest walls.	4	0.68
11-Female stopping in the nest above in second instar embryos.	4	0.68
12-Female stopping in the nest together with the protonymphs.	29	4.92
13-Female excluding conspecifics from previously built chamber.	3	0.51
14-Matriphagy.	3	0.51
15-Female bringing food to her nymphs	42	7.13
16-Males offering prey to nymphs	94	16
Total	589	100

n = 3) left the nest and gathered around the mother and attacked by grasping the mother's legs and pedipalps (3 ± 1 min, X ± SD, n = 3; time to attack). The young fed through the leg joints of the mother. The mother remained motionless as she was consumed (40 ± 5 min, X ± SD, n = 3; time used by nymphs feeding on mother's body, Figs. 1–4). Immediately, in the next step, the mother's exoskeleton was thrown out of the bark piece by the nymphs. Without the mother, nymphs began to hunt cooperatively.

In the classic definition of degrees of social behavior by Wilson (1971), eusocial species are characterized as having members of the same generation using a composite nest, cooperation in brood care, overlap of generations with offspring assisting parents and reproductive division of labor. In *P. nidificator* we did not identify a worker caste. Nevertheless, we consider this pseudoscopion as a permanent social species. In arachnids, Plateaux-Quénu et al. (1997) defined as permanent social species, ''a group of individuals of both sexes generally with overlapping generations which cooperate in the construction of a common nest, prey capture and care of the young.'' These authors consider permanent social species as synonymous with cooperative, non-territorial permanently social species (Plateaux-Quénu et al. 1997).

The trade off between individual sacrifice and colony welfare is well evident in the case of defense, and sometimes this altruistic behavior is accompanied by anatomical specialization (Hölldobler & Wilson 1990). The presence of a sting, used to defend the colony against vertebrates in the honey bees, some genera of ants, social polistine and polybiine wasps, constitutes a remarkable example of convergence in social behavior (Hermann & Blum 1981). There is no anatomical specialization in *P. nidificator* or other arachnids to facilitate matriphagy. However, the simple occurrence of matriphagy in pseudoscorpions and other invertebrates (e.g. Evans et al. 1995; Kim et al. 2000), can be also pointed out as example of convergence in social behavior.

According to Evans et al. (1995), extreme forms of parental care, such as matriphagy, may be frequent among spiders that typically produce single clutches. We did additional laboratory observations in 38 colonies of *P. nidificator* during the reproductive season of 2003. Of these 38 colonies, in 7 the female was maintained alone and she was able to produce only one brood. In the other 31 colonies, females were maintained in the colony and they produced two or more additional clusters, in general three (n = 26). The observation that females alone did not produce additional broods suggests that solitary females may have a smaller reproductive output than that females living in groups. We suggest that the social life in *P. nidificator*, with adults hunting cooperatively, can reduce the chances of cannibalism and improve reproductive conditions for many individuals. In Araneae, Elgar & Crespi



Figures 1–4.—Schematic illustrations of matriphagy in the pseudoscorpion *Paratemnoides nidificator*. 1. Female and protonymphs resting inside the silk chamber (sc), near entrance hole (eh); 2. The mother goes out to the nest and raises her pedipalps. The brood begin to leave the nest; 3. Nymphs gather around the mother and attack by grasping the mother's legs (arrow) and pedipalps; 4. The young feed through the joints of mother's pedipalps (a), legs (b) and abdome (c). Scale = 1.0 mm.

(1992) suggested that by reducing cannibalism among groups of siblings, matriphagy may facilitate the evolution of social behavior (Crespi 1992). We suggest that here also, matriphagy may be an important part of the evolution of sociality in this group.

To our knowledge this is the first record of matriphagy in pseudoscorpions and *P. nidificator* serves as a good model for the difficult assessment of the costs and benefits of altruistic behavior (Krebs & Davies 1993). Further studies could help to clarify proximate and evolutionary causes of matriphagy in pseudoscorpions. Many questions deserve further research. For example, do nymphs survive better as a consequence of matriphagy? Does matriphagy occur in starving colonies in the same mannner as it occurs with isolated females? Could the *P. nidificator* mother be maximiting her ultimate number of offspring by this extreme form of altruism, similar to that reported to spiders (Kim et. al 2000)? These and other questions confirm there is still much to be learned.

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