

EGG COVERING BEHAVIOR OF THE NEOTROPICAL HARVESTMAN *PROMITOBATES ORNATUS* (OPILIONES, GONYLEPTIDAE)

Rodrigo Hirata Willemart: Departamento de Zoologia, Instituto de Biociências,
Universidade de São Paulo, Caixa Postal 11461, 05422-970, São Paulo, SP, Brazil

ABSTRACT. The egg covering behavior of the laniatorid harvestman *Promitobates ornatus* was studied. Females of this species laid eggs isolated, on soil. After laying an egg, the female started scraping the substrate next to the egg, picking up debris, and attached the earth particles to the egg. After she scraped one area, she rotated around the egg, stopped turning, and restarted the collection of debris from another site. Alternation of scraping and changing body position was repeated twice or more until the female completed the egg covering. Data on egg size, duration of egg laying and egg covering, and duration of embryonic development are also provided.

Keywords: Laniatores, Mitobatinae, biology, care, maternal investment

In the Laniatorine suborder of Opiliones, females lay eggs that are either clustered (Canals 1936; Capocasale & Bruno-Trezza 1964; Mitchell 1971; Juberthie & Muñoz-Cuevas 1971; Matthiesen 1975; Goodnight & Goodnight 1976; Pinto-da-Rocha 1993; Ramires & Giarretta 1994; Gnaspini 1995; Machado & Oliveira 1998) or isolated (Canals 1936; Juberthie 1965, 1972; Cokendolpher & Jones 1991), on a large variety of substrates, such as leaves, moss, rocks, bark crevices and soil.

Among the Laniatores (unless otherwise indicated, all species mentioned below belong to the family Gonyleptidae), different forms of parental investment have been described in the literature, ranging from the oviposition site selection to egg guarding. Egg guarding has been observed in one species of Cosmetidae and one of Stynopsidae and in seven species of Gonyleptidae (see Gnaspini 1995 for references), and is usually performed by females. Paternal care has seldom been reported (Rodríguez & Guerrero 1976; Mora 1990; Martens 1993) and there is no record of biparental care in harvestmen, although Machado & Oliveira (1998) reported males of *Goniosoma longipes* (Roewer 1913) near the eggs, and taking care of eggs when the female was experimentally removed.

Scotolemon lespesi Lucas 1860 (Juberthie 1965), *Cynorta cubana* (Banks 1909) (Cosmetidae) (Juberthie 1972), *Pachylus quina-vidensis* Muñoz-Cuevas 1969 (Juberthie &

Muñoz-Cuevas 1971), *Vonones sayi* (Simon 1879) (Cosmetidae) (Cokendolpher & Jones 1991) as well as two other species of cosmetids and six species of gonyleptids (Canals 1936) are known to cover eggs with debris.

The behavior of covering eggs has never been described in detail. The only mention of how egg covering occurs was by Canals (1936), who reported “scraping of the substrate with the anterior legs” by the female. Again, he did not specify which species did this. This paper provides the first detailed description of egg covering behavior in harvestmen, based on data from *Promitobates ornatus* (Mello-Leitão 1922) (Mitobatinae).

Three female *P. ornatus* were used for this study. One of them (identified as *Po1*) was collected on 24 January 1999 in Carlos Botelho State Park, São Miguel Arcanjo county. The other two (identified as *Po2* and *Po3*) were collected on 27 July 1999 in Paranapiacaba (= Alto da Serra), Santo André county. Both localities are representative of tropical rain forest in São Paulo state, southeastern Brazil. I maintained *Po1* with a conspecific male at room temperature in a terrarium with damp soil, a wet piece of cotton, and hard surfaces such as stones and plastic blocks. *Po2* and *Po3* were kept in a second terrarium under the same conditions, but with six other conspecifics including males and females. In both of the cases, the artificial light : dark periods were irregularly distributed throughout



Figure 1.—Drawing of an egg of *Promitobates ornatus* after the covering was completed, showing soil particles (black spots) and a fragment of root (arrow) attached to it.

the day. The harvestmen were fed once a week with dead arthropods such as isopods, mosquitoes, drosophilids, pieces of *Tenebrio obscurus* larvae and a variety of plant items (papaya, sugar beet, boiled carrots, beans and rice) and industrial food (cream cheese, cooked ground beef, and bread). They accepted all the items mentioned. All observations were conducted between August 1999 and December 1999.

Females of *P. ornatus* laid isolated eggs over soil surfaces. During oviposition, the female *P. ornatus* stood at legs III and IV, with legs I and II extended forward. The ovipositor extended forward to the genital operculum, at 20° below the horizontal body axis, and the egg slid slowly along it, until the distal part of the ovipositor was reached. At this moment, the female bent the ovipositor bringing it close to the substrate and deposited the egg. Only one egg was laid in each event. In the two cases in which I observed nearly the entire act of oviposition, the times spent for one egg to be laid were 3.4 and 3.5 min. The mean egg length was 1.29 ± 0.16 mm ($n = 8$, range = 1.05–1.40 mm), approximately 25% of the female body length (5.10, 5.15, and 5.20 mm). Females laid eggs in the morning ($n = 5$; one not included in Table 1), afternoon ($n = 3$) and at night ($n = 2$), and so apparently did not favor a particular time of day for oviposition.

The time spent by *P. ornatus* to lay one egg was similar to that in other laniatorean species—e.g., 4–12 min for *Pachylus quinamav-*

idensis (Juberthie & Muñoz-Cuevas 1971). The general egg-laying behavior was also similar among the species studied so far, and follows the general description of Juberthie & Muñoz-Cuevas (1971). However, after laying an egg, *P. ornatus* waved legs I over the egg occasionally touching it. Thereafter, the female started scraping the substrate next to the egg with alternate movements of legs I, picking up debris. She then raised legs I and strongly pressed them simultaneously or one at a time against the egg, leaving earth particles attached to it. While scraping, some bigger particles were occasionally brought near the egg, without adhering to it. After she scraped the substrate from one area, she rotated around the egg, stopped turning, and restarted the collection of soil particles from another site. The female's rotation was either clockwise or counterclockwise, with no apparent rule concerning direction or angle of rotation. Alternation of scraping and changing body position was repeated twice or more until the egg covering was complete (Table 1). The mean time spent during egg covering was 37 ± 11 min ($n = 9$, range = 20–50 min). Occasionally, between two events of scraping, the female would pass her legs I between the chelae of her chelicerae. This explains why the total time is greater than the sum of partial time periods in Table 1. Before leaving the site, the female tapped the substrate around the egg with the first pair of legs. In one case, 2.3 h elapsed between covering one egg and laying the next one.

Promitobates ornatus apparently does not always choose an appropriate site for collection of soil particles. Female *Po1* twice laid an egg in sites where she was unable to turn herself around the egg, although she tried to, because the egg was laid too close to a vertical substrate. In addition, females *Po1* and *Po2* were observed scraping stones instead of earth surfaces, using the same behavioral patterns described earlier. Thus, the quality of the substrate used for collection of soil particles is probably not the factor that determines the time spent in egg covering. It should be noted, however, that the females always laid their eggs on soil, indicating that they probably recognized and selected soil surfaces for oviposition.

Females of *P. ornatus* did not abort egg laying and egg covering when disturbed by light

Table 1.—Change of body position during nine covering events by three females of *Promitobates ornatus* (*Po1*, *Po2*, and *Po3*). The second column represents the positions adopted by the female. In all cases, 0° is horizontally at left and the angles of rotation have to be counted clockwise. Partial time periods follow the sequence of the location of the female relative to the egg. The lines are organized by animal and hour.

Female	Location of female relative to egg	Partial time periods (min)	Total time (min)	Hour when egg covering started
<i>Po1</i>	0°/225°/0°/60°/0°/110°/180°	4/11/4/1/4/9/2	36	0830
<i>Po1</i>	0°/225°/180°/270°	13/9/6/5	34	0919
<i>Po1</i>	0°/225°/0°/65°/135°	9/10/7/10/5	45	1058
<i>Po1</i>	0°/270°/45°/135°	7/12/6/19	45	1135
<i>Po1</i>	0°/90°/135°	12/6/5	24	1500
<i>Po1</i>	0°/90°/225°	6/7/6	20	0010
<i>Po2</i>	0°/180°/340°	24/10/16	51	1836
<i>Po3</i>	0°/270°/180°/90°	15/10/4/19	49	1515
<i>Po3</i>	0°/45°/290°	10/11/7	29	1950

($n = 5$) or by the approach of other harvestmen of approximately the same body size [a conspecific male ($n = 1$) and *Ilhaia cuspidata* Roewer 1913 male introduced in the terrarium ($n = 1$)]. On one occasion, a female stopped egg covering and remained motionless when touched on the dorsum with a thin paintbrush. In this case, she waved her second pair of legs searching for the stimulus. Fleeing only occurred when she touched the paintbrush with her second pair of legs.

This reluctance to abandon the eggs has been described in two other Gonyleptidae. Light did not cause females of *Goniosoma proximum* (Mello-Leitão 1922) with eggs to flee (Ramires & Giaretta 1994) and females of *Acanthopachylus aculeatus* (Kirby 1819) guarding eggs fled only under very intense light (Capocasale & Bruno-Trezza 1964). However, in contrast with the behavior displayed by *P. ornatus*, females of *Pachylus quinamavidensis*, while laying an egg, reacted to approaching conspecific males springing with the palps extended towards the male (Juberthie & Muñoz-Cuevas 1971).

No droplets of exocrine gland secretion were noticed on *P. ornatus*' body while laying or covering an egg, but it could be that secretions are added to the legs as they are passed between the chelicerae. Clawson (1988) noted females of two species of Palpatores would rub the exocrine gland openings over their oviposition sites, and suggested this behavior was to mark the sites.

An average of 30 ± 4.97 days ($n = 5$; range = 23–36) of embryonic development was necessary for nymphs of *P. ornatus* to hatch,

less than the 30–60 days found for *Goniosoma spelaeum* (Mello-Leitão 1933) (Gnaspini 1995) and the 45–64 days for *Goniosoma longipes* (Machado & Oliveira 1998). These differences are tentative since temperature greatly influences the duration of embryonic development, and as mentioned above, the laboratory temperature was not controlled during this study. Egg development took 16–27 days for *Cynorta cubana* at 20–28 °C (Juberthie 1972), 13 days at 26 °C and 23–27 days at 20 °C for *Erginulus clavotibialis* (Cambridge 1904) (Goodnight & Goodnight 1976), and 20–38 days for *Vonones sayi* with the temperature ranging from 5–20 °C (Coken-dolpher & Jones 1991).

Several invertebrates are known to feed on harvestmen eggs—from conspecifics to flatworms, ants, reduviid bugs, staphylinid beetle larvae, and crickets (Capocasale & Bruno-Trezza 1964; Juberthie & Muñoz-Cuevas 1971; Mora 1990; Gnaspini 1995; Machado & Oliveira 1998). In that context, the energy invested in parental care may be justified because of the resulting (presumed) protection from predation (Alcock 1993). Egg covering in *P. ornatus* lasts an average of 37 min, and the process repeats for each egg laid. Nevertheless, this investment is certainly not as costly as the investments made by females of *Goniosoma spelaeum* and *G. longipes*, which lay clustered eggs and stay with their offspring until the dispersion of the nymphs (sometimes 60–80 days between laying eggs and dispersion) (Gnaspini 1995; Machado & Oliveira 1998).

By laying isolated eggs *P. ornatus* avoids the risk of losing several eggs if an egg happens to be noticed by a predator. Covering eggs with debris is interpreted as a way to hide them from predators (Canals 1936; Juberthie 1972; Cokendolpher & Jones 1991), thus increasing the chances of the embryo's survival. I believe that, in addition to the fact that camouflage makes the eggs difficult to be seen, it may also be effective against predators that use tactile clues. A wandering predator may pass over the egg without noticing it because of the soil particles adhered to the egg. In theory, the greater the number of particles attached and the more uniformly they are distributed on the egg surface, the more effective would be the protection. I believe that there is a strong relationship between the act of changing the body position radially around the egg and the effectiveness of the process. As suggested by Mitchell (1971) for eggs laid in crevices, egg guarding would be of little selective value if the egg is difficult to find.

ACKNOWLEDGMENTS

This paper has been greatly improved by the suggestions of my advisor P. Gnaspini, to whom I am deeply grateful. I am also indebted to J. Berry, J. Cokendolpher, G. Machado, R. Suter and an anonymous referee for helpful comments. I thank M.R. Hara for rearing some animals used in this study and R. Pinto-da-Rocha for identification of the harvestmen. F. Garcia provided assistance with computer matters.

LITERATURE CITED

- Alcock, J. 1993. *Animal Behavior: An Evolutionary Approach*. 5th ed., Sinauer Associates, Sunderland. 626 p.
- Canals, J. 1936. Observaciones biológicas em aracnidos del orden Opiliones. *Revista de Chilena de Historia Natural* 40:61–63.
- Capocasale, R. & L. Bruno-Trezza. 1964. Biología de *Acanthopachylus aculeatus* (Kirby, 1819) (Opiliones: Pachylinae). *Revista de la Sociedad Uruguaya de Entomología* 6:19–32.
- Clawson, R.C. 1988. Morphology of defense glands of the opilions (daddy longlegs) *Leiobunum vittatum* and *L. flavum* (Arachnida: Opiliones: Palpatores: Phalangiidae). *Journal of Morphology* 196:363–381.
- 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.
- Gnaspini, P. 1995. Reproduction and postembryonic development of *Goniosoma spelaeum*, a cavernicolous harvestman from southeastern Brazil (Arachnida: Opiliones: Gonyleptidae). *Invertebrate Reproduction and Development* 28: 137–151.
- Goodnight, M.R. & 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.
- Juberthie, C. 1965. Données sur l'écologie, le développement et la reproduction des Opilions. *Revue d'Ecologie et de Biologie du Sol* 2:377–396.
- Juberthie, C. 1972. Reproduction et développement d'un opilion Cosmetidae, *Cynorta cubana* (Banks), de Cuba. *Annales de Spéléologie* 27: 773–785.
- Juberthie, C. & Muñoz-Cuevas 1971. Sur la ponte de *Pachylus quinamavidensis* (Opilion, Gonyleptidae). *Bulletin de la Société d'Histoire Naturelle de Toulouse* 107:468–474.
- Machado, G. & P.S. Oliveira. 1998. Reproductive biology of the Neotropical harvestman (*Goniosoma longipes*) (Arachnida, Opiliones: Gonyleptidae): Mating, oviposition behaviour, brood mortality, and parental care. *Journal of Zoology* 246:359–367.
- Martens, J. 1993. Further cases of paternal care in Opiliones (Arachnida). *Tropical Zoology* 6:97–107.
- Matthiesen, F.A. 1975. Sobre a postura de *Disco-cyrtus pectinifemur* Mello-Leitão, 1937 (Opiliones, Gonyleptidae). *Ciência e Cultura* (São Paulo) 27 suppl:372.
- Mitchell, R.W. 1971. Egg and young guarding by a Mexican cave-dwelling harvestman, *Hoplobunus boneti* (Arachnida). *Southwestern Naturalist* 15:392–394.
- Mora, G. 1990. Paternal care in a Neotropical harvestman, *Zygopachylus albomarginis* (Arachnida, Opiliones: Gonyleptidae). *Animal Behaviour* 39:582–593.
- Pinto-da-Rocha, R. 1993. Invertebrados cavernícolas da porção meridional da Província Espeleológica do Vale do Ribeira, sul do Brasil. *Revista Brasileira de Zoologia* 10:229–255.
- Ramires, E.N. & A.A. Giaretta. 1994. Maternal care in a Neotropical harvestman, *Acutisoma proximum* (Opiliones, Gonyleptidae). *Journal of Arachnology* 22:179–180.
- Rodriguez, C.A. & S. Guerrero. 1976. La historia natural y el comportamiento de *Zygopachylus albomarginis* (Chamberlin) (Arachnida: Opiliones: Gonyleptidae). *Biotropica* 8:242–247.

Manuscript received 20 March 2000, revised 30 November 2000.