

SHORT COMMUNICATION

MATERNAL OR PATERNAL EGG GUARDING? REVISITING PARENTAL CARE IN TRIAENONYCHID HARVESTMEN (OPILIONES)

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ABSTRACT. Based on a photo published in a book on New Zealand arachnids, I propose here that the cases of maternal care described by Forster in 1954 should be considered as paternal care. Maternal care is therefore restricted to the superfamily Gonyleptoidea, while paternal care has evolved in five phylogenetically independent lineages of Opiliones, including representatives of the superfamilies Travunioidea, Epedanoidea, and Gonyleptoidea.

Keywords: Evolution, *Karamea*, Laniatores, Soerensenellinae

In 1954, Ray Forster published a comprehensive study on New Zealand harvestmen in which he provided a detailed taxonomic account of the family Triaenonychidae and also described basic aspects of the natural history of some species. As far as I know, this work was the first record of maternal care in the order Opiliones. Based on field and laboratory observations, the author stated that all New Zealand representatives of the subfamily Soerensenellinae lay small groups of eggs ($n = 10\text{--}20$) on the undersurface of logs or rocks, which are guarded by the female. Some additional information is presented: “At intervals of a few days or a week further eggs are deposited so that in some cases egg masses of some 60–100 eggs may be found, some of which are hatching, while others are found at all stages, often including newly laid eggs” (Forster 1954).

There are several differences in the behavioral patterns of guarding females and guarding males in harvestmen, which are probably a consequence of the different selective pressures leading to the evolution of maternal care (via natural selection) or paternal care (probably via sexual selection). Perhaps the most striking difference is that females care for batches containing eggs in only one stage of embryonic development, while males care for batches containing eggs in several stages of embryonic development, likely from the result of different oviposition events (Machado et al. 2004). Therefore, the behavioral pattern of oviposition described for the New Zealand Soerensenellinae contrasts with all other harvestman species that present maternal care and is remarkably similar to the species that present

paternal care (see Machado et al. 2004). Unfortunately no photograph or drawings were provided in Forster’s paper and no voucher specimens were mentioned for the behavioral observations; thus it is not possible to examine the individuals studied by Forster in order to determine the identity of the sex that provides care.

More recently, Ray and Lynn Forster published a book called “Spiders of New Zealand and Their Worldwide Kin” (Forster & Forster 1999), which contains a brief description of the general biology of the New Zealand harvestmen, mostly based on the data previously presented in his paper of 1954. The book provides a color photo of an individual of *Karamea* sp. (Triaenonychidae, Soerensenellinae) guarding an egg-batch (Figure 1). This photo is highly informative since it clearly shows that the parental individual is a male and not a female. Many triaenonychid males are easily recognized due to the size of their swollen chelicerae and, in some species, also to the shape of the ocularium, which bends forwards while in females it is an erect spine (Lawrence 1937; Maury & Roig-Alsina 1985). Moreover, it is also possible to recognize in the photo that the eggs are in different stages of embryonic development (as described by Forster 1954), which is congruent with the multiple ovipositions observed in paternal harvestmen. Thus, Figure 1 provides unequivocal evidence that at least in this species of the genus *Karamea* the guarding individuals are males. However, there is no reason to believe that this case is an exception since Forster (1954) clearly states that all New Zealand Soerensenellinae show the same reproductive pattern.

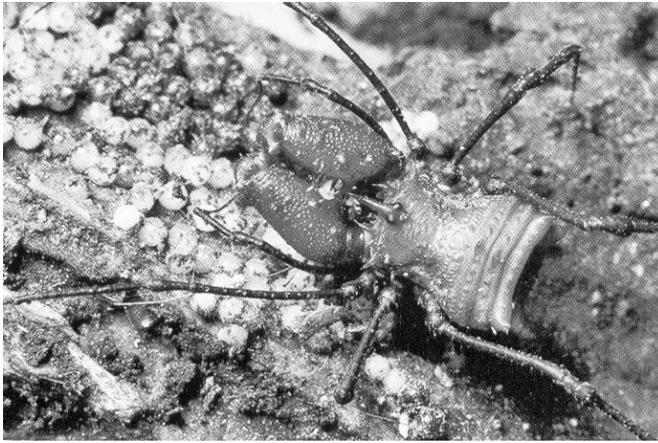


Figure 1.—Male of the triaenonychid harvestman *Karama* sp. (Soerensenellinae) caring for eggs in different embryonic stages (noted by the difference in size and coloration) under a rotting log in New Zealand. Photo by Forster & Forster (1999), reproduced here with the permission of the University of Otago Press.

Consequently, paternal care, and not maternal care, is probably the rule in the subfamily. A final piece of information that can be extracted from the photo, which has never been mentioned by Forster, is that the debris is attached to the eggs, probably by the ovipositing females. This behavior has been previously described for several harvestman species of the families Cosmetidae and Gonyleptidae that present no care or exclusive maternal care (references in Willemart 2001), but it is the first record of its existence in a paternal species.

Debate about the existence of paternal care has been commonplace in the behavioral literature (see examples in Tallamy 2001), but misinterpretations about the sex of the guarding individuals are somewhat rare. Tallamy et al. (2004) recently showed that, with the assassin bug *Atopozelus pallens*, the females and not the males are responsible for egg protection. Curiously, like the case of triaenonychids reported here, the sexual dimorphism is quite evident and males and females can be easily recognized in the field. Another interesting case of mistaken parental identity is found in giant water bugs (Heteroptera: Belostomatidae) in which males of the subfamily Belostomatinae brood eggs laid by the females on their backs (Smith 1997). Since there is no clear sexual dimorphism among belostomatines, the parental behavior was originally attributed to females (Dimmock 1887). Surprisingly the mistake was not corrected for several years (Slater 1899), despite the fact that females are clearly unable to lay eggs on their own dorsum.

A putative explanation for Forster's mistake is that he was influenced by the widespread occurrence of maternal care in arthropods and the total absence of paternal care in arachnids until that moment. The first case of paternal assistance in the

arachnids was reported only at the end of the 1970s when Rodríguez & Guerrero (1976) described males of the manaosbiid harvestman *Zygopachylus albomarginis* Chamberlain 1925 guarding eggs and early hatched nymphs inside mud nests in Panama. Even if we take arthropods as a whole, the number of cases of paternal care in the literature by the 1950s was low (see references in Tallamy 2001). On the other hand, maternal care has been reported as early as the 18th and 19th centuries for non-social insects (e.g., Modeer 1764) and arachnids (e.g., Latreille 1802).

The presence of paternal care in the New Zealand triaenonychids has important implications for the evolution of the forms of parental care in the order Opiliones, particularly among the Laniatores. Maternal care is therefore restricted to the superfamily Gonyleptoidea, occurring in the families Cosmetidae, Cranidae, Gonyleptidae, and Stygnopsidae (see references in Machado & Raimundo 2001; Machado & Warfel 2006). The first real case of maternal assistance in harvestmen belongs to the gonyleptid *Acanthopachylus aculeatus* (Kirby 1818) from Uruguay (Capocasale & Bruno-Trezza 1964). Paternal care, on the other hand, has evolved in five phylogenetically independent lineages of Opiliones: once in Soerensenellinae triaenonychids (superfamily Travunioidea), once in podoctids (superfamily Epedanoidea), once in assamiids, and at least twice in gonyleptids (superfamily Gonyleptoidea) (see references in Machado et al. 2004).

I thank Wendy Harrex from the Otago University Press for giving me the permission to reproduce the photo of the male *Karama*, Adriano B. Kury for identifying the sex of the individual in Figure 1, Rogelio Macías Ordóñez, Jeffrey W. Shultz, and two anonymous reviewers for comments on the

manuscript. GM is supported by grants from Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP, proc. #02/00381-0).

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Manuscript received 26 March 2006, revised 17 October 2006.