

Research article

Amphisexual care in *Acutisoma proximum* (Arachnida, Opiliones), a neotropical harvestman with exclusive maternal care

B.A. Buzatto¹ and G. Machado²

¹ Programa de Pós-graduação em Ecologia, Instituto de Biologia, Universidade Estadual de Campinas, Campinas, Brazil,
e-mail: bruno.buzatto@gmail.com

² Departamento de Ecologia, Instituto de Biociências, Rua do Matão, trav. 14, n° 321, Cidade Universitária, 05508–900, São Paulo, SP, Brazil,
e-mail: glaucom@ib.usp.br

Received 5 August 2008; revised 13 and 29 October 2008; accepted 25 November 2008
Published Online First 15 December 2008

Abstract. We provide observational and experimental evidence that territorial males of the maternal harvestman *Acutisoma proximum* temporarily care for clutches that are left unattended by females from their harems. The evolution of paternal care in harvestmen from a territory-based polygynous mating system is discussed.

Keywords: Evolution, Gonyleptidae, male territoriality, paternal care, polygyny.

Exclusive postovipositional paternal care is the rarest form of parental investment among arthropods, and all described cases in Arachnida are restricted to the order Opiliones (Machado and Macías-Ordóñez, 2007). The most important cost of paternal care is probably the loss of mating opportunities because a trade-off is expected to exist between parental effort and mating effort (Trivers, 1972). However, this reproductive cost may be reduced when males defend a territory where multiple females lay their eggs, since territorial males may increase their fitness by indirectly defending these eggs against predation (Williams, 1975). In fact, the possibility that paternal care evolved from a territory-based polygynous mating system has been suggested for fish, anurans (Williams, 1975; Ridley, 1978), and some harvestmen (Mora, 1990; Machado and Raimundo, 2001). Additionally, if paternal care is a sexually selected trait, males providing care should be preferred by females and obtain a greater number of copulations than males that are unable and/or unwilling to provide care (Tallamy, 2000, 2001).

Acutisoma proximum (Opiliones: Gonyleptidae) is a polygynous harvestman whose mating system contains components of both resource defense and female defense polygyny (Buzatto and Machado, 2008). At the beginning of the reproductive season, males fight other males for the possession of territories on the vegetation where females will later oviposit, as is typical of resource defense polygyny. Females have a marked preference for specific host plant species, and males establish their territories in areas where these host plants are especially abundant. Later in the reproductive season, males reduce their patrolling activity on the vegetation and focus on guarding individual females that are ovipositing inside their territories, as occurs in female defense polygyny. After oviposition, females take care of their eggs for approximately 37 days, defending them against the attack of predators (Buzatto et al., 2007). During the caring period, females may desert their clutches for brief intervals to take shelter during the coldest hours of the day. Moreover, clutches may also end up unattended when the parental female dies during the caring period. In the present study, we tested if territorial males of *A. proximum* exhibit amphisexual care, i.e., if they take over the guard of clutches when caring females desert or are experimentally removed. The existence of amphisexual care in this species would support the hypothesis that male care in harvestmen evolved from a territory-based polygynous mating system (Mora, 1990; Machado and Raimundo, 2001).

The study was conducted at Intervalos State Park (24°14'S/48°04'W, 800 m a.s.l.), southern São Paulo state, south-eastern Brazil. The *A. proximum* population studied here was found on the vegetation flanking a small river (5 m wide) inside the forest (for details on the study

site see Buzatto et al., 2007). Approximately 800 h of focal observations were conducted on 29 harems between December 2006 and March 2007. These harems were composed of one territorial male and up to six caring females. In February 2007, 11 caring females from the focal harems were experimentally removed from their clutches and kept alive in plastic vials. The presence of territorial males on unattended clutches was monitored on six instantaneous scans a day (at 9, 11, 14, 16, 21 and 23 h) during 10 consecutive days.

Since there is no evidence that females of *A. proximum* are able to clean the eggs and actively protect the offspring against fungal attack, defense against egg-predators is probably the main function of maternal care in this harvestman (Buzatto et al., 2007). In order to test if males that were caring for eggs after female removal also exhibited aggressive responses against potential egg-predators, four caring males were experimentally approached by a female of the harvestman *Promitobates ornatus* (a known predator of *A. proximum* eggs, Buzatto et al., 2007). Afterward, it was recorded whether these males attacked the individuals of *P. ornatus* or fled away abandoning the clutch.

In six out of the 11 experimental clutches, after 4–192 h from female removal, the territorial males were found resting on the clutches in a typical caring position (Fig. 1). Those males stood with the clutches for up to eight days, but all of them temporarily abandoned their clutches a few times during this period (mean frequency of care = 31.5 %, range = 6–100 %). Only one of the males responded aggressively to the approach of a potential egg predator, attacking the female *P. ornatus* in the same way caring females were seen to repel conspecifics (see Buzatto et al., 2007). The other three males abandoned the clutches without showing any aggressive reactions towards the “intruder”, but later returned to their clutches.



Figure 1. After the clutch of a caring *Acutisoma proximum* female had been experimentally removed, the territorial male resident in the area took care of the clutch for up to eight days.

Furthermore, in four out of the 18 unmanipulated harems, one of the caring females naturally disappeared during the period of maternal care, probably due to the mortality caused by parasitoids (Diptera: Phoridae) that attack individuals of *A. proximum* in the study area (unpublished data). In all these cases, the territorial males also took over guarding the eggs. Those males stayed on the clutches from two to nine consecutive days, and the frequency that they were recorded on the clutches ranged from 80 % to 100 % of the observations. One male stayed with the offspring for six days after the nymphs had hatched. Another male was seen consuming a few eggs from his clutch during the first hours after female disappearance, but later stayed five more days on the clutch without eating any more eggs.

Amphisexual behavior has already been recorded in two other Goniosomatinae species (*Acutisoma longipes* and *Goniosoma albicriptum*), whose males have been observed temporarily taking care of unattended clutches (Machado and Oliveira, 1998; Willemart and Gnaspini, 2004). In the present study, we have observed *A. proximum* males providing amphisexual care under natural conditions and also induced this behavior by experimentally removing caring females from several males' harems. Although male care is temporary, this behavior may be crucial (especially just before hatching), since egg predators can consume entire clutches in a few days (Buzatto et al., 2007). However, the frequency and intensity of care-giving between males and females is markedly different, since males frequently left the clutches unattended and rarely repelled potential egg-predators. These results contrast with those obtained for the burying beetle *Nicrophorus vespilloides* (Coleoptera: Silphidae) and for the assassin bug *Rhynocoris tristis* (Heteroptera: Reduviidae), in which individuals of both sexes take care of the offspring with similar efficiency (Smiseth et al., 2005; Beal and Tallamy, 2006). We suggest that harem holders of *A. proximum* are not willing to pay the potential injury costs of offspring defense against large egg predators because the possession of their territories depends on the integrity of their weapons (pedipalps and second pair of legs), which in turn is related to their ability to repel conspecific males (Buzatto and Machado, 2008).

The amphisexual care recorded here has at least two behavioral similarities with the exclusive post-zygotic paternal care described for other harvestman species: (1) like most paternal species, males do not stay on their clutches all the time, and leave them unattended for some time (generally hours), probably in order to forage (Machado et al., 2004); (2) like *Iporangaia pustulosa* (Gonyleptidae), males may consume some eggs of their clutches (Machado et al., 2004), which may be viewed as a means of acquiring energy without abandoning the clutch or the territory. Our results on amphisexual care in *A. proximum* provide support to the hypothesis that male care in harvestmen, even for short periods, is likely to occur when males defend a territory that is also an

oviposition site. However, it is still not clear whether paternal care in the group has evolved from no care or from female care, since in both cases males may be attached to a territory (Machado and Macías-Ordóñez, 2007). Given that male care has evolved at least seven times independently in the order Opiliones (Machado, 2007), the group offers an ideal opportunity to investigate this question using a comparative approach.

Acknowledgments

To the staff of Intervalos State Park for logistical support, to G.S. Requena for helping in the fieldwork, and to Roberto Munguía Steyer, Douglas W. Tallamy, and two anonymous reviewers for comments on an early version of the manuscript. The study was supported by fellowships from the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP, 02/00381–0 and 03/05427–0) and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES).

References

- Beal C.A. and Tallamy D.W. 2006. A new record of amphisexual care in an insect with exclusive paternal care: *Rhynocoris tristis* (Heteroptera: Reduviidae). *J. Ethol.* **24**: 305–307
- Buzatto B.A. and Machado G. 2008. Resource defense polygyny shifts to female defense polygyny over the course of the reproductive season of a neotropical harvestman. *Behav. Ecol. Sociobiol.* **63**: 85–94
- Buzatto B.A., Requena G.S., Martins E.G. and Machado G. 2007. Effects of maternal care on the lifetime reproductive success of females in a Neotropical harvestman. *J. Anim. Ecol.* **76**: 937–945
- Machado G. 2007. Maternal or paternal egg guarding? Revisiting parental care in triaenonychid harvestmen (Opiliones). *J. Arachnol.* **35**: 202–204
- Machado G. and Oliveira P.S. 1998. Reproductive biology of the Neotropical harvestman (*Goniosoma longipes*) (Arachnida, Opiliones: Gonyleptidae): mating and oviposition behaviour, brood mortality, and parental care. *J. Zool.* **246**: 359–367
- Machado G. and Macías-Ordóñez R. 2007. Reproduction. In: *Harvestmen: The Biology of Opiliones* (Pinto-da-Rocha R., Machado G. and Giribet G., Eds), Harvard University Press, Cambridge. pp 414–454
- Machado G. and Raimundo R.L.G. 2001. Parental investment and the evolution of subsocial behaviour in harvestmen (Arachnida Opiliones). *Ethol. Ecol. Evol.* **13**: 133–150
- Machado G., Requena G.S., Buzatto B.A., Osses F. and Rossetto L.M. 2004. Five new cases of paternal care in harvestmen (Arachnida: Opiliones): implications for the evolution of male guarding in the Neotropical family Gonyleptidae. *Sociobiology* **44**: 577–598
- Mora G. 1990. Parental care in a neotropical harvestman, *Zygopachylus albomarginis* (Arachnida: Gonyleptidae). *Anim. Behav.* **39**: 582–593
- Ridley M. 1978. Paternal care. *Anim. Behav.* **20**: 904–932
- Smiseth P.T., Dawson C., Varley E. and Moore A.J. 2005. How do caring parents respond to mate loss? Differential responses by males and females. *Anim. Behav.* **69**: 551–559
- Tallamy D.W. 2000. Sexual selection and evolution of exclusive paternal care in arthropods. *Anim. Behav.* **60**: 559–567
- Tallamy D.W. 2001. Evolution of exclusive paternal care in arthropods. *Annu. Rev. Entomol.* **46**: 139–165
- Trivers R.L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man* (Campbell B., Ed), Aldine Press, Chicago. pp 136–179
- Willemart R.H. and Gnaspini P. 2004. Breeding biology of the cavernicolous harvestman *Goniosoma albicriptum* (Arachnida, Opiliones, Laniatores): sites of oviposition, egg-batches characteristics and subsocial behaviour. *Invertebr. Reprod. Dev.* **45**: 15–28
- Williams G.C. 1975. *Sex and Evolution*. Princeton University Press, Princeton. 200 pp

To access this journal online:
<http://www.birkhauser.ch/IS>
