Bull. Br. arachnol. Soc. (2001) **12** (3), 144–150

Behavioural repertory and notes on natural history of the Neotropical harvestman *Discocyrtus oliverioi* (Opiliones: Gonyleptidae)*

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Summary

Discocyrtus oliverioi is a Neotropical harvestman that is commonly found in urban areas of Uberlândia, Minas Gerais state, south-eastern Brazil. This paper describes the daily activity pattern, gregariousness, and reproductive biology of this harvestman and provides the first detailed ethogram for a harvestman species. The study was conducted in the laboratory, where 13 females and 5 males were maintained in two terraria from November 1998 to November 1999. Twenty-five behavioural acts were observed and classified in six groups of activities: foraging, social interactions, resting, exploration, cleaning or grooming, and reproduction. The individuals were inactive during the day, and at night they foraged, fed and interacted with other individuals. Five multi-species aggregations of *D. oliverioi*, *Discocyrtus* sp. and *Ilhaia* sp. (Gonyleptidae) were found in the field under fallen trunks. Females of *D. oliverioi* reproduced throughout the year, with the number of eggs per batch being about 25. After laying each egg, females use their first pair of legs to attach pieces of wood and soil to the egg. Females provide parental care and stay over the offspring protecting them against predators for about 22 days. After hatching, the nymphs remain aggregated under the female for up to one week and then they disperse.

Introduction

Most harvestman species live in moist environments, such as caves and forests, where they are frequently found under fallen trunks, rocks and among leaf litter (Edgar, 1990). They are generally photophobic and nocturnal foragers which show a wide variety of feeding habits, ranging from scavengers to predators (Savory, 1938; Phillipson, 1960; Gnaspini, 1996). Although primarily solitary, some harvestman species can form large aggregations (Coddington *et al*., 1990; Machado *et al*., 2000). The most common reproductive mode in the order involves copulation, although parthenogenesis may occur in some species (Phillipson, 1959; Tsurusaki, 1986). The forms of parental investment found in harvestmen show a remarkable variety and among the species of the suborder Laniatores it includes microhabitat selection for oviposition, egg-hiding, and guarding of eggs and nymphs by females or males (Machado & Raimundo, in press).

Behavioural repertory studies and natural history observations are important for understanding the biology and ecology of a great variety of organisms (Alcock, 1997; Krebs & Davies, 1993). Despite the fact that studies on harvestman biology have increased in the last decade, specially for laniatorean species in the Neotropical region (see Gnaspini, 1995, 1996; Machado & Oliveira, 1998; Machado *et al*., 2000 for references), ecological and behavioural information for the order is still scarce. Moreover, hitherto there has been no information about the behavioural repertory (ethogram) for a harvestman species in the literature. This study describes the daily activity pattern, gregariousness, and reproductive biology of the harvestman *Discocyrtus oliverioi* H. Soares (Gonyleptidae: Pachylinae) and provides the first detailed ethogram for a harvestman species.

Methods

Study area

The individuals of *Discocyrtus oliverioi* used in this study were collected in the Experimental Garden of the Universidade Federal de Uberlândia (18°53′S, 48°15′W; 863 m alt.), Minas Gerais state, south-eastern Brazil. The garden has a total area of 485 m^2, predominantly covered by trees, and is located in an urban region. The local climate has two well-defined seasons: one dry-cold from April to September, with mean monthly rainfall of 37.2 mm and temperature of 20.9°C, and one wet-warm from October to March, with mean monthly rainfall of 117.8 mm and temperature of 25.2°C (data from Estação Climatológica do Departamento de Geografia, UFU for the year 1999).

Behavioural repertory and ethogram

The biology of *D. oliverioi* was studied in the laboratory (Laboratório de Ecologia Comportamental e de Interações, IB-UFU) from November 1998 to November 1999. The animals (13 females and 5 males) were maintained in two terraria (20.5 × 44.5 cm, 27.5 cm high) containing soil, leaves and a branch, with conditions of light and moisture similar to the field (see study area). Nineteen individuals of the harvestman *Ilhaia* sp. (Gonyleptidae) and two individuals of *Discocyrtus* sp., which are commonly found together with *D. oliverioi* in the field, were also placed in the terraria. All individuals were equally divided in the terraria, and the sex ratio (females:males) for the two commonest species in each container was approximately 2:1. The animals were fed with live termite workers (Insecta: Isoptera), freshly chopped pieces of worms (Annelida: Oligochaeta), honey solution and an artificial diet for ants (Bhatkar & Whitcomb, 1970).

Six hours of field observations and another 6 h of observations in the laboratory (20 sessions of 36 min — *ab libitum* sampling, *sensu* Altmann, 1974)

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were carried out at night during January 1999 in order to identify and describe the behaviours of *D. oliverioi*. Descriptions of each behavioural act are presented in Table 1. In the next stage, 100 h (30 sessions of 200 min — *ad libitum* sampling, *sensu* Altmann, 1974) of quantitative observations were performed throughout the year on captive individuals. These observations were conducted between 1900 and 0300h with a red lamp to avoid disturbing the animals. Ten minutes before starting the observations, 10 termite workers and 3 pieces of worms (each 1 cm long) were offered as food. The data recorded in these samples were used to prepare an ethogram.

The activity pattern of *D. oliverioi* was quantified at 1 h intervals during a 24 h period. Sampling at each interval consisted of counting during 5 min the number of individuals performing the different types of behavioural acts. These observations were carried out on three different days during January 1999.

Voucher specimens have been deposited in the Museu da Biodiversidade do Cerrado (MBC-Uberlândia, MG-Brazil) and in the Museu de Zoologia da USP (MZSP-São Paulo, SP-Brazil).

Results

Behavioural repertory and activity pattern

Twenty-five behavioural acts were observed for *D. oliverioi* and classified into six groups of activities: foraging, social interactions, resting, exploration, cleaning or grooming, and reproduction (Tables 1 and 2). The commonest group of activities was exploration, which included walking about and touching the substrate with the first two pairs of legs (Table 2). Resting was also a frequent behavioural act and the individuals showed a tendency to rest in groups. Self-grooming activities were performed by both males and females, and leg-threading was done mainly to clean the first three pairs of legs (Table 2). Only females were involved in parental care activities (Table 2).

Individuals of *D. oliverioi* were inactive during most of the day, staying immobile in their shelters (Fig. 1). Occasionally, some individuals were observed foraging during the day. The harvestmen were most active at night and during this period they foraged, fed and interacted with other individuals (conspecifics or not) (Fig. 1). However, individuals do not seem to leave the shelter every night to forage.

Food was located upon contact with the second pair of legs and caught with the pedipalps and chelicerae. In the laboratory, individuals accepted both live (termites) and dead animals (pieces of worms). The item caught was carried to the shelter to be consumed. In the shelter, animals were seen fighting for food ($n=16$) and, in two cases, the item was stolen from the owner of the food by one conspecific and by one individual of *Ilhaia* sp.

Aggregations

In the field, five multi-species aggregations of harvestmen were found under fallen trunks. Three species were resting together: *Discocyrtus oliverioi*, *Discocyrtus* sp. (Pachylinae), and *Ilhaia* sp. (Gonyleptinae), all of the family Gonyleptidae. The occurrence of each species and

Foraging

Feeding: To manipulate organic matter using the chelicerae and pedipalpi, and to insert it into the mouth (Macías-Ordóñez, 1997).

Fighting for food: Any aggression toward another individual (conspecific or not) possessing food. It involves attack with pedipalpi and the first two pairs of legs.

Social interactions

Touching other individuals: Physical contact between two individuals (conspecific or not) established with the first or second pairs of legs, and without aggressive reactions by either individual.

Attacking other individuals: Aggressive approach toward another individual (conspecific or not). It involves bouncing the body against, chasing or grabbing the opponent's leg and pulling (Macías-Ordóñez, 1997).

Resting

Alone: To remain isolated, with the legs retracted over the body, and with the body clearly in contact with the substrate (Macías-Ordóñez, 1997).

In group: Similar to the above, but in this situation a group of at least 3 individuals are 0–2 cm apart from each other and with legs overlapping (Machado *et al*., 2000).

Exploration

Walking about: To walk with the second pair of legs extended sideways without touching the substrate.

Touching the substrate: To remain in the same place, constantly tapping the substrate with the first or second pairs of legs.

Self-grooming

Leg-threading: Process of cleaning in which each leg is held in the chelicerae and passed through the mouth-parts until the end of the tarsus is reached (Hillyard & Sankey, 1989).

Cleaning the pedipalps: Process in which the pedipalps are passed through the mouth-parts.

Reproduction

Copulation: To remain in a face-to-face position with the male grasping the female pedipalps with his pedipalps. It includes intermittent genital intromissions by the male by assuming a perpendicular position with respect to the female (Macías-Ordóñez, 1997).

Oviposition: To extrude the ovipositor and lay one egg on the substrate.

Brood guarding: To remain over an egg-batch with the body in contact with the eggs and the legs retracted over the body, or standing up tapping the eggs with the first two pairs of legs.

Protecting eggs: To clearly react (by moving) at the approach of another individual (conspecific or not) to the egg-batch. It involves bouncing the body against, chasing or grabbing the intruder's leg and pulling.

Table 1: Definition of each behavioural act of the harvestman *Discocyrtus oliverioi*.

the sex ratios in the aggregations are presented in Table 3. When disturbed by the collector, individuals of *Discocyrtus* sp. and *D. oliverioi* fled but individuals of *Ilhaia* sp. remained motionless with the legs retracted over the body — in this position, the dark brown coloration of the animals is extremely cryptic against a background of mud. Even when persistently disturbed or manipulated the individuals of these three species rarely release repugnatorial substances.

One complete aggregation was collected, transported to the laboratory, and placed in the same terrarium. The group was composed of two males and six females of *D. oliverioi*, one male and one female of *Discocyrtus* sp., and four males and five females of *Ilhaia* sp. In the laboratory, the individuals of these three species re-established the aggregation under a trunk, despite the presence of at least two other shelters in the container. Isolated individuals of these three species collected in the field were placed in another terrarium and also formed multi-species aggregations.

Mating and egg-laying

As in most laniatorean harvestmen, there is no precopulatory courting behaviour in *D. oliverioi*. Males stop in front of females and the copulation occurs immediately without any previous interaction between the mating pair. During copulation the male and female remain in a face-to-face position and the male grasps the female's pedipalps with his pedipalps, while the penis passes through the female's chelicerae and penetrates her genital opening. Throughout the copulation process the male touches the female's body with his first and second pairs of legs — which may be interpreted as copulatory courting. At the end of copulation, immediately after the mating pair separate, both individuals perform leg-threading behaviour, as also described for *D. pectinifemur* Mello-Leitão (Matthiesen, 1982).

Females lay their eggs on the same day or on the day after copulation. The females ($n=9$) were observed touching intensively a specific place in the substrate with

Behavioural acts	**Frequency of behavioural acts (%)**		
	Males ($n=2$) (545)	Females ($n=6$) (1623)	Total ($n=8$) (2168)
Foraging	6.05	8.31	7.76
Feeding on termites	0.55	3.33	2.63
Feeding on worm pieces	4.40	4.00	4.11
Feeding on honey solution	0.18	0.31	0.28
Fighting for food	0.92	0.67	0.74
Social interactions	2.02	1.48	1.61
Touching individual of *Ilhaia* sp. with legs	0.18	0.62	0.51
Touching individual of *D. oliverioi* with legs	0.37	0.25	0.28
Attacking individual of *Ilhaia* sp.	0.55	0.18	0.27
Attacking individual of *D. oliverioi*	0.92	0.43	0.55
Resting	12.11	11.39	11.58
Alone	6.24	4.74	5.12
In group	5.87	6.65	6.46
Exploration	69.91	69.37	69.51
Walking about	20.18	18.85	19.19
Touching the substrate with first legs	18.72	18.05	18.22
Touching the substrate with second legs	31.01	32.47	32.10
Self-grooming	8.07	6.27	6.74
Leg-threading — first pair	2.20	2.03	2.08
Leg-threading — second pair	2.75	1.91	1.94
Leg-threading — third pair	2.02	1.29	1.66
Leg-threading — fourth pair	0.73	0.55	0.60
Cleaning the pedipalps	0.37	0.49	0.46
Reproduction	1.28	1.90	1.76
Copulation	1.28	0.43	0.65
Oviposition	0	0.49	0.37
Brood guarding	0	0.49	0.37
Protecting eggs against males of *D. oliverioi*	0	0.06	0.05
Protecting eggs against males of *Ilhaia* sp.	0	0.06	0.05
Protecting eggs against females of *D. oliverioi*	0	0.25	0.17
Protecting eggs against females of *Ilhaia* sp.	0	0.12	0.10
Others	0.56	1.28	1.04
Pressing the body against the substrate, touching eggs (guarding females), and cannibalising eggs			
Total	100.0	100.0	100.0

Table 2: Behavioural repertory and frequency of each behavioural act for 8 captive individuals of the harvestman *Discocyrtus oliverioi*; n=total number of individuals observed, and between parentheses the total number of behavioural acts observed for each category.

Discocyrtus oliverioi		*Discocyrtus* sp.		*Ilhaia* sp.		Total no. of individuals
Male	Female	Male	Female	Male	Female	
3	2	4	2	24	31	66
2	4	1	1	9	18	35
1	3	0	2	3	10	19
2	6	1	1	4	5	19
1	1	0	2	1	3	8
17.0%		9.5%		73.5%		147

Table 3: Species occurrence within five different multi-species aggregations of harvestmen in an urban area of Uberlândia, Minas Gerais state, south-eastern Brazil.

the first and second pairs of legs before laying their eggs. The oviposition can last several hours or, in some cases, more than one day. The female lays groups of eggs, one at a time, in a process similar to that described for other harvestmen (see Juberthie & Muñoz-Cuevas, 1971; Machado & Oliveira, 1998). After laying each egg, females of *D. oliverioi* attach pieces of wood and soil to it with legs I and II. This process can last from 1 to 2 minutes for each egg laid.

Parental care and sources of egg mortality

Females of *D. oliverioi* provide parental care and stay near their eggs and the first instar juveniles, probably protecting them against predators (Fig. 2). Females did not leave their eggs to feed, to take water or to accomplish other activities apart from guarding. Guarding females attacked any individual, conspecific or not, that approached closer than 2 cm to the egg-batch. Nine fights were observed between guarding females and other harvestmen. These fights lasted from 5 to 30 s and in every case the guarding female won the combat. In one case the attacker (an adult female of *D. oliverioi*) ate one egg before the guarding female reacted. After the intruder's detection the mother attacked and successfully repelled the cannibalistic female. Two egg-batches were attacked by fungi, and guarding females did not eat or remove these eggs or the fungi from their batches.

The mean number of eggs in an egg-batch was 25.46 ± 32.34 SD ($n=9$; range =8–69) and the duration of embryonic development was 21.83 ± 4.30 days ($n=9$). Recently laid eggs were white in colour and measured on average 1.25 ± 0.08 mm in diameter ($n=20$). The eggs darkened with development and just before hatching the average diameter was 1.33 ± 0.05 mm ($n=20$). This increase of 13.2% in egg volume is probably caused by water intake (Machado & Oliveira, 1998). After hatching the young remained aggregated under the female for up to one week and then they dispersed. Females reproduced throughout the year (Table 4) and one female in the laboratory oviposited twice 32 days apart; there were 20 eggs in the first clutch but only 8 in the second.

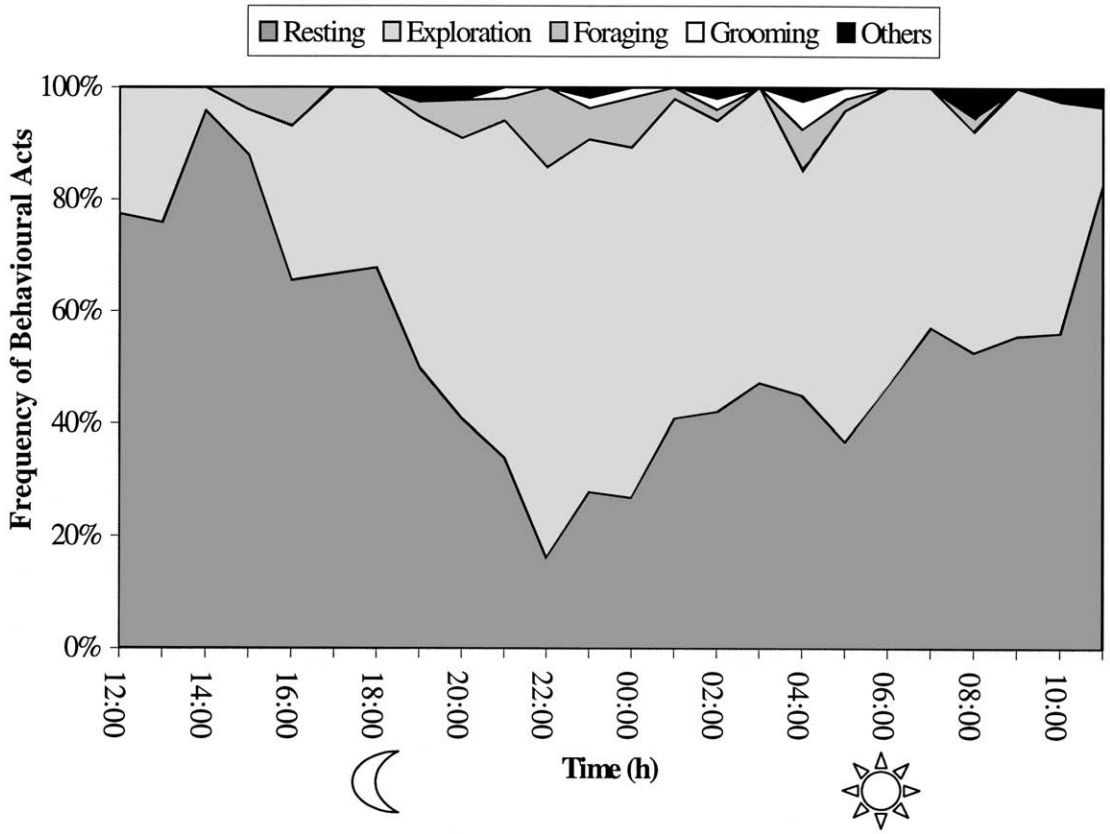

Fig. 1: Daily activity pattern of the harvestman *Discocyrtus oliverioi*. The data are based on three different days of samples and were obtained from 8 captive individuals. The moon and the sun indicate dusk and dawn, respectively.

Fig. 2: Marked female of *Discocyrtus oliverioi* (*c.* 6.5 mm) guarding her eggs in the field. Note the debris on the surface of the eggs.

Discussion

The general behaviour of *Discocyrtus oliverioi* is very similar to that of other Gonyleptidae, especially that of the subfamily Pachylinae (see Acosta *et al.*, 1995; Capocasale & Bruno-Trezza, 1964). All species of this subfamily that have been studied are nocturnal foragers that feed on small, soft-bodied arthropods and/or dead animal matter. They also hide during the day, sheltering in small aggregations. Like *Acanthopachylus aculeatus* (Kirby), individuals of *D. oliverioi* carry prey into the shelter before feeding. Although this strategy possibly protects foraging harvestmen from predation, it can result in food robbing by other individuals inside the shelter.

Since there is no information about behavioural repertories and ethograms for other harvestmen species, it is difficult to make detailed comparisons with the results obtained in the present study. For ants, the most studied arthropod group regarding behavioural repertories, it is common to find 30 or more different acts (see Hölldobler & Wilson, 1990). In these eusocial insects, behaviours related to cleaning (grooming) and foraging are commonly the most frequent acts observed (e.g. Brandão, 1978; Wilson, 1976). For the harvestman *D. oliverioi*, 25 behavioural acts were observed in which self-grooming, foraging and exploration formed a large percentage of the total. The same behavioural pattern has also been observed for the tailless-whipspider *Charinus asturius* (Amblypygi: Charinidae) (Pinto-da-Rocha *et al.*, in press). As the ethogram of *D. oliverioi* was done in the laboratory it is important to stress that captive conditions can impose constraints for some kinds of behaviours or promote others. However, for harvestman species reared in similar conditions, ethograms can be a starting point for comparisons of energy allocation for different activities as well as behavioural repertories in both qualitative and quantitative ways.

Month	Number of egg-batches
November 1998	1
December 1998	0
January 1999	0
February 1999	0
March 1999	1
April 1999	0
May 1999	2
June 1999	3
July 1999	0
August 1999	1
September 1999	1
October 1999	0
November 1999	1

Table 4: Number of egg-batches of the harvestman *Discocyrtus oliverioi* produced throughout the year. These data were obtained from 13 captive females.

At present, harvestmen are not considered to have a well developed chemical orientation and it is possible that they are strongly dependent on touching for receiving stimuli from the environment (Macías-Ordóñez, 1997). Although harvestmen have no antennae, they use their legs (mainly the second pair) as a sensitive organ to touch the substrate, food and other individuals. In insects it is common to observe individuals passing the antennae and the hind legs through the mouth parts to clean them. Among harvestmen leg-threading is a corollary activity (Edgar, 1971) and in *D. oliverioi* self-grooming was mainly used to clean the sensorial legs. This behaviour has also been recorded for other arachnid orders in which the species have sensory organs in the legs, such as tailless-whipspiders (Pinto-da-Rocha *et al.*, in press) and whipscorpions (P. Gnaspini, pers. comm.), or in the pedipalps, as in pseudoscorpions (Weygoldt, 1969). The legs of harvestmen have several chemical and mechanical receptors (Edgar, 1963). These organs appear to be highly sensitive, allowing individuals to recognise conspecifics, to determine the sex of other individuals and possibly to assess some microhabitat conditions in the selection of oviposition sites. Thus, leg-cleaning may be necessary to preserve the efficiency of these functions (Edgar, 1971).

Multi-species aggregations in Neotropical harvestmen have been described recently for three other species of the family Gonyleptidae: *Despirus montanus* Mello-Leitão (Mitobatinae), *Eugyndes* sp. (Pachylinae), and *Holoversia nigra* Mello-Leitão (Gonyleptinae) (Machado & Vasconcelos, 1998). Although there are several explanations for the gregariousness in harvestmen (see Holmberg *et al.*, 1984), some evidence suggests that this behaviour is related to the selection of places with more suitable microclimatic conditions and/or to group defence (Machado *et al.*, 2000). Based on field and laboratory observations it is difficult to assess the role of the multi-species aggregations of *D. oliverioi*, *Discocyrtus* sp. and *Ilhaia* sp., but both current hypotheses can be applied. The three species could be sharing shelters such as fallen trunks which conserve moisture and are light protected, or may gain benefit from the presence of other individuals in the group through the dilution effect (*sensu* Krebs & Davies, 1993). Individuals of the three species do not release repugnatorial substances when disturbed — rejecting the hypothesis of defence by the collective action of repulsive secretions

(Holmberg *et al*., 1984; Machado *et al*., 2000). This result contrasts with other studies on laniatoreans and reaffirms the need for an experimental approach to gregarious behaviour in harvestmen.

Eggs of harvestmen are exposed to several sources of mortality, such as inter- and intra-specific predation and fungal attack (Gnaspini, 1995; Machado & Oliveira, 1998). Several harvestman species are known to cover their eggs with debris and leave the offspring without additional care (Canals, 1936; Cokendolpher & Jones, 1991; Juberthie, 1965, 1972). Like *Pachylus quinamavidensis* Muñoz-Cuevas (Juberthie & Muñoz-Cuevas, 1971), females of *D. oliverioi* cover the eggs with debris and remain over them actively defending the offspring against predators. Covering the eggs with soil particles has been interpreted as a way to camouflage them on the substrate (Cokendolpher & Jones, 1991; Juberthie, 1972), but it can also prevent egg dehydration and/or decrease fungal infection. The latter suggestion is especially relevant since females of *D. oliverioi* seem to be unable to protect their eggs against fungal attack.

The forms of parental investment present in harvestmen of the genus *Discocyrtus* include maternal care, found in *D. pectinifemur* (Matthiesen, 1982) and *D. oliverioi* (present study), and egg-hiding by females of *D. prospicuus* (Holmberg) (Canals, 1936) and *D. dilatatus* Sörensen (L. E. Acosta, pers. comm.). This scenario is similar to that found among the New Zealand harvestmen of the family Triaenonychidae. That family is divided into two subfamilies: the Triaenonychinae, in which females leave their eggs hidden in the substrate, and the Soerensenellinae, in which females show maternal care (Forster, 1956). The genus *Discocyrtus* is highly variable morphologically and its monophyly is uncertain (R. Pinto-da-Rocha, pers. comm.). As previously verified for the Triaenonychidae, the presence of maternal care can be useful for separating groups of species in this genus. Thus, in association with the classical taxonomic approach, more studies on reproductive biology could provide additional tools for harvestman systematics (see De Queiroz & Wimberger, 1993).

Acknowledgements

We thank R. Pinto-da-Rocha for identification of the harvestmen species. P. Gnaspini, R. Macías Ordóñez, S. Koehler, R. L. G. Raimundo, P. S. Oliveira, and two anonymous reviewers provided helpful comments on an earlier draft of the manuscript. This research was supported by the Brazilian CNPq through a doctoral fellowship to GM and an undergraduate fellowship to AEC.

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