

Spatial distribution, mobility, gregariousness, and defensive behaviour in a Brazilian cave harvestman *Goniosoma albiscriptum* (Arachnida, Opiliones, Gonyleptidae)

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Abstract—This study provides information on population dynamics and behaviour (gregariousness and defensive tactics) of the Brazilian cave harvestman *Goniosoma albiscriptum* (Goniosomatinae). Through a mark-recapture study, we observed that this species regularly uses the cave during the day, leaving it to forage on the vegetation after dusk (i.e., a troglonexene species). There were nine groups within the cave, composed of females and males, the latter being the only sex that moved from one group to another (although rarely). Distinct groups used distinct openings of the cave to leave the shelter after dusk. *Goniosoma albiscriptum* showed a variety of mechanical defensive behaviours, and also exuded scent gland secretions. During dryer and colder months (between April and August), adult and subadult harvestmen aggregated on the cave walls. The individuals that composed the aggregations were not always the same ones. Reproductive activity (detected by the presence of egg batches) was negatively correlated with formation of aggregations. We suggest that intolerance towards conspecifics during the reproductive period may inhibit the formation of aggregations.

Keywords: harvestman; gregarious behaviour; mobility; Opiliones; population ecology.

INTRODUCTION

Population dynamics, defined as the relationship between a group of individuals of a single species within a particular area and environmental factors, can provide important data for evolutionary and ecological theory (Solomon, 1969; Ricklefs and Miller, 2000). The study of population dynamics of a particular species depends not only on understanding the responses of the individuals to the physical and biological

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environments, but also on how the individual activities are manifested and affect the dynamics of their groups (Ricklefs and Miller, 2000).

Cavernicolous species have traditionally been subdivided into three categories: troglobites, which are restricted to cave environments; troglaphiles, which have populations that complete their life cycle in caves as well as populations that complete their life cycle outside caves; and troglaxenes which inhabit caves but must leave them in order to feed and/or reproduce (Howarth, 1983; Gnaspini and Hoenen, 1999).

Harvestmen encompass about 4500-5000 species (Adis and Harvey, 2000) and have traditionally been divided in the suborders Cyphophthalmi, Palpatores and Laniatores (e.g., Shultz, 1998), although sometimes the first two are grouped in the single suborder Cyphopalpatores (e.g., Martens et al., 1981), or Palpatores is split into the suborders Eupnoi and Dyspnoi (e.g., Giribet et al., 2002). Typically, harvestmen are nocturnal foragers that inhabit humid environments (Berland, 1949), including caves. However, some are diurnal (Hoenen and Gnaspini, 1999) and others live in arid to semi-arid habitats (Cokendolpher et al., 1993). They feed mainly on other animals but also on vegetal matter (see references in Willemart, 2002).

Some harvestmen species are known to form aggregations that include three to 70 000 individuals (see references in Machado et al., 2000). Several explanations have been proposed to understand why harvestmen aggregate, and few studies have provided data on the dynamics of these aggregations (see Machado *et al.*, 2000).

Harvestmen belonging to the gonyleptid subfamily Goniosomatinae include several troglaxenic species that reproduce in caves (see references in Willemart and Gnaspini, 2004), but leave the shelter at night to forage (see references in Gnaspini et al., 2003). With respect to ecology and behaviour, this subfamily is the best-known group of Laniatores.

In order to provide further comparative information on goniosomatines and laniatoreans as a whole, and considering that the number of detailed works about population dynamics and gregariousness of harvestmen is still scarce, we report on the spatial distribution and mobility of a Brazilian cavernicolous harvestman *Goniosoma albiscriptum* Mello-Leitão, 1932. Since defensive behaviour and gregariousness may influence the distribution of individuals of this species in caves (see Machado et al., 2000), we also provide data on these topics.

MATERIALS AND METHODS

Study area

This study was conducted in Quarta Divisão cave (23°38'S, 46°22'W), in Ribeirão Pires, state of São Paulo, southeastern Brazil (see Gnaspini and Trajano, 1994; in that paper, the species studied herein was erroneously identified as *Goniosoma proximum* (Mello-Leitão 1922)). This granitic cave is formed by a conduit of 130 m,

which is crossed by a stream (~60 cm wide, <10 cm deep) (fig. 1). It has several openings (formed at the contact among large rock boulders) that open to a tropical secondary rainforest.

Fieldwork and marking methods

Preliminary daily visits to the cave were made twice in September 1999 and once in October 1999, to familiarise ourselves with the cave and the marking technique. From December 1999 to March 2001 the cave was visited once each month, during the day, for a mark-recapture study. In addition, the cave was visited on ten more occasions between October 1999 to April 2001, in order to make nocturnal observations of behaviour, using headlamps covered with red plastic filters.

Adult males and females and subadult males (which can be distinguished by the degree of armature, size and colour — see Gnaspini, 1995 and references therein) found in the cave were captured, marked, and then released in the exact place they were found. The developmental stage, location, and sex of all captured animals were noted.

When aggregations (=groups of three or more individuals with their legs overlapped — cf. Machado et al., 2000) were found, we also noted the number of individuals of each sex, and if it was on an exposed or non-exposed place. An aggregation was considered to be at an exposed place when the individuals were resting, within the hypogean environment, on a cave wall that faced an illuminated and open area (epigean environment or opening at the ceiling to the hypogean environment). Sites that did not fit this definition were considered to be non-exposed places.

To mark the harvestmen we used four coloured dots of enamel paint at the dorsum, femur and tibia of legs III and IV (modified from Gnaspini, 1996). Each animal had an individual mark (left legs and dorsum), which allowed individual recognition, and a 'first capture' mark (right legs), which corresponded to the month that the animal was first captured, as an extra insurance to make sure of the coding method.

In the monthly visits to the cave, we measured the temperature and relative humidity of the epigean environment and of ten locations in the hypogean environment, always starting at 14:30 h, using a portable whirling psychrometer. When manipulating the individuals, we noted any defensive behaviours exhibited.

Voucher specimens are deposited in the Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZSP).

Statistical analysis

We estimated the population size in the whole cave using the Fisher-Ford methodology (Blower et al., 1980) with a computer program developed by the junior author. Although we also tried to use Jolly and Manly-Parr methodologies, a low number of recaptures from the earlier months of study precluded this method.

Remaining analyses were conducted with SIGMASTAT statistical software version 2.0. This software tests for homoscedasticity and normality before analysing

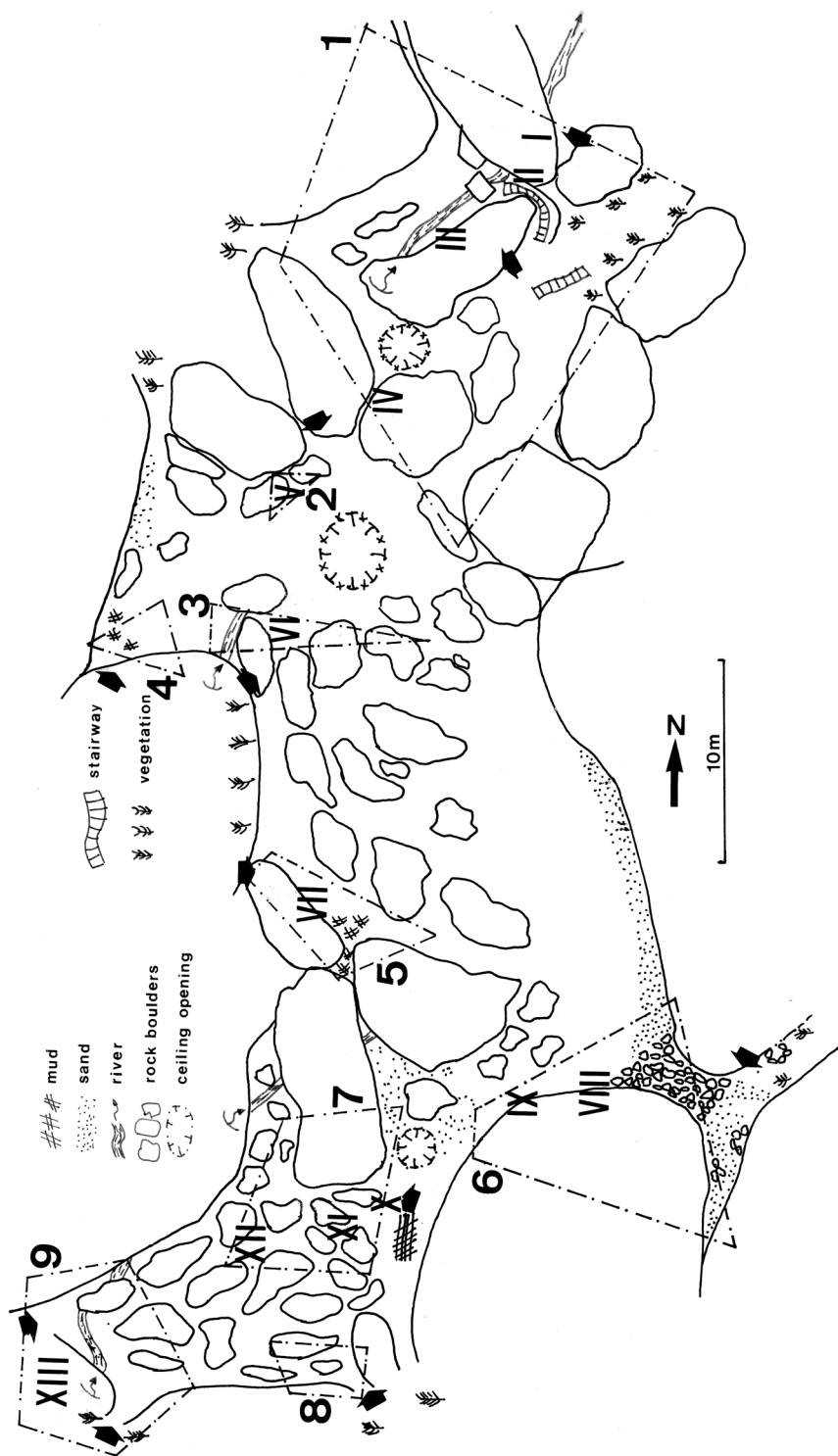


Figure 1. Map of Quarta Divisão cave, São Paulo, SP, southeastern Brazil. Polygons and Arabic numbers indicate the groups, Roman numbers indicate the locations where the aggregations were seen, and arrows show the entrances where individuals were seen leaving the cave after dusk.

the data with parametric tests. We compared our P values to $\alpha = 0.05$. The tests used in each case are indicated throughout the text. We used medians instead of averages to present our results since data were not normally distributed (see Zar, 1996).

RESULTS

Spatial distribution within the cave and mobility

Throughout the study, 260 individuals were marked and the total sex ratio was 1 : 1.4 (107 males and 153 females). Immatures younger than subadults were not included in the count since they were rarely found. The median number of individuals recaptured per monthly trip was 44.5 (range = 26-67), and the median number of individuals captured for the first time per monthly trip was 12.5 (range = 3-35). Therefore, the recapture rate was very high (median = 68.5%; range = 41.0-94.1%). Except for the first 2 months (when we found numbers larger than 300, probably due to a methodology bias that generally occurs in the first months; Blower et al., 1980), the population size residing in the cave was estimated to vary between 100 and 200 individuals during the 1.5 years sampled, with a daily survival index of 0.996. Since we found groups composed of the same marked individuals more than once in some regions of the cave, and only there, it seems that there are distinct groups that inhabit specific locations in the cave.

The distribution of the animals suggests that there are nine groups in the cave (fig. 1). A few males moved between groups ($n = 9$, 3 being subadults). Five males moved, respectively, from group 1 to 2, 1 to 3, 1 to 6, 1 to 7, and 2 to 3. Two males moved from group 3 to 5, and two from 7 to 9. No male returned to its original group after leaving it. Females sometimes moved away from conspecifics to oviposit (Willemart and Gnaspini, 2004), but were never found in two different groups.

Aggregations

In some regions of the cave, on vertical, horizontal or inclined walls, we found aggregations, either at exposed ($n = 2$: locations I and VII in fig. 1 and table 1) or non-exposed places ($n = 32$). Aggregations were formed by adult and subadult males, and by adult females. Immatures younger than subadults were never present within aggregations. The median number of individuals per aggregation was 4.5 (range = 3-10; $n = 32$). The average sex ratio within the aggregations was 1 : 2.3 female biased (table 1). Although individuals within aggregations changed, they tended to remain in the same region of the cave and so in the same group.

As temperature (Kruskal-Wallis: $H = 3.936$; d.f. = 9; $P = 0.916$) and humidity (Kruskal-Wallis: $H = 16.113$; d.f. = 9; $P = 0.065$) did not differ among the ten different locations studied inside the cave, we chose one of them (location

Table 1.

Characteristics of the aggregations of *Goniosoma albiscriptum* observed in the Quarta Divisão cave, southeastern Brazil. All dates are in the year 2000. ag = aggregation.

ag. #	Number of individuals	Females	Males (subadults)	Unknown sex	Location in the cave (fig. 1)	Date when the aggregation was seen for the first time
1	7	6	1	—	IV	30 April
2	8	8	—	—	II	30 April
3	4	3	1	—	IX	30 April
4	5	—	—	5	VIII	30 April
5	4	3	1	—	VII	30 April
6	4	4	—	—	X	30 April
7	6	5	1	—	IV	25 May
8	3	0	3	—	XII	25 May
9	6	4	2	—	XII	25 May
10	3	0	3(2)	—	XIII	25 May
11	4	3	1	—	IV	3 June
12	8	5	3	—	I	3 June
13	3	1	1	1	V	3 June
14	10	7	2	—	VI	3 June
15	7	4	3(2)	—	VII	3 June
16	6	4	2(2)	—	XIII	3 June
17	5	3	1	1	IV	17 June
18	4	3	1	—	IV	17 June
19	5	5	—	—	VII	17 June
20	3	2	1	—	VII	17 June
21	8	4	4	—	XIII	17 June
22	5	4	1	—	IV	02 July
23	4	3	1	—	III	02 July
24	6	3	3	—	VI	02 July
25	3	3	—	—	III	02 July
26	3	1	2	—	IX	02 July
27	6	4	1	1	XI	02 July
28	3	3	—	—	IV	30 July
29	9	6	3	—	III	30 July
30	3	3	—	—	IV	30 August
31	3	2	1	—	VII	30 August
32	4	2	2(2)	—	XIII	30 August

II in fig. 1) as representative of the hypogean environment. Annual variation in hypogean and epigeal temperature and humidity are presented in figures 2 and 3. We only found aggregations between April and August, which are the colder and drier months of the year (fig. 4). However, during the months in which aggregations were found, there was no correlation between the number of aggregations and meteorological features (Spearman rank order: epigeal temperature: $r_s = 0.671$; $P = 0.233$; $n = 5$; epigeal humidity: $r_s = -0.287$; $P = 0.683$; $n = 5$; hypogean temperature: $r_s = 0.671$; $P = 0.233$; $n = 5$; hypogean humidity: $r_s = 0.412$;

Table 2.

Marked individuals of *Goniosoma albiscriptum* captured more than once in aggregation in the Quarta Divisão cave, southeastern Brazil. The numbers indicate the aggregations according to Table 1. The Roman numbers between parentheses indicate the location of the aggregation in the cave, according to fig. 1. The last column corresponds to the date when the individual was last captured being aggregated or not.

Individual	30 April	25 May	3 June	17 June	2 July	30 July	30 August	Last capture
Females								
1	–	–	16 (XIII)	21 (XIII)	–	–	–	17 June 2000
2	1 (IV)	7 (IV)	–	–	–	–	–	4 March 2001
3	1 (IV)	–	11 (IV)	18 (IV)	–	–	30 (IV)	6 February 2001
4	1 (IV)	7 (IV)	11 (IV)	–	–	–	–	28 October 2000
5	1 (IV)	7 (IV)	–	–	–	–	–	28 October 2000
6	1 (IV)	7 (IV)	11 (IV)	–	–	–	–	4 March 2001
7	2 (II)	–	–	–	23 (III)	–	–	4 March 2001
8	5 (VII)	–	–	19 (VII)	–	–	–	17 June 2000
9	5 (VII)	–	15 (VII)	–	–	–	–	2 July 2000
10	5 (VII)	–	15 (VII)	–	–	–	–	2 July 2000
11	5 (VII)	–	–	19 (VII)	–	–	–	17 June 2000
12	5 (VII)	–	–	–	–	–	31 (VII)	5 January 2001
13	–	–	–	17 (IV)	22 (IV)	–	–	4 March 2001
14	–	–	15 (VII)	19 (VII)	–	–	31 (VII)	30 November 2000
15	–	–	15 (VII)	19 (VII)	–	–	–	02 July 2000
16	–	–	15 (VII)	20 (VII)	–	–	31 (VII)	3 December 2000
17	–	–	16 (XIII)	–	–	–	32 (XIII)	30 July 2000
18	–	–	–	–	22 (IV)	29 (III)	30 (IV)	30 August 2000
19	–	–	–	–	23 (III)	28 (IV)	–	3 December 2000
20	–	–	–	–	25 (III)	29 (III)	–	4 March 2001
21	–	–	–	–	25 (III)	28 (IV)	30 (IV)	30 September 2000
22	6 (X)	–	–	–	26 (IX)	–	–	28 October 2000
23	6 (X)	–	–	–	26 (IX)	–	–	30 August 2000
24	6 (X)	–	–	–	26 (IX)	–	–	30 August 2000
Males								
25	1 (IV)	7 (IV)	11 (IV)	17 (IV)	–	–	–	4 March 2001
26	5 (VII)	–	–	–	–	–	31 (VII)	5 January 2001
27	–	–	14 (VI)	–	24 (VI)	–	–	4 March 2001
28	–	–	15 (VII)	20 (VII)	–	–	–	17 June 2000
29	–	–	–	18 (IV)	22 (IV)	–	–	2 July 2000

$P = 0.450$; $n = 5$). The number of aggregations found was negatively correlated to the number of egg batches found per month (Spearman rank order: $r_s = -0.762$; $P = 0.0028$; $n = 12$) (see Willemart and Gnaspi, 2004). There was no monthly difference in the number of individuals per aggregation (ANOVA: $F_{4,18} = 1.316$; $P = 0.302$).

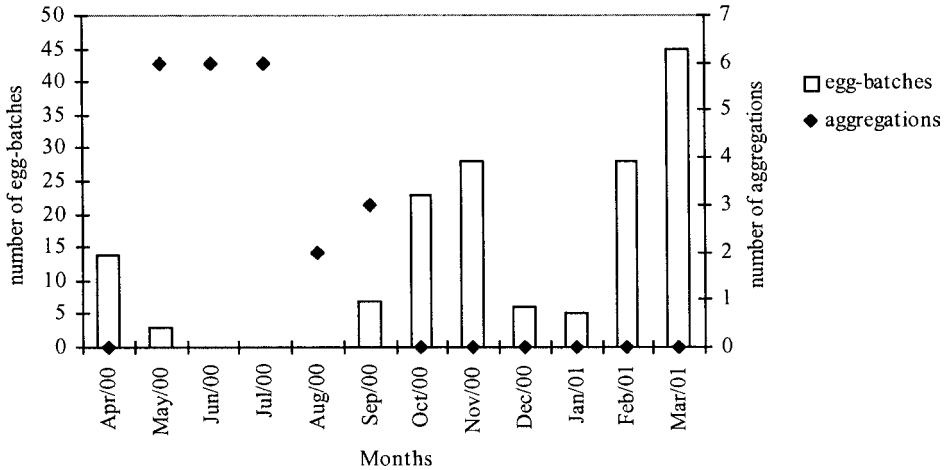


Figure 2. Number of aggregations of *Goniosoma albiscriptum* versus the number of egg batches found in Quarta Divisão cave during each month.

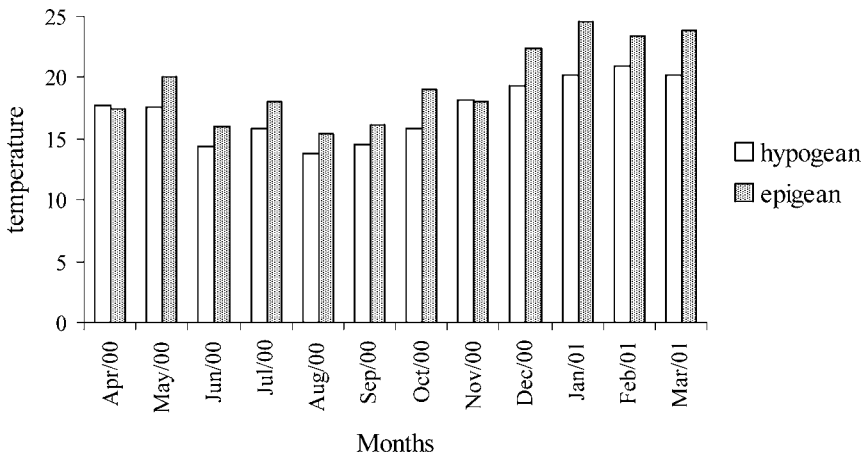


Figure 3. Annual variation of epigeal and hypogean temperature in the region of Quarta Divisão cave.

Foraging

During the day, except for some males that guarded females (Willemart and Gnaspini, 2004), individuals of *G. albiscriptum* stayed inside the cave in a resting position (i.e., the body was close or in contact with the substrate and the legs were flexed and brought close to the body). At night, some individuals left the cave to forage. They moved slowly towards the epigeal environment, alternating between walking, motionless in the resting position, and motionless but in the active position (i.e., with the legs radially spread around the body, supporting the body off the substrate). When walking, they tapped the substrate with legs I and II. Different groups used different cave openings to reach the forest. It is not known if the same

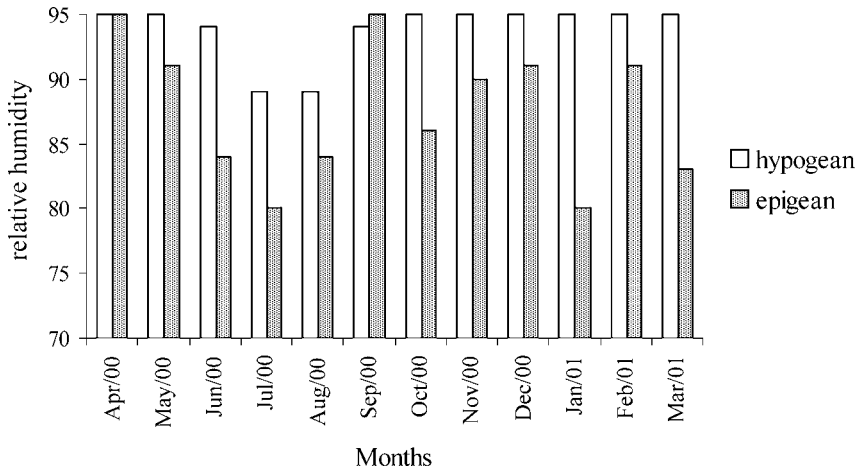


Figure 4. Annual variation of epigeal and hypogean relative humidity in the region of Quarta Divisão cave.

individuals always used the same opening because none was seen leaving the cave more than once. However, it seems that each group uses the nearest openings to reach the forest (see fig. 1), since distinct individuals of the same group were seen using the same closest opening, on different days. Only one observation was made on feeding: an adult male was seen eating a cane fly (Diptera, Tipulidae) at an opening during the day.

Defensive behaviour

Fleeing was the most common defensive behaviour when we touched the individuals with our fingers. Falling from the wall to the ground (the usual behaviour among *Goniosomatinae* species — see Gnaspini and Cavalheiro, 1998; Machado et al., 2000) was seldom observed. When handled by femur IV, individuals of *G. albiscryptum* stayed motionless with legs radially extended. If persistently handled, they tried to seize our fingers with their spiny pedipalps and bite with their chelicerae. Males would try to pinch our fingers between their fourth coxae and femur. Concerning chemical defence, when handled by the legs, individuals of *G. albiscryptum* released enteric fluid from their mouth, and this fluid accumulated in the posterior part of the dorsal scutum. The same behaviour was sometimes observed when we touched or illuminated the harvestmen with headlamps without red filters. If handled by the abdomen or cephalothorax, after having released the enteric fluid, they released secretions from their scent glands. These secretions mixed with the enteric fluid and either accumulated between legs II and III or moved along the lateral grooves of the dorsal scutum and accumulated on its posterior border. They were also able to eject and direct the scent glands secretions towards the stimulus. Third to fifth instar immatures and subadults behaved as adults, except for pinching with legs IV, which was only observed among subadults and adults.

We observed no difference between the defensive reaction of a harvestman alone and a harvestman in aggregation. It should be stressed, however, that when aggregated, and therefore with the legs overlapped, there was a mechanical transmission of the stimulus: if one individual fled, the others detected the movement and also started fleeing.

DISCUSSION

Relationship between G. albiscriptum and the cave

Since several marked individuals were often seen leaving the cave at dusk, others were seen at night foraging in the forest, and they were all seen again in the cave during the study, we can assume that they leave the cave to forage and return regularly to it. Since we never found individuals outside the cave during the day, we assume that this population is restricted to the cave. We hence consider this species as a troglone, as *G. spelaeum* (Mello-Leitão, 1933) (Gnaspirini, 1996) and *G. longipes* (Roewer, 1913) (Machado et al., 2000). It should be mentioned, however, that in another location (Boracéia Biological Station, at Salesópolis, São Paulo, SP — which is around 50 km from the studied cave), individuals of *G. albiscriptum* have been collected in the epigeal environment during the day while resting on rocks.

Philopatry and male displacements

Our study about spatial distribution and movements inside the cave showed a high recapture rate, which was also the case of *G. spelaeum* (Gnaspirini, 1996). A second important fact is that individuals of *G. albiscriptum* were almost always seen at the same cave region where they were before (with only a few exceptions). Combining these two pieces of information, we conclude that this species shows a high degree of philopatry, as detected for the two species mentioned above.

Breeding is a costly phenomenon for females, demanding adequate food intake. Since finding food may be easier in familiar environments, this is thought to be the reason why philopatry is more common in females than in males (Wrangham, 1980; Waser and Jones, 1983), which is in accordance to our data. Individuals of *G. albiscriptum* resting on a known place of the cave would find the epigeal environment (where they forage) more easily than individuals resting on unknown places of the cave. Therefore, the advantage of being philopatric would be the main factor responsible for keeping the groups separated.

The males that moved to another group did not return, suggesting that it would be a case of dispersion instead of occasional movement within a single population, and only nine out of 260 individuals moved between groups, suggesting that these might be distinct groups (see also Gnaspirini, 1996: only three individuals out of more than a thousand marked individuals moved between the two distinct groups of the same

cave). A similar pattern was found by Pires and Fernandez (1999), who studied a metapopulation of the marsupial *Microureus demerarae* (Thomas, 1905) in which only males moved between populations. In our study, evidence from reproductive data and/or genetic structure would be important to clarify whether these groups are relatively isolated, and therefore if we could call it a metapopulation (see Hanski and Simberloff, 1997).

The difference in the mobility of adult males and females is also found among other arachnid groups, such as scorpions (Scorpiones) and spiders (Araneae) (Foelix, 1996; Benton, 2001), but has so far been reported in only a few harvestmen, such as the laniatorean *Zygopachylus albomarginis* Chamberlin, 1925, of which the females wander in search of male nests (Rodríguez and Guerrero, 1976; Mora, 1990) and the Eupnoi *Leiobunum vittatum* Say 1821, of which males wait on rocks for wandering females (Macías-Ordóñez, 1997).

Ecology of aggregations

Many possible reasons for aggregations have been proposed (see Holmberg et al., 1984; Machado et al., 2002). Harvestmen aggregations seem to be somewhat common in Gonyleptidae (Laniatores), Phalangiidae and Sclerosomatidae (Eupnoi), although nothing can be said about other groups because they are not well studied from a natural history point of view. In our study, the choice of an adequate dark and humid place fails to explain why aggregations were found in such different locations of the cave, e.g., very tight and protected crevices and places exposed to wind (see also Machado et al., 2001). It should be mentioned that although aggregations were more frequent in protected than in exposed places, there are many more protected than exposed areas in the cave. However, aggregations do appear during winter, which is the season with lower temperatures and humidity. Aggregation to improve mating success also seems unlikely because most individuals of *G. albiscryptum* do not reproduce when aggregations are formed, as discussed below.

As concluded by Holmberg et al. (1984) for an Eupnoi, defensive purposes seem to be the most plausible explanation for aggregation in this species as well. Because either isolated or grouped harvestmen generally stay motionless during the day, animals that are willing to prey on these harvestmen in the cave must be either active searchers (see Riechert and Luczak, 1982 for discussion), or ambushers that stay on the routes of the harvestmen when they are leaving the cave, especially when these harvestmen generally use the same routes (as is the case of the studied goniosomatines). Considering the predators that have been recorded for other goniosomatines (see Gnaspini, 1996; Pellegatti-Franco and Gnaspini, 1996; Machado et al., 2000), the grey 'four eyed' opossum, *Philander opossum* Linnaeus, 1758 (Mammalia, Didelphidae), fits perfectly in the first case whereas the assassin bug, *Zelurus travassosi* (Costa-Lima, 1940) (Heteroptera, Reduviidae), seems to fit in the second case (PG, pers. obs.). The two potential cave predators of *G. albiscryptum* are the ctenid spider *Enoploctenus cyclothorax* (Bertkau, 1880) and *P. opossum*. *E. cyclothorax*, although seen throughout the cave day and night, and

known to try to prey on goniosomatine harvestman (Machado *et al.*, 2000), is a sit-and-wait predator (Willemart and Kaneto, 2004), and generally leaves the cave at night to forage (P. Gnaschini, pers. obs.). In addition, *E. cyclothorax* has had its prey taken by *G. longipes* and, independently, has been seen backing up after attacking *G. spelaeum* (Sabino and Gnaschini, 1999). Therefore, it would not threaten at least adults of *G. albiscriptum*. *Philander opossum* was often seen wandering throughout the cave after dusk. Thence, it is probable that the defensive advantages of aggregations, such as dilution effect, the strengthening of the repulsive signal by concomitant exuding of scent glands secretions, mechanical alarm by leg movement when any attacked harvestman tries to flee, alarm pheromone through the scent glands, and confusion effect (Machado *et al.*, 2002, and references therein) increase harvestmen chances of survival when attacked by opossums.

It has been proposed that although harvestmen first aggregated as a result of searching for adequate microclimatic conditions, it also became useful for defensive purposes (Machado, 2002). Relating this point to our data, why does *G. albiscriptum* not aggregate also in the warmer and more humid months if it would be advantageous (for defence purposes) to them?

We would like to propose an alternative hypothesis to explain this 'intermittent' gregariousness, based on the trade-off between defence and reproduction. Being aggregated is probably advantageous to the harvestmen against predators, as discussed above. Therefore, there must be a strong selective pressure that inhibits its formation in the rest of the year. Examining the conditions leading to the formation of aggregations, we understand that non-aggressiveness to conspecifics is maybe the most obvious requirement (see also Machado, 2002). However, females of *G. albiscriptum* are not tolerant to conspecifics the whole year. This harvestman exhibits parental care of eggs and first instar immatures, and conspecifics are known to prey on the eggs (Willemart and Gnaschini, 2004). It has been proposed (Willemart and Gnaschini, 2004) that egg-guarding females are found significantly more on exposed places than non-guarding females, possibly to avoid conspecific egg predation, because non-guarding females and males are mainly found in non-exposed places of the cave. Moreover, egg-guarding females react aggressively towards intruders, including conspecifics (Willemart and Gnaschini, 2004). Thus, females cannot be tolerant to conspecifics in periods of reproduction. In fact, reproductive activity was negatively correlated to the number of aggregations found (fig. 4). Moreover, it should be stressed that, when not guarding eggs/immatures, females tended to be gregarious, since the sex ratio seems to be more female biased within aggregations than when the whole population is considered. Therefore, females changed from being attracted to aggregations during non-guarding periods to being intolerant to aggregations during egg-guarding periods. In our evolutionary scenario, females that did not become intolerant towards aggregations during the reproductive period had more eggs eaten (Machado & Oliveira, 1998) and left fewer descendants than those who did become intolerant. Males were seen reacting aggressively towards conspecific males in the presence and even in the absence of females (Willemart

and Gnaspini, 2004) in months in which reproduction occurred. Occasional fights may reduce fitness of males, as shown by Willemart (2001), who reported the amputation of legs, and death in the days following male-male contests in another *Goniosomatinae* species. We therefore suggest that intolerance to conspecifics in the months of reproductive activity may inhibit the formation of aggregations, despite the advantages to individuals. As reproduction seems to be related to meteorological features (Willemart and Gnaspini, 2004), the latter would indirectly be related to the formation of aggregations. Broadly speaking, it would be a case of an individual activity (reproduction) that affects the dynamics of the whole group (non-formation of aggregations) (Ricklefs and Miller, 2000).

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