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Research article

Maternal care, defensive behavior, and sociality in neotropical *Goniosoma* harvestmen (Arachnida, Opiliones)

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Summary. *Goniosoma* includes large and conspicuous species of harvestmen that occur exclusively in the Brazilian Atlantic forest. This paper reports on the parental activities, defensive behavior, and gregariousness of five species of *Goniosoma*, and also summarizes the published biological data for the genus. The behavioral patterns within the genus are discussed and a hypothesis for the emergence of gregariousness in the group is presented. Several *Goniosoma* live inside caves, mainly as trogloxenes. Although species of the genus comprise only 5% of the harvestmen fauna in Brazil, they account for 20.6% of all harvestmen species recorded in Brazilian caves. In addition to several morphological and physiological features that may favor the occupation of caves, species of *Goniosoma* also present subsocial behavior, which may confer a special advantage in this particular environment. Female protection is crucial for egg survival since predators may consume entire batches in a single night. Most species of *Goniosoma* form dense diurnal aggregations ranging from three to 200 individuals (mainly subadults and adults of both sexes). In a hypothetical scenario for the evolution of sociality in the *Goniosoma*, physiological constraints acting on individual harvestmen would lead to a behavioral response for the selection of sites with appropriate microclimatic conditions. The lack of cannibalism among adults and subadults may favor tolerance towards conspecifics, and may represent a pre-adaptation to gregariousness. The derived functions of gregarious behavior may include strengthening of the defensive signal through the collective release of a repugnant secretion, the dilution effect, and promptness in fleeing a predator attack as a consequence of the additional alarm role of scent gland secretions. These defensive functions may overcome the costs of group living and may be responsible for the maintenance of gregariousness in *Goniosoma*.

Key words: Cave, chemical defense, gregariousness, presocial behavior, subsociality.

Introduction

There is little information on neotropical harvestmen, except for the genus *Goniosoma* Perty (Arachnida, Opiliones, Gonyleptidae), in which the ecology and behavior of several species have already been studied (Bristowe, 1925; Pinto-da-Rocha, 1993; Ramires and Giaretta, 1994; Gnaspini, 1995, 1996; Gnaspini and Cavalheiro, 1998; Machado and Oliveira, 1998; Machado et al., 2000, 2001, 2002; Sabino and Gnaspini, 1999). *Goniosoma* includes large and conspicuous species of harvestmen that occur exclusively in the Brazilian Atlantic forest. Despite the importance of the genus as a model for ecological and behavioral studies, the taxonomy of *Goniosoma* remains confusing. About 40 species are currently recognized, but more species will probably be added as systematic studies of the group advance (M.B. Silva, pers. comm.).

Maternal care has been recorded for all species of *Goniosoma* studied so far (Pinto-da-Rocha, 1993; Ramires and Giaretta, 1994; Gnaspini, 1995; Machado and Oliveira, 1998; Machado et al., 2001). Females lay their eggs mainly on a rocky substrate and care for them for 45–64 days. After hatching, first-instar nymphs remain aggregated under the guarding female for up to two weeks before dispersing (Gnaspini, 1995; Machado and Oliveira, 1998).

Several species of *Goniosoma* form dense diurnal aggregations consisting mainly of subadults and adults of both sexes. Among these gregarious species are *G.* aff. *badium* (Pinto-da-Rocha, 1993), *G. longipes* (Machado et al., 2000), *G. catarina* (Machado et al., 2001), *G.* aff. *proximum* (Machado et al., 2002), and *G. spelaeum* (P. Gnaspini, pers. comm.). In general, individuals aggregate at protected sites, such as rock fissures, and close to a water source. The number of aggregated individuals ranges from three to about 200 and, upon manipulation, they collectively discharge scent gland secretions (Machado et al., 2000, 2002).

Defensive behaviors in animals may be divided into primary responses, which operate regardless of the presence of

a predator, and secondary responses, which operate in the presence of a predator (Edmunds, 1974). Among harvestmen, especially the large Gonyleptidae such as *Goniosoma*, secondary defensive mechanisms have been studied the most (Capocasale and Bruno-Trezza, 1964; Acosta et al., 1993; Gnaspini and Cavalheiro, 1998; Machado et al., 2000). These defenses include both mechanical (attack with the pedipalps and pinching with spines) and chemical (releasing of repugnant secretions) responses. Evasive responses, such as fleeing, are also commonly used by *Goniosoma* (Gnaspini and Cavalheiro, 1998; Machado et al., 2000) and other long-legged harvestmen species (Hillyard and Sankey, 1989).

This paper reports on the parental activities, defensive behavior, and gregariousness of five species of *Goniosoma* occurring in different regions of Brazil, and also summarizes the published biological data for the genus. The behavioral patterns within the genus are discussed and a hypothesis for the emergence of gregariousness in the group is presented.

Materials and methods

The observations described here were made during fieldwork from 1998 to 2002, and included visits to several localities in the Brazilian Atlantic forest. Table 1 shows the species studied and the localities where they were found. An aggregation was considered any group of at least three harvestmen that were close enough to each other for their legs to overlap (cf. Machado et al., 2000). Whenever possible, the aggregations were collected and the individuals were counted and their sex determined. The dorsal scute length of females caring for offspring was measured and a sample of eggs was collected and preserved in 70% ethanol. In the laboratory, the egg diameter was measured with calipers to the nearest 0.02 mm. Continuous recording (sensu Martin and Bateson, 1986) was made of relevant behavioral events, such as interactions between individuals and defensive responses. Voucher specimens were deposited in the Museu de Zoologia da Universidade de São Paulo (MZSP), São Paulo, Brazil.

Results

Maternal care

The eggs of all *Goniosoma* species studied so far are laid about 1–5 mm apart, in a single layer, and are generally covered by a thick mucous layer. Recently laid eggs are cream colored and have a mean diameter ranging from 1.44 to 1.58 mm (Table 2). The eggs darken with development and may reach an average diameter of 2.3 mm before hatching (Table 2). The increase in egg volume occurs as a result of water intake during embryonic development. The number of eggs laid varies widely within and among species, and ranges from 26 to 204 (Table 2).

The egg batches were located mainly in poorly-illuminated, wet sites (1–2 m from a water source), such as in gaps between rocks along river margins (e.g. *G. catarina, G. discolor, G. proximum,* and *G.* aff. *proximum*) and in caves (*G. geniculatum*, *G. indistinctum*, *G. longipes*, *G. spelaeum*, and *G.* aff. *badium*). Females cared for the eggs and first instar nymphs before they dispersed. For *G.* aff. *proximum* (this study), *G. longipes* (Machado and Oliveira, 1998), and *G. spelaeum* (Gnaspini, 1995), ovipositions occurred throughout the year, indicating that there was no seasonal interruption in the reproductive activities of these species.

Potential egg-predators and fungal attack

Cave crickets (Ensifera, Phalangopsidae), which feed on *G. longipes* eggs, were commonly found near (10–50 cm) egg batches of *G. geniculatum* and *G. indistinctum* (Table 3). For the non-cavernicolous species (*G. discolor*, *G.* aff. *proximum*, and *Goniosoma* sp.n.1), the potential egg predators found near the batches were predacious tiger beetles (Coleoptera, Cicindellidae) and ants. Table 3 summarizes the current information on potential predators of *Goniosoma* eggs. One egg batch of *G. indistinctum* and five egg batches of *G.* aff. *proximum* were attacked by fungi, with the number of infected eggs ranging from 1 (1.3% of the total) to 38 (100% of the eggs).

Defensive behavior

All species of *Goniosoma* studied so far rely on similar defensive mechanisms (Bristowe, 1925; Gnaspini, 1996; Gnaspini and Cavalheiro, 1998; Machado et al., 2000). Fleeing is the most common response upon disturbance by touch or illumination with artificial light. Individuals also sometimes try to escape by dropping from the substrate to the ground, and this behavior appears to be more common among guarding females. On the ground, the fallen individuals remain motionless for a while, probably to avoid detection by the potential predator. Attacking the aggressor with the pedipalps and trying to bite with the chelicerae is a frequent behavior upon manipulation. When handled by the fourth pair of legs, males move the femur IV vigorously in order to pinch with the sharp projections of the femur and coxa IV.

The manipulation of individuals may also cause the release of scent gland secretions. Initially, a transparent,

Table 1. The species of *Goniosoma* studied and the localities in the Brazilian Atlantic forest where they were found. *Goniosoma* sp.n.1 is a new species (M.B. Silva, pers. comm.) and the biological notes presented here precede its formal description

Species	Locality	State	Habitat	Elevation (m)
G. aff. *proximum*	Ilha do Cardoso	São Paulo	forest stream	100
G. discolor	Ubatuba	São Paulo	forest stream	100
G. geniculatum	Nova Friburgo	Rio de Janeiro	granitic cave	900
G. indistinctum	Alto Caparaó	Minas Gerais	granitic cave	700
Goniosoma sp.n.1	Itororó	Bahia	hematite boulders	1100

Table 2. Life history traits related to the habitat occupation, reproduction, and gregariousness of several *Goniosoma* species. When the sample size (n) for the quantitative categories was smaller than 10, only the range is presented. In the remaining cases, the mean ± SD is shown, with the range in parentheses

Species	Cave dweller	Female size (mm)	Number of eggs	Egg diameter (mm)		Increase in volume	Oviposition substrate	Gregarious habits	Number of individuals
				Recently laid	Prior to hatching				
G. aff. *badium* [a]	yes	?	72–105 (n = ?)	–	–	–	calcareous rocks	yes	9–34 (n = ?)
G. aff. *proximum* [b,c]	no	7.80 ± 0.22 (n = 14)	95.1 ± 31.9 (3–165; n = 18)	1.46 ±0.08 (n = 10)	1.89 ± 0.10 (n = 10)	29.5%	granitic rocks	yes	19.5 ± 18.4 (3–79; n = 82)
G. catarina [d]	no	8.1 (n = 1)	ca. 100	–	–	–	granitic rocks	yes	16–37 (n = 3)
G. geniculatum [b]	yes	7.96 ± 0.25 (n = 18)	47–156 (n = 2)	1.58 ± 0.04 (n = 10)	2.11 ± 0.06 (n = 10)	33.5%	granitic rocks	yes	30–50 (n = 3)
G. discolor [b]	no	6.90 ± 0.28 (n = 10)	26–93 (n = 9)	1.44 ± 0.12 (n = 10)	1.85 ± 0.07 (n = 10)	28.5%	granitic rocks	yes	3–10 (n = 5)
G. indistinctum [b]	yes	7.0 (n = 1)	97 (n = 1)	–	1.86 ± 0.10 (n = 10)	–	granitic rocks	yes	–
G. longipes [e]	yes	7.83 ± 0.24 (n = 33)	131.05 ± 38.62 (27–209; n = 33)	1.44 ± 0.09 (n = 20)	1.91 ± 0.12	43%	granitic rocks	yes	34.2 ± 38.1 (7–200; n = 30)
G. proximum [f]	no	7.4–7.8 (n = 2)	49–77 (n = 3)	–	2.01 ± 0.18 (n = 15)	–	granitic rocks	no	–
G. spelaeum [g]	yes	~8.0	30–120	–	2.1–2.3 (n = ?)	–	calcareous rocks	yes	?
Goniosoma sp.n.1 [b]	no	7.56 ± 0.20 (n = 11)	85–173 (n = 4)	1.51 ± 0.08 (n = 10)	1.91 ± 0.19 (n = 10)	24.8%	hematite rocks	no	–

Sources: [a] Pinto-da-Rocha (1993); [b] This study; [c] Machado et al. (2002); [d] Machado et al. (2001); [e] Machado and Oliveira (1998) and Machado et al. (2000); [f] Ramires and Giaretta (1994); [g] Gnaspini (1995) and pers. comm.

inodorous droplet (enteric fluid) is released through the mouthparts and oozes throughout the lateral margins of the dorsal scute. Thereafter, a yellowish secretion with a sour smell is released by the exocrine glands located above the second pair of legs. This secretion also oozes throughout the margins of the body and mixes with the transparent liquid. The scent secretion may also be released as the enteric fluid passes near the opening of the scent glands, or even may be sprayed directly towards the aggressor with no prior release of oral liquid. Upon contact with human skin, the repugnant secretions of all species produced reddish spots, suggesting the presence of a quinone. The chemical composition of the scent gland secretion consists of two alkyl-1,4-benzo-quinones in *G. spelaeum* (Gnaspini and Cavalheiro, 1998) and *G. longipes* (G. Machado and J.R. Trigo, unpub. data), and four alkyl-1,4-benzoquinones in *G.* aff. *proximum* (Machado et al., 2002).

Gregariousness

Aggregations of *Goniosoma* consisted of motionless individuals (bodies 0–5 cm apart from each other), with their legs extensively overlapped, and were found during the daytime in wet, poorly-illuminated places. Just before dusk, the aggre-gations dispersed, and the individuals left the diurnal shelter to forage. The mean number of individuals per aggregation ranged from 3 to about 200 (Table 2). The mean sex ratio in aggregations of *G.* aff. *proximum* was nearly 1:1 (X ± SD = 1.07 ± 1.39; range = 0.25–7; n = 82 aggregations), in contrast to *G. longipes* in which the sex ratio was female biased (X ± SD = 1.8 ± 1.5; range = 0.3–5.3; n = 28 aggregations).

Discussion

Cave colonization and parental care

Caves are characterized by darkness, high moisture, little variation in temperature throughout the year, and low food availability (Barr, 1968), characteristics that may impose constraints on the colonization of caves by epigean animals (Gnaspini and Hoenen, 1999). The lack of light restricts cave colonization by visually oriented animals and makes occupation by photosynthetic organisms impossible. Generally, animal groups with cavernicolous representatives show nocturnal habits in the external environment and this feature may be a pre-adaptation for the occupation of caves. Indeed, cave-

Table 3. Potential predators of *Goniosoma* eggs based on literature data. The asterisk (*) indicates species found preying on eggs in the field. The sources for the cited species are the same as in Table 2

Species	Potential predators of *Goniosoma* eggs
G. aff. *badium*	*Zelurus travassosi* (Heteroptera: Reduviidae), *Strinatia* sp. (Ensifera: Phalangopsidae), and conspecifics
G. aff. *proximum*	*Pachycondyla* sp. and *Camponotus* sp. (Hymenoptera: Formicidae), *Oxychila* sp. (Coleoptera: Cicindelidae), and conspecifics
G. catarina	Conspecifics
G. discolor	Conspecifics
G. geniculatum	Cave crickets (Ensifera: Phalangopsidae) and conspecifics
G. indistinctum	Cave crickets (Ensifera: Phalangopsidae) and conspecifics
G. longipes	*Odontomachus chelifer* (Hymenoptera: Formicidae), *Zelurus travassosi** (Heteroptera: Reduviidae), *Strinatia* sp.* (Ensifera: Phalangopsidae), and conspecifics*
G. proximum	Conspecifics
G. spelaeum	*Zelurus travassosi** (Heteroptera: Reduviidae), *Sepedophilus* sp.* (Coleoptera: Staphylinidae), *Strinatia brevipenis* (Ensifera: Phalangopsidae), and conspecifics
Goniosoma sp.n.1	Ants (Hymenoptera: Formicidae) and conspecifics

dwelling arthropods rely mostly on non-visual structures, such as antennae or antenniform legs (Gnaspini and Hoenen, 1999 and references therein). Many cavernicolous species also show special adaptations to the scarcity of food, including a high resistance to starvation and/or an omnivorous and opportunistic diet (Barr and Holsinger, 1985). Harvestmen are an arachnid order with many cavernicolous species (Goodnight and Goodnight, 1981; Pinto-da-Rocha, 1995) and the presence of several of the morphological and physiological pre-adaptations cited above may explain their success in the colonization of caves.

Several representatives of the genus *Goniosoma* live in caves, mainly as trogloxenes (Gnaspini, 1996; Machado et al., 2000), i.e., they use the caves for shelter and as reproductive sites, but need to leave this habit to forage outside. Although species of *Goniosoma* comprise only 5% of the harvestmen fauna in Brazil, they account for 20.6% of all harvestmen species recorded in Brazilian caves (Pinto-da-Rocha, 1995). In addition to several morphological and physiological features that may favor the occupation of caves, species of *Goniosoma* present subsocial behavior, which may confer a special advantage in this particular environment. Subsociality includes brooding eggs and guarding young, as well as provisioning offspring before and after birth, and supporting them after nutritional independence (Clutton-Brock, 1991). Maternal assistance to eggs and nymphs has been reported for several harvestmen species and appears as the most elaborate form of parental investment in the order Opiliones (Machado and Raimundo, 2001).

Trivers (1972) proposed that maternal care will evolve when the individual's benefit (in terms of offspring survival) overrides the costs of parental behavior. Constant exposure to heavy predation may be an important selective pressure favoring the evolution of parental care if unprotected eggs have a high chance of being consumed (Wilson, 1971; Tallamy and Denno, 1981). Inside caves, the scarcity of food and the strong predation pressure (cave fauna consists mainly of predators and detritivores) may lead to a situation in which the maternal care confers an overall benefits to females. Despite the physiological costs of such behavior, unprotected eggs may have a low chance of survival. Indeed, for *G. longipes*, in which females reproduce inside caves, maternal care is crucial for egg survival since predators (mainly conspecifics and cave crickets) may consume entire batches in a single night (Machado and Oliveira, 1998). The results presented here show that most *Goniosoma* species seem to be exposed to these sources of egg mortality since similar egg predators were found near the guarding females (Table 3).

Defensive behavior and gregariousness

Arachnids are essentially solitary, predatory organisms that need to modify their behavior in order to interact with conspecifics. Among spiders and scorpions in particular, this behavioral modification is based on a period of non-aggression or tolerance that, in most species, corresponds to the sexual and parental phases (Foelix, 1996; Mahsberg, 2001). The few arachnid species that show social behavior are characterized by a suppression of cannibalistic habits among siblings, and an extended association between the parents and offspring. Therefore, at least among spiders, the subsociality is the most common route to achieve more complex forms of social behavior (Avilés, 1997).

Although detailed molecular studies have not yet been done, there are two main reasons to believe that individuals in harvestmen aggregations are not genetically related: (a) the individual composition of the groups varies from one day to another (G. Machado, unpublished data) and (b) after 5–14 days of maternal assistance the newly hatched offspring disperse and spend at least five instars (ca. 10 months) in a solitary life before joining a given group. Thus, there is apparently no direct connection between subsocial behavior and the evolution of gregariousness in *Goniosoma*. These observations weaken the possibility of kinship selection as a selective pressure leading to gregariousness in harvestmen, and also have an heuristic relevance for the comprehension of the evolution of sociality among non-related individuals. Perhaps the most important behavioral feature that differentiates harvestmen from spiders and scorpions is the lack of cannibalism among adults. Most records of cannibalism in harvestmen are of adults eating eggs or early instar nymphs (Edgar, 1971; Goodnight and Goodnight, 1976; Mora, 1990; Machado and Oliveira, 1998). Despite their carnivorous habits, harvestmen are generalist feeders with a tendency to necrophagy (Gnaspini, 1996; Machado et al., 2000). The non-cannibalistic habits of adults may have favored conspe-
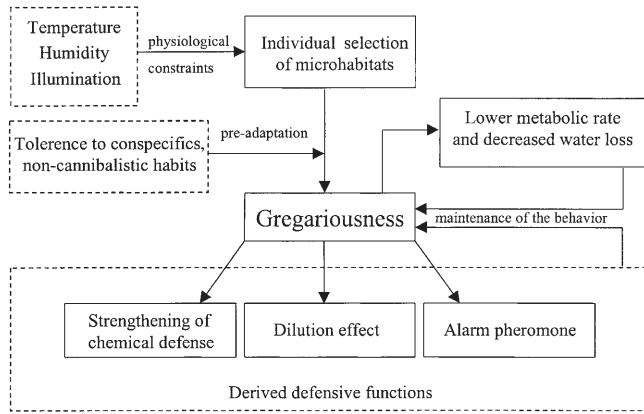
Figure 1. Hypothetical scenario for the evolution of gregariousness in harvestmen of the genus *Goniosoma*. Physiological constraints acting on individual harvestmen may lead to the selection of sites with appropriate temperature, humidity, and illumination. The lack of cannibalism among individuals may favor the tolerance of conspecifics, and may be a pre-adaptation to gregariousness. The derived functions of gregarious behavior in *Goniosoma* harvestmen may include strengthening of the defensive signal through the collective release of the scent gland secretion, the dilution (sensu Vulinec, 1990), and a promptness to flee a predator attack in response to the alarm role of defensive secretions. These defensive functions, allied with the physiological advantages of group living (such as lower metabolic rate and decreased water loss), may overcome the costs of living in a group and may contribute to the maintenance of gregariousness in *Goniosoma*

cific tolerance and the evolution of gregarious behavior in harvestmen (Fig. 1).

Among gregarious web-building spiders, the primary selective advantages favoring group living are derived from foraging benefits (Uetz and Hieber, 1997). For most insects, however, defense seems to be the main advantage achieved with gregariousness (Vulinec, 1990). Several hypotheses have been proposed to explain the adaptive relevance of harvestmen aggregations, including mating, defense, and hydro- and thermoregulation (Holmberg et al., 1984; Machado et al., 2000). The data presented here suggest that the gregariousness in *Goniosoma*, which is characterized by non-sexual, non-familial interindividual attraction, is not the result of chance but is a social phenomenon. Group living in the genus may confer defensive advantages to an individual harvestman in three different ways (Fig. 1). First, aggregations may strengthen the repulsive signal of the scent gland secretions to predators (Holmberg et al., 1984; Machado and Vasconcelos, 1998; Machado et al., 2000). Chemical studies have shown that the secretions produced by *Goniosoma* are mainly benzoquinones (Gnaspini and Cavalheiro, 1998; Machado et al., 2002), which are widespread predator deterrents among arthropods (Blum, 1981). Second, resting in a group may decrease the risks of being singled out by a predator, according to the dilution effect, which have been shown to reduce individual chance of predation by wasps in social spiders (Uetz and Hieber, 1994). Third, at least in *G.* aff. *proximum*, the scent gland secretion also works as an alarm pheromone such that larger groups respond faster to the chemical stimulus because of the increased number of sen-

sorial legs used for surveillance (Machado et al., 2002). This finding does not exclude the possibility that the scent gland secretion also works as an aggregation pheromone. In the leaf bug *Nezara viridula* the scent secretion, primarily used for defense, can elicit an alarm or attract conspecifics, depending on the concentration (Lockwood and Story, 1987).

Despite the defensive benefits, gregarious behavior in *Goniosoma* may be induced primarily by microclimatic factors, such as relative humidity, temperature, and degree of illumination (Holmberg et al., 1984; Machado et al., 2000), since harvestmen are more susceptible to dehydration than most other arachnids (Hillyard and Sankey, 1989). Microclimatic factors, such as relative humidity, temperature, and light conditions may have a general influence on gregariousness in arthropods (Buxton, 1932). For some beetles (Copp, 1983; Rasa, 1997), cockroaches (Dambach and Goehlen, 1999), millipedes (Dangerfield, 1993), and isopods (Friedlander, 1965), gregarious behavior is a strategy used primarily to reduce body water loss, since grouped individuals lose less water than solitary ones. The same is true for the harvestman *Vonones ornata* (Cosmetidae), in which the metabolism of aggregated individuals is 12% lower than that of single individuals (Anderson, 1993). A lower metabolic rate reduces energy expenditure and spiracular water loss in several tracheate arthropods, including arachnids (Hadley, 1994). This phenomenon may also occur in *Goniosoma* and gregariousness could act as a behavioral mechanism for regulating and reducing evaporation among grouped individuals. Thus, it seems reasonable to suppose that the defensive functions of gregarious behavior in *Goniosoma* have evolved as a by-product of a primarily behavioral response to environmental stress (Fig. 1; see also Machado et al., 2002).

The importance of behavioral studies in a variety of related species lies mainly in the basic information that can be used to test evolutionary hypotheses about the origin and maintenance of several life history traits (Brooks et al., 1995). Recently, several researchers have used behavioral characters to construct phylogenies (De Queiroz and Wimberger, 1993). Information on the behavior of organisms can be useful in both ecological and systematic studies (Wenzel, 1992; Miller and Wenzel, 1995). The genus *Goniosoma* is certainly the most studied among neotropical harvestmen. The amount of published information on *Goniosoma*, coupled with a phylogeny for the genus, would allow researchers to test hypotheses about the evolution of characters such as the colonization of caves, gregariousness, the chemical nature of the scent gland secretions, and life history traits associated with subsociality.

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