

SHORT COMMUNICATION

Paternal care in a Neotropical harvestman (Opiliones: Cosmetidae) from Costa Rica

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Abstract. Although relatively rare among harvestmen in the superfamily Gonyleptoidea, paternal care has been observed in the families Manaosbiidae and Gonyleptidae, but not previously in the Cosmetidae. In this study, we describe multiple observations of egg guarding by adult males of an undescribed species of cosmetid harvestman from Volcán Cacao, Guanacaste Province, Costa Rica. Observations were made from 26–28 July 2010, during the wet season. In this species, males only guard eggs after dusk, leaving eggs unattended during the day. Based upon differences in color and size, males guarded eggs through several stages of development. When guarding, males contacted the first two pairs of legs with the eggs. Oviposition sites consisted of the undersides of leaves of small plants, with eggs closely packed together in a single layer covered by abundant, transparent mucus. The largest, darkest eggs were located near the distal tip of the leaf.

Keywords: Behavioral ecology, Central America, egg guarding, polyandry, reproduction

In this study, we describe multiple observations of egg guarding by adult males of an undescribed species of cosmetid harvestman in Central America. Among Neotropical harvestmen of the suborder Laniatores, parental care may take several forms including the guarding of nymphs and the burying, hiding, carrying, or guarding of eggs (Machado & Raimundo 2001) and is performed by the adult female or male (Machado & Macías-Ordóñez 2007). Maternal care, though generally more common, is restricted to the Gonyleptoidea, including species in the families Cosmetidae (Goodnight & Goodnight 1976), Cranidae (Machado & Warfel 2006; Hunter et al. 2007), Gonyleptidae (Machado & Raimundo 2001) and Stygnopsidae (Mitchell 1971). In contrast, exclusive paternal care is relatively rare and is known to occur in species from the families Assamiidae (Martens 1993), Gonyleptidae (Hara et al. 2003; Machado et al. 2004), Manaosbiidae (Rodríguez & Guerrero 1976; Mora 1990), Podoctidae (Martens 1993) and Triaenonychidae (Forster 1954, but see Machado 2007). True biparental care of eggs or nymphs has not been conclusively demonstrated. However, in *Goniosoma longipes* (Gonyleptidae), males will assume parental care if the guarding female is removed (Machado & Oliveira 1998).

In general, there are considerable, consistent differences between the sexes with respect to egg guarding behavior. In the field, maternal care is essential for preventing egg predation by insects, including ants (Machado & Oliveira 2002) and crickets (Machado & Oliveira 1998). In the manaosbiid harvestman *Zygopachylus albomarginis*, adult males effectively protect eggs against fungal growth and cannibalism by conspecifics (Mora 1990). The guarding of eggs by male harvestmen may also attract females, enabling these individuals to mate more frequently than conspecifics that are not associated with eggs (Nazareth & Machado 2010). In species with maternal care, females generally only guard eggs of the same age (same stage of development), and the eggs are guarded continuously (Machado & Macías-Ordóñez 2007). In contrast, males often guard eggs of different ages (multiple stages of development) and may regularly leave the eggs to undertake other activities, such as foraging (Hara et al. 2003; Machado et al. 2004).

We observed cosmetid harvestmen in the field from 26–28 July 2010 at Cacao Field Station (10°55'15.79"N, 85°28'3.53"W, elev. 1049 m) on the southwestern slope of Guanacaste National Park, Guanacaste Province, Costa Rica. The forested habitat in this area features a canopy height of approximately 20 m with an understory composed of small plants, generally less than 0.5 m in total height. During evening observations (2100–2300 h), air temperature was approximately 20–21° C and relative humidity was nearly 99%, with little to no wind or rain.

Over the three-day period, we observed four instances of paternal care. Egg batches (A, B, C and D) were observed for 15-min periods each, at approximately 12 and 24 h increments following their discovery. All eggs were covered in a thick, transparent mucus coat (Fig. 1A, B). Egg batches A, C and D occurred on the underside of leaves of the same species of small unidentified plant (Sapotaceae), while egg batch B (Fig. 1B) was on the underside of a leaf of *Symphonia globulifera* (Clusiaceae). On 26 July 2010 at 2100 h, we located egg batches A and B on the underside of leaves from plants that were 30 cm tall. The plants were no more than 2 m apart and the eggs and guarding males were on the undersides of leaves, approximately 10 cm above the ground (Fig. 1A). When initially disturbed, the adult males actively waved legs I and II over the eggs and occasionally touched them, most frequently with leg I. Egg batch A contained 39 eggs at two different stages of development (based on egg color and size). Egg batch B had approximately 150 eggs representing at least two different stages of development. We photographed the egg batches and marked their location with flagging. At 0800 h the following day, we relocated the unattended egg batches. We briefly searched the surrounding leaf litter and adjacent plants, but did not find either male. Later that evening (27 July) at 2100 h, we returned and found that both males had resumed guarding their eggs. We observed the males, collected the leaf containing the eggs and male, placed them into the same container and monitored them for 72 h. Males continued guarding eggs, but no hatching occurred over this interval, so we preserved the eggs and the males in 70% ethanol.

During the evening of 27 July, we discovered two additional egg batches, approximately 10 m from the first two batches. Egg batch C was 5 cm above the ground on the underside of a leaf and contained

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Figure 1.—Paternal care by an undescribed species of cosmetid harvestman. A. Male guarding an egg batch on the underside of a leaf (Sapotaceae) that is approximately 10 cm above the litter. B. Egg batch with eggs at two developmental stages on the distal tip of leaf of *Symphonia globulifera* (Clusiaceae). The eggs are covered in a thick mucus coat, and those closest to the leaf margin are darker and seem to have been laid first.

17 eggs at two different stages of development. When disturbed, the guarding male actively waved legs I and II over the eggs. Egg batch D was approximately 4 m away from batch C and was 10 cm above the ground. This batch had 57 eggs at two different stages of development. We observed and photographed the batches and marked their locations with flagging. At 0800 h on the following day, we returned and found the eggs unguarded. We did not collect these eggs.

Our natural history observations offer new and important insights into the reproductive biology of Laniatores harvestmen and the evolution of paternal care. The ovipositional pattern and paternal care that we observed has previously only been reported for species from the sister subfamilies Caelopyginae and Progonyleptoidellinae of the Gonyleptidae (Machado et al. 2004). In these gonyleptid harvestmen, eggs are 1) deposited on the undersurface of leaves; 2) laid from the apex to the base of the leaf; 3) covered in a thick mucus coat and 4) guarded by males during postzygotic development. Cosmetid harvestmen are not phylogenetically closely related to this group; thus, our observations represent the first report of a new, independent event in the evolution of paternal care in harvestmen.

In several gonyleptid harvestmen that exhibit paternal care, sexual dimorphism with respect to body size and the armature of leg IV is generally reduced (Kury & Pinto-da-Rocha 1997; Pinto-da-Rocha 2002). However, in other species with paternal care, strong sexual dimorphism is associated with defense by the male of a specific and scarce resource, such as a tree hole (Machado et al. 2004; Nazareth & Machado 2009). In the cosmetid species that we examined there was little sexual dimorphism with respect to body size or the armature of leg IV. However, this species is unique among the 133 formally described cosmetid species from Central America (Townsend et al. 2010), because males only have four tarsomeres on leg I, whereas females have five. In addition, the two most basal tarsal segments on leg I are enlarged in the male, but not in the female. Given that sexual differences in the relative size of the basal tarsomeres are very common among cosmetid harvestmen, it seems likely that this dimorphism reflects sexual selection for intra- or intersexual communication, rather than egg guarding.

Our observations represent important contributions to the natural history of harvestmen in the family Cosmetidae, the second largest group of Neotropical (> 700 described species) harvestmen. Little is known about the fecundity, frequency of reproduction, parental care, or preferences for oviposition sites of most species (Machado & Macías-Ordóñez 2007). In two Nearctic cosmetid species of *Vonones*, females produce a single batch of 85 or more eggs and cover or hide them (Goodnight 1958; Cokendolpher & Jones 1991). Oviposition sites include fallen tree trunks, leaf litter and the inside crevices of moist wood (Machado & Macías-Ordóñez 2007). In other Neotropical cosmetid species from the Caribbean and South America, females lay one or two batches of 90–240 eggs and generally cover and hide their eggs (Canals 1936; Juberthie 1972; Friebe & Adis 1983). The only cosmetid harvestman from Central America that has been studied is *Erginulus clavotibialis* (Goodnight & Goodnight 1976). In this species females produce a single batch of 90–100 eggs, with oviposition occurring in spaces under tree bark or in crevices. In contrast to other cosmetid species, however, female *E. clavotibialis* actively guard their eggs.

During our field observations we observed that egg batches were only guarded by males at night, and that each batch contained eggs at different stages of development. These behavioral patterns are similar to those observed in other Neotropical harvestmen (Hara et al. 2003; Machado et al. 2004). In the manausbiid *Zygopachylus albomarginis* (Mora 1990) and the gonyleptid *Iporangaia pustulosa* (Machado et al. 2004), rival males consume unprotected eggs. Machado et al. (2004) provided three possible explanations for why male parental care is discontinuous, including the hypotheses that 1) males lack sufficient energy reserves to sustain extended guarding periods, so they must leave eggs to forage; 2) males actively guard the eggs at a distance during the day and protect them from conspecifics or other predators; and 3) males use the time away from guarding the eggs to search for additional mates. Additional field studies that involve monitoring the behavior of males guarding egg batches as well as the survival of egg batches that are guarded and unguarded (through male removal) are needed to assess the efficacy of paternal care in this species.

In most species of harvestmen, eggs grow larger and change color during development, gradually darkening before hatching (Gnaspiñi 2007). In gonyleptid harvestmen that oviposit on the undersurface of leaves, the first eggs that are laid by females are closest to the apex (Machado et al. 2004). On the basis of the position of the eggs and their different sizes and colors, we infer that these males guard batches of eggs through several developmental stages. We also infer that eggs at different stages of development are the result of different oviposition events, by one or more females. In 11 species of gonyleptid harvestmen, males mate multiple times and guard eggs produced by multiple females (Machado & Macías-Ordóñez 2007). Thus, we hypothesize that the cosmetid species in our study also exhibits a polygynic mating system. Additional field studies that

involve the mark-recapture of females in the vicinity of guarding males are needed to assess this hypothesis.

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LITERATURE CITED

- Canals, J. 1936. Observaciones biológicas en arácnidos del orden Opiliones. *Revista Chilena Historia Natural* 40:61–63.
- Cokendolpher, J.C. & S.R. Jones. 1991. Karyotype and notes on the male reproductive system and natural history of the harvestman *Vonones sayi* (Simon) (Opiliones, Cosmetidae). *Proceedings of the Entomological Society of Washington* 93:86–91.
- Forster, R.R. 1954. The New Zealand harvestmen (sub-order Laniatores). *Canterbury Museum Bulletin* 2:1–329.
- Friebe, B. & J. Adis. 1983. Entwicklungzyklen von Opiliones (Arachnida) im Schwazwasser-Überschwemmungswald (Igapó) des Rio Tarumã Mirim (Zentralamazonien, Brasilien). *Amazoniana* 8:101–110.
- Goodnight, C.J. 1958. Two representatives of a tropical suborder of opilionids (Arachnida) found in Indiana. *Proceedings of the Indiana Academy of Sciences* 67:322–323.
- Goodnight, M.L. & C.J. Goodnight. 1976. Observations on the systematics, development, and habits of *Erginulus clavotibialis* (Opiliones: Cosmetidae). *Transactions of the American Microscopical Society* 95:654–664.
- Gnaspini, P. 2007. Development. Pp. 455–472. *In* Harvestmen: The Biology of Opiliones. (R. Pinto-da-Rocha, G. Machado & G. Giribet, eds.). Harvard University Press, Cambridge, Massachusetts.
- Hara, M.R., P. Gnaspini & G. Machado. 2003. Male guarding behavior in the Neotropical harvestman *Ampheres leucopheus* (Mello-Leitão, 1922) (Opiliones, Laniatores, Gonyleptidae). *Journal of Arachnology* 31:441–444.
- Hunter, R.K., D.N. Proud, J.A. Tibbetts, J.A. Burns & V.R. Townsend, Jr. Parental care in the neotropical harvestman *Phaveicranaus calcariferus* (Opiliones, Laniatores, Cranidae). *Journal of Arachnology* 35:199–201.
- Juberthie, C. 1972. Reproduction et développement d'un opilion Cosmetidae, *Cynorta cubana* (Banks) de Cuba. *Annales Spéléologie* 27:773–785.
- Kury, A.B. & R. Pinto-da-Rocha. 1997. Notes on the Brazilian harvestmen genera *Progonyleptoidellus* Piza and *Iporangaia* Mello-Leitão. *Revista Brasileira de Entomologia* 41:109–115.
- Machado, G. 2007. Maternal or paternal egg guarding? Revisiting parental care in triaenonychid harvestmen (Opiliones). *Journal of Arachnology* 35:202–204.
- Machado, G. & R. Macías-Ordóñez. 2007. Reproduction. Pp. 414–454. *In* Harvestmen: The Biology of Opiliones. (R. Pinto-da-Rocha, G. Machado & G. Giribet, eds.). Harvard University Press, Cambridge, Massachusetts.
- Machado, G. & P.S. Oliveira. 1998. Reproductive biology of the Neotropical harvestman *Goniosoma longipes* (Arachnida, Opiliones, Gonyleptidae): mating and oviposition behaviour, brood mortality, and parental care. *Journal of Zoology* 246:359–367.
- Machado, G. & P.S. Oliveira. 2002. Maternal care in the Neotropical harvestman *Bourguyia albiornata* (Arachnida, Opiliones): oviposition site selection and egg protection. *Behaviour* 139:1509–1524.
- Machado, G. & R.L.G. Raimundo. 2001. Parental investment and the evolution of subsocial behaviour in harvestmen (Arachnida Opiliones). *Ethology Ecology & Evolution* 13:133–150.
- Machado, G., G.S. Requena, B.A. Buzatto, F. Osses & L.M. Rossetto. 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.
- Machado, G. & J. Warfel. 2006. First case of maternal care in the family Cranidae (Opiliones, Laniatores). *Journal of Arachnology* 34:269–272.
- Martens, J. 1993. Further cases of paternal care in Opiliones (Arachnida). *Tropical Zoology* 6:97–107.
- Mitchell, R.W. 1971. Egg and young guarding by a cave-dwelling harvestman, *Hoplobunus boneti* (Arachnida). *Southwestern Naturalist* 15:392–395.
- Mora, G. 1990. Paternal care in a Neotropical harvestman, *Zygopachylus albomarginis* (Arachnida, Opiliones: Gonyleptidae). *Animal Behavior* 39:582–593.
- Nazareth, T.M. & G. Machado. 2009. Reproductive behavior of *Chavesincola inexpectabilis* (Opiliones, Gonyleptidae) with description and independently evolved case of paternal care in harvestmen. *Journal of Arachnology* 37:127–134.
- Nazareth, T.M. & G. Machado. 2010. Mating system and exclusive postzygotic paternal care in a Neotropical harvestman (Arachnida: Opiliones). *Animal Behaviour* 79:547–554.
- Pinto-da-Rocha, R. 2002. Systematic review and cladistic analysis of the Caelopyginae (Opiliones, Gonyleptidae). *Arquivos de Zoologia* 36:357–464.
- Rodríguez, C.A. & S. Guerrero. 1976. La historia natural y el comportamiento de *Zygopachylus albomarginis* (Chamberlin) (Arachnida: Opiliones: Gonyleptidae). *Biotropica* 8:242–247.
- Townsend, V.R. Jr., C. Viquez, P.A. VanZandt & D.N. Proud. 2010. Key to the Cosmetidae (Arachnida, Opiliones) of Central America, with notes on penis morphology and sexual dimorphisms. *Zootaxa* 2414:1–26.

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