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Daily activity schedule, gregariousness, and defensive behaviour in the Neotropical harvestman *Goniosoma longipes* (Opiliones: Gonyleptidae)

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In this paper we provide a field account of some aspects of the behavioural biology of *Goniosoma longipes* (Roewer), a harvestman which commonly occurs in caves in South-east Brazil. During daytime, solitary and aggregated individuals can be found resting on the cave walls. Just after sunset, however, many individuals leave the cave to forage for live and dead arthropods. Foraging individuals return to the cave before dawn. Aggregations of *G. longipes* contain on average 34 individuals (range 7–200), and the groups are usually found close to the water source and away from the cave entrance. The main predators of *G. longipes* are the spider *Ctenus fasciatus* Mello-Leitão (Ctenidae) and the opossum *Philander opossum* (L.) (Didelphidae). Upon disturbance solitary and aggregated individuals may either flee, or drop from the cave wall or vegetation. The harvestmen can also release a repugnatory liquid upon manipulation, and aggregated individuals collectively discharge this secretion toward the aggressor before fleeing. The activity schedule of *G. longipes* shows that individuals need to leave the cave periodically to forage, and therefore the population can be considered trogloxene. Data on the food items collected by *G. longipes* indicate that the harvestman is a generalist predator which also feeds on dead animal matter. Gregarious behaviour is considered relatively common among harvestmen and has been interpreted in several ways. We suggest that gregarious behaviour in *G. longipes* may be related with the choice of more suitable microconditions in the cave habitat and/or with group chemical defence.

KEYWORDS: Defensive behaviour, foraging, activity rhythms, *Goniosoma*, gregariousness, harvestmen, Opiliones.

Introduction

Most harvestman species live in moist forests, and are frequently found under fallen trunks, among the leaf litter, and inside caves (Edgar, 1990). Although primarily solitary and nocturnal foragers, some harvestmen can form large aggregations during the day (Coddington *et al.*, 1990), and many species present a

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wide diversity of feeding habits, ranging from scavengers to predators (Phillipson, 1960; Capocasale and Bruno-Trezza, 1964; Edgar, 1971). Harvestmen exhibit an array of behavioural defence techniques (Cokendolpher, 1987), but the use of repugnatorial secretions is probably the most common tactic employed by members of the suborder Laniatores (Duffield *et al.*, 1981; Holmberg, 1983).

Cavernicolous species in general show a nocturnal and cryptobiotic habit, use non-visual sensitive structures, and have an omnivorous and opportunistic diet (Barr and Holsinger, 1985). An ecological and evolutionary classification of cavernicolous species divided them into three categories (see Holsinger and Culver, 1988): (1) the troglobites comprise the strictly cavernicolous species which complete the whole life-cycle in this environment; (2) troglophiles include the species which use the cave habitat as shelter, and complete the life-cycle either in this environment or outside the caves; (3) the trogloxenes include species which have to leave the cavernicolous environment to complete part of the life-cycle. It is difficult to discriminate between troglophiles and trogloxenes since both may be found either in cave habitats or in the neighbouring external environment. According to Gnaspini (1996), the inclusion of cave animals into one of these three categories requires a detailed study of the biology of the species, including the activity schedules.

The Neotropical genus *Goniosoma* Perty (Laniatores: Gonyleptidae) includes large and conspicuous harvestmen inhabiting caves, rock crevices, and tree trunks, and the biology of some species has already been studied from an ecological and behavioural point of view (Bristowe, 1925; Ramires and Giaretta, 1994; Gnaspini, 1995, 1996; Machado and Oliveira, 1998). The harvestman *G. longipes* (Roewer) has a widespread distribution in Southeast Brazil where populations are recorded in sandstone (Gnaspini and Trajano, 1994) and granitic caves (Machado and Oliveira, 1998). In the latter environment many individuals are seen resting on the cave walls, which is also the preferred oviposition site (further details in Machado and Oliveira, 1998). In this paper we provide a field account of some aspects of the behavioural biology of *G. longipes* such as daily foraging schedule, gregarious behaviour, and defensive tactics.

Materials and methods

Study area

Fieldwork was carried out in the Parque Florestal do Itapetinga (23°10′S; 46°25′W), near Atibaia, São Paulo State, South-east Brazil. The area is a microbasin formed by small perennial streams (approximately 60 cm wide) that flow on granitic and/or sandy beds. In some places the rivers are covered by large granitic boulders that form small caves. The local climate has two well-defined seasons. The dry/cold season lasts from April to September, with mean monthly rainfall of 72 mm and temperature of 17°C. Winter frosts are frequent in June and July. The wet/warm season lasts from October to March, with a mean monthly rainfall of 182 mm and temperature of 21°C.

Behavioural observations

The biology of *Goniosoma longipes* was studied in two granitic caves (30 m and 300 m long) crossed by rivers. Preliminary field data were taken weekly from August to November 1995. Further data were regularly taken at 7–14-day intervals from March 1996 to June 1998, totalling over 500 h of fieldwork. The observations inside the caves were made with a flashlight covered by a red filter to avoid disturbing the organisms. Rare events, such as the attack by predators, were recorded continuously, following the procedure suggested by Martin and Bateson (1986).

We considered an aggregation to be any group of at least three harvestmen whose legs were overlapping (figure 2). All individuals found aggregated were measured for dorsal scutum length and sexed. We also measured the distance of the aggregates from the river and from the cave entrance. All harvestmen from five aggregations were individually marked with different colour codes on the dorsal scutum with enamel paint (Testors Co., Rockford, USA). Nocturnal observations were made outside the caves, where we searched for individuals with prey items. While manipulating or collecting the harvestmen, we recorded all the behavioural responses of the individuals, such as attempts to escape, and the discharge of odoriferous secretions.

The activity schedule of *G. longipes* was quantified at 2 h intervals during a 24 h period (1–2 May 1998). Sampling at each interval consisted of counting during 30 min the number of individuals leaving or entering the cave, as well as those stationary at the cave entrance. The routes taken by foraging harvestmen in the cave were also recorded.

Voucher specimens of *G. longipes* are deposited in the Museu de Zoologia da Universidade de São Paulo (MZUSP).

Results

Foraging and activity schedule

During daytime, individuals of *Goniosoma longipes* can be found resting in the caves either isolated or forming stationary aggregations. In the afternoon, approximately 1 h before dusk, the aggregations disperse and the individuals move toward the entrance of the cave, where they remain stationary until complete darkness. Many individuals leave the cave in the first hour after sunset, although the harvestmen are also seen abandoning the cave up to 4 h after dusk (figure 1). Brood-caring females, however, never leave the cave to forage (see Machado and Oliveira, 1998).

The vast majority (97%) of foraging harvestmen ($n = 54$) used two trails when leaving or returning to the cave. At night, most of the individuals were found motionless in the external environment, clinging on the vegetation and with the second pair of legs extended sideways. Some individuals were seen walking slowly, rubbing the substratum with the second pair of legs. Marked harvestmen were found up to 70 m from the cave. *Goniosoma longipes* feed mainly on live or dead arthropods and on other organisms with little sclerotized skin (table 1). The food item is usually captured with a fast movement by the harvestman's pedipalps, and seized by the chelicerae. The prey can either be consumed on the spot ($n = 3$), or carried into the cave ($n = 5$). Some individuals (adults and juveniles) remaining in the cave may prey on conspecific eggs (see Machado and Oliveira, 1998). The return of the foraging individuals to the cave peaked 1 h before dawn (figure 1). Two hours after dawn the harvestmen regrouped in the cave.

Gregarious behaviour

The aggregations of *G. longipes* consisted of groups of motionless individuals 0–5 cm apart from each other, and with legs widely overlapping (figure 2). The groups contained on average 34.2 individuals (SD = 38.1; range = 7–200; $n = 30$),

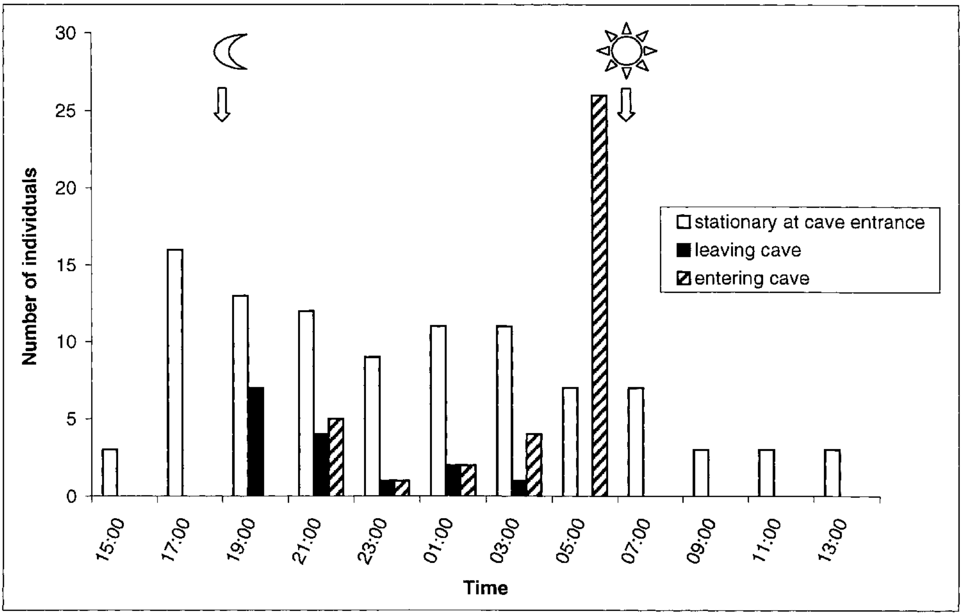

FIG. 1. Activity schedule of *Goniosoma longipes* at Parque Florestal do Itapetinga, South-east Brazil. The moon and the sun indicate dusk and dawn, respectively.

Table 1. Food items caught by individuals of *Goniosoma longipes* at Parque Florestal do Itapetinga, South-east Brazil. Prey presenting clear signs of decay were categorized as dead items.

Food item	Number of items dead/alive
Annelida	
Hirudinea	1/0
Oligochaeta	0/1
Arachnida	
Opiliones (Gagrellidae)	1/0
Insecta	
Diptera (Tipulidae)	0/1
Hymenoptera	
(Formicidae)	1/0
(Vespidae)	1/0
Lepidoptera	
(adult moth)	2/1
(larvae of moth)	0/1
Orthoptera (legs fragments)	1/0
Insect remains wrapped in silk	1/0
Total	8/4

and were formed by adults and juveniles. The mean sex ratio in the aggregations was female-biased (1.8 ± 1.5; range = 0.3–5.3; $n = 28$). Harvestmen aggregated on the exposed cave wall (78%) or inside breaches (22%; $n = 30$). The groups were usually close to a water source such as the cave river or a dripping fissure (2.8 ± 2.1 m; range = 0.9–8.0 m; $n = 28$), and away from the cave entrance (6.2 ± 2.5 m; range = 1.5–9.0 m; $n = 28$). Although harvestman aggregations can remain in the

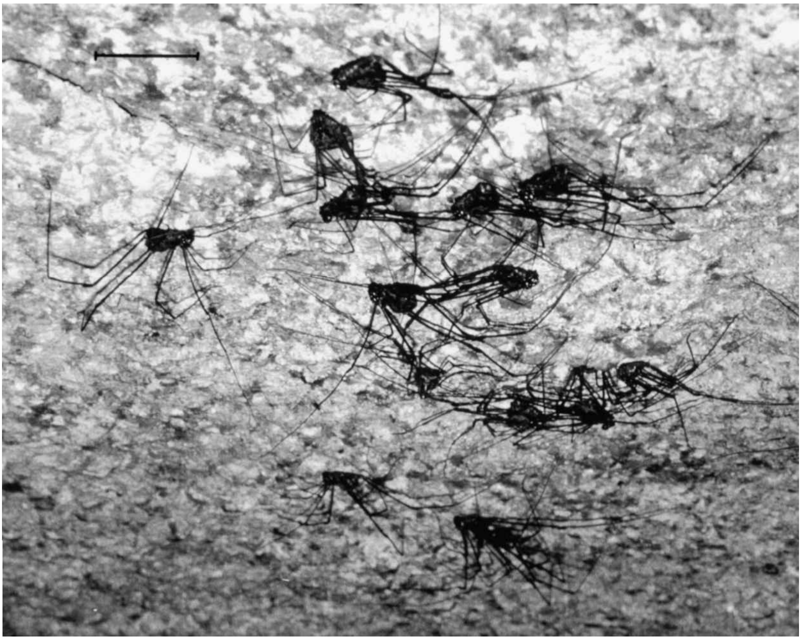

FIG. 2. Small aggregation of *Goniosoma longipes* on a cave wall at Parque Florestal do Itapetinga, South-east Brazil. Note the overlapping of legs. Scale bar = 2 cm.

same site for up to 4 months ($n = 2$), on one occasion a group moved closer to the cave river during the peak of the 1996 dry season (June to September). Aggregations were never found on the cave ceiling or on the floor.

Predators and parasites of Goniosoma longipes

The spider *Ctenus fasciatus* Mello-Leitão (Ctenidae) was twice seen feeding on juvenile *G. longipes* (3rd and 5th instars). Foraging activity by the opossum *Philander opossum* (L.) (Mammalia: Didelphidae) inside the caves was usually nocturnal. *Goniosoma* fragments were found both in the stomach contents of one opossum collected in the study area, as well as in two faeces found inside the caves.

Individuals of *G. longipes* were frequently infected by fungi on the dorsal scutum. Fungal attack was mostly directed toward the eye mound ($n = 13$) and the region between coxae I and III ($n = 6$). A detailed inspection of two preserved harvestmen revealed that the fungus is saprophytic since it does not penetrate the cuticle. In the laboratory we also recorded the death of one adult female parasitized by four dipteran larvae.

Defensive behaviour

The most common defensive behaviour of solitary and aggregated individuals of *G. longipes* was to flee when disturbed. For instance, two females of the spider *Enoploctenus cyclothorax* (Bertkau) (Ctenidae) were seen attacking adult males of *G. longipes*. On both occasions the harvestmen escaped by fleeing. Bristowe (1925) also described a defensive behaviour in *G. longipes* in which the harvestman, when handled by the 4th pair of legs, moves vigorously femur IV so as to promote a pinch between the sharp projections of the femur and trochanter IV. Attacking with the pedipalps before seizing or pinching the aggressor was very common. These two types of mechanical defensive behaviours were observed more frequently in adult males. Another common behaviour upon disturbance was to fall from the wall or vegetation to the ground. In this case the harvestman quickly hides under stones and/or stays motionless (feigning dead) during some time, as also recorded for *G. spelaeum* (Mello-Leitão) (Gnaspini and Cavalheiro, 1998), and many cosmetids (Eisner *et al.*, 1978; Kaestner, 1980). Brood-guarding females frequently exhibit this behaviour.

Finally, individuals of *G. longipes* can release a repugnatory liquid upon manipulation. Aggregated harvestmen collectively discharge this secretion before fleeing ($n = 28$ aggregations). The repellent liquid is released in drops, or sprayed directly toward the aggressor. In the first case a large transparent drop slips along the lateral area of the scutum, runs by capillarity in tegumentary grooves, and accumulates in the posterior portion of the body (enteric fluid). If persistently disturbed, a second fluid can also be secreted by the repugnatorial glands which adds to the previously colourless fluid a yellowish coloration and a characteristic sour smell. The mixture of these secretions promotes red stains on human skin. Overall, the delivery of the defensive secretions in *G. longipes* occurs much in the same way as described by Acosta *et al.* (1993) for the other gonyleptid *Pachyloidellus goliath* Acosta.

Discussion

Harvestmen generally hide in wet and dark sites during daytime (Capocasale and Bruno-Trezza, 1964; Anuradha and Parthasarathy, 1976) and many species are photophobic (Savory, 1938). The conditions of moisture and temperature tend to be highly constant in cave habitats (Gautier *et al.*, 1988). At night, humidity at ground and vegetation level increases and allows harvestmen to leave their shelters and extend their foraging range (Phillipson, 1960). The activity rhythm displayed by *G. longipes* shows that the individuals use the cave as shelter and reproductive site (see Machado and Oliveira, 1998) but need to leave the cave periodically to forage at night. Therefore the studied population can be considered trogloxene and not an occasional user of the cave habitat.

The traffic from and toward the cave by *G. longipes* seems to be influenced by the photoperiod since the harvestmen leave the cave just after dusk and return before dawn. Such a daily activity pattern is also reported for many cavernicolous bat species (Kunz, 1982). Foraging individuals of *G. longipes* use the same route within the cave, both when entering or leaving the shelter. A similar behaviour was also reported for G. *spelaeum* (Gnaspini, 1996) and field experiments are needed to test if route fidelity in *Goniosoma* is mediated by chemical cues or if the harvestmen have a spatial memory of the trail, or both.

Harvestmen apparently do not have specialized predators but can be eaten by spiders, heteropterans and several vertebrates such as toads, lizards and mammals (Bristowe, 1949; Edgar, 1971; Gnaspini, 1996). However, Pellegati-Franco and Gnaspini (1996) showed that the cavernicolous harvestman G. *spelaeum* is an important item in the diet of the opossum *P. opossum* throughout the dry/cold season in south-eastern Brazil. In the same region, *Goniosoma* aff. *badium* (Pinto-da-Rocha, 1993) and G. *spelaeum* (Gnaspini, 1996) were often seen being eaten by the assassin bug *Zelurus travassosi* (Costa-Lima) and the spider *Ctenus fasciatus*. Although these three predators were also seen in the caves of our study area, we only observed one entire event of predation. A possible explanation for this fact is the low density of invertebrate predators in the caves. Moreover, the hunting activity of the opossum in the caves occurs mainly at night and in this period the observations were focused on the behaviour of *G. longipes* in the external environment. Another possible predator of *G. longipes* present in the study area is the large spider *Enoploctenus cyclothorax*, which was seen attacking the harvestman.

Harvestmen are usually considered as predators or scavengers (Berland, 1949; Bristowe, 1949; Cloudsley-Thompson, 1958; see review in Gnaspini, 1996). According to our field observations, *G. longipes* is a generalist predator, which can also feed on dead animal matter. The insect remains wrapped in silk (see table 1) may suggest food robbing from spiders. Food robbing has already been described for a *G. longipes* female, which was seen stealing a moth prey from the large spider *Enoploctenus cyclothorax* (Sabino and Gnaspini, 1999). Contrary to G. *spelaeum* which feeds outside the cave (Gnaspini, 1996), *G. longipes* may consume its prey on the spot or carry it into the cave prior to ingestion. Capocasale and Bruno-Trezza (1964) described a similar behaviour for the harvestman *Acanthopachylus aculeatus* (Kirby) (Laniatores: Gonyleptidae), which also transports prey into the shelter before consumption. This strategy possibly protects foraging harvestmen from predation and kleptoparasitism.

Harvestmen may exhibit a number of defensive and evasive traits when disturbed (Duffield *et al.*, 1981; Acosta *et al.*, 1993). For members of the suborder Palpatores leg autotomy is considered the most frequent and efficient defensive behaviour (Roth and Roth, 1984). Fleeing is also relatively common in species of long-legged harvestmen, such as the Palpatores and several Laniatores (Bristowe, 1925; Edgar, 1971). Although autotomy has not been recorded for *G. longipes*, fleeing and falling from the cave wall were very frequently exhibited by isolated and aggregated individuals when disturbed by light. On the other hand, physical disturbance usually provokes the discharge of repellent secretions by *G. longipes*. Field and captivity observations suggest that the repugnatory secretion can deter predators such as ants (Capocasale and Bruno-Trezza, 1964; Duffield *et al.*, 1981), and in some Laniatores the fluid is also a powerful antibiotic against bacteria, protozoa and fungi (Estable *et al.*, 1955; see also Cokendolpher, 1993). The defensive role of these secretions in *G. longipes* is still to be experimentally assessed.

The role of harvestmen secretion for intraspecific communication is unclear. Wagner (1954) suggests that the secretion acts as an aggregation pheromone, but there is no evidence supporting this hypothesis. Holmberg (1983) suggests that the secretion produced by the harvestmen serves as an alarm pheromone. Field observations with *G. longipes* apparently support this hypothesis, since the collective fleeing is preceded by the discharge of the fluid.

Gregariousness has already been described for many species of Palpatores (Anuradha and Parthasarathy, 1976; Coddington *et al.*, 1990; Cockerill, 1988 and included references), but there are few records of gregarious behaviour among Laniatores. In Brazil there are reports of gregariousness in *Goniosoma* aff. *badium* (9–34 individuals; Pinto-da-Rocha, 1993), *G. spelaeum* (P. Gnaspini, personal communication), and in *Despirus montanus* Mello-Leitão, *Holoversia nigra* Mello-Leitão and *Eugyndes* sp. which form multi-species aggregations (5–35 individuals; Machado and Vasconcelos, 1998). Although gregarious behaviour is considered relatively common among harvestmen (Coddington *et al.*, 1990), little is known about its ecological meaning. According to Holmberg *et al.* (1984) this behaviour has been interpreted in several ways. The first interpretation is that harvestmen groups result from many individuals choosing places with decreased risk of dehydration and low exposure to light. The aggregations of *G. longipes* were found close to a water source, in complete darkness, and protected from wind—which seems to support this suggestion. Therefore the common choice of a suitable site within the cave probably favours gregariousness in *G. longipes*. Females of *G. longipes* also prefer similar sites for oviposition (Machado and Oliveira, 1998).

A second hypothesis states that the overlapping legs of compactly aggregated individuals reduce air movement and consequently decrease evaporation and dehydration. Aggregations of *Leiobunum paessleri* (Roewer) (Palpatores: Leiobunidae) form a compact mass (2.5 individuals per cm^2) which probably reduces the air flow between individuals in the group (Holmberg *et al.*, 1984). Since aggregations of *G. longipes* have a low density of individuals (0.013 indiviuals per cm^2), and do not form a compact mass as in *L. paessleri*, it is very unlikely that the aggregate can block air flow or retain humidity between the harvestmen.

Another hypothesis suggests that gregariousness increases the defensive ability against predators by the collective action of the repulsive fluid secreted by the group (Holmberg *et al.*, 1984). The behavioural data on *G. longipes* support this suggestion since the aggregated individuals immediately discharge the repugnatorial fluid upon physical disturbance. The gregarious harvestman *Pachyloidellus goliath* (Laniatores: Gonyleptidae) also discharges a repugnatorial liquid when the group is disturbed (Acosta *et al.*, 1993). A fourth hypothesis states that harvestman aggregation would have a mating function (Holmberg *et al.*, 1984), but this is unlikely for *G. longipes* since the mating pairs in this species are formed in isolation (Machado and Oliveira, 1998).

Finally, it is also possible that gregariousness may decrease the individual risk of predation through a dilution effect (*sensu* Krebs and Davies, 1987; see also Machado and Vasconcelos, 1998). Our results suggest that gregarious behaviour in *G. longipes* may be related to the choice of more suitable microconditions in the cave habitat and/or with group chemical defence. Further experiments are needed to assess the ecological meaning of gregariousness across different harvestman species.

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