

Aspects of the population ecology of *Goniosoma* sp. (Arachnida Opiliones Gonyleptidae) in limestone caves in southeastern Brazil

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The new species of *Goniosoma* found in the city of Pains, Brazil, is well distributed in the caves of the region, occurring in 55 out of 62 visited caves. The species is still being described. This study aimed to evaluate oscillations in population sizes and to show possible allometric variations between individuals. The caves presented more constant temperature and relative humidity than the external environment. In Dona Rita cave the population of *Goniosoma* sp. varied between 48 and 140 individuals; in São Lourenço cave, between 45 and 346 individuals; in Isaías cave, between 93 and 509 individuals, and in Sorvetão cave, between 27 and 125 individuals. Despite the different sizes, the populations presented similar oscillations, reaching maximum values in June and July and then decreasing until October. No migration events were observed between the nearest caves, about 250 m apart. The species is troglomen, leaving the cave regularly to feed on the nearest trees and rocky walls and returning in the morning. A Principal Components Analysis (PCA) revealed a sexual dimorphism in the size of the second leg and its femur; the males with average leg length of 16 cm and femur length of 4.5 cm and the females with average leg length of 9 cm and femur length of 2.5 cm.

KEY WORDS: Brazil, caves, *Goniosoma* sp., population ecology.

Introduction	14
Methodology	15
Results	17
Population dynamics	17
Distribution patterns, gregariousness and parental care	18
Defensive behaviour	21
Activity schedule, foraging, predators and parasites	22
Sexual dimorphism and allometric comparisons	23
Discussion	23
Acknowledgements	27
References	28
Appendix 1	30

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INTRODUCTION

The harvestmen occur almost exclusively in moist habitats, such as on tree trunks and litter in forests and inside caves (EDGAR 1990). They are generally photophobic organisms, inactive during the day: they move at night to feed on small arthropods, decomposing organic matter or plant debris (PHILLIPSON 1960, CAPOCASALE & BRUNO-TREZZA 1964, EDGAR 1971). For orientation, they use the second pair of legs, which are elongated and have sensorial function. Although primarily solitary, some harvestmen can be found in aggregations, mainly during the day (CODDINGTON et al. 1990). The members of the suborder Laniatores can produce repugnatorial secretions, used in their defense (DUFFIELD et al. 1981, HOLMBERG 1983, COKENDOLPHER 1987). Many harvestmen have cestodes, trematodes, dipterans, wasps and mites as parasites (COKENDOLPHER 1993).

There are records for six families of harvestmen in Brazilian caves (PINTO-DA-ROCHA 1996a). Individuals of Gonyleptidae have been recorded in several caves in the country, but most families are restricted to few a caves (Minuidae, Tricommatidae, Cosmetidae, Stygnidae, and Gagrellidae). Among the six families listed, only Minuidae and Gonyleptidae have been found in Minas Gerais state (PINTO-DA-ROCHA 1995).

Harvestmen, as other cave organisms, can show different degrees of morphological, physiological and behavioral specializations (HOLSINGER & CULVER 1988, based on Schiner-Racovitza's system). Troglaxens are those that can be found regularly in caves but have to leave the cave to feed; thus so they are unable to complete their entire life cycle inside caves. Many of these organisms act as importers of energy from the external environment, often being primarily responsible for the energy input in permanently dry caves. Troglaphiles can complete their life cycle in the external environment or in caves. Troglobites are the most specialized organisms, occurring only in caves. These animals can show morphological, physiological, and/or behavioral specializations, probably evolved either in response to the selective pressures found in caves or to the absence of normal external selective pressures. Of the 5,000 harvestmen species found in the world, nearly 115 live in the cave habitat, of which 82 are obligatory troglobites (RAMBLA & JUBERTHIE 1994).

Only three species of troglobite harvestmen are known from Brazil: *Spaeleoleptes spaeleus* Soares 1966 (Minuidae), *Iandumoema uai* Pinto-da-Rocha 1996 (PINTO-DA-ROCHA 1996b) (Gonyleptidae) and *Pachylospeleus strinatii* Silhavy 1974 (Gonyleptidae). However, troglaphile harverstmen are more common, and many species occur in the States of São Paulo, Paraná, Minas Gerais, Goiás, and Pará. The Brazilian troglaxen species are *Paecilaema* sp., from Goiás, and the species of the genus *Goniosoma*: *Goniosoma badium* Kock 1839, inhabiting the caves of Paraná, *Goniosoma longipes* Roewer 1913 and *Goniosoma spelaeum* Mello-Leitão 1933 which occur in the State of São Paulo. The genus *Goniosoma* Perty 1833 (Gonyleptidae) include large harvestmen with a wide distribution in the Neotropics. The biology and ecology of some species of this genus have been studied (RAMIRES & GIARETTA 1994; GNASPINI 1995, 1996; MACHADO & OLIVEIRA 1998).

The present work aims to answer the following questions:

1. What are the sizes of four *Goniosoma* sp. populations in different caves from the karst area of Pains, Minas Gerais State, Brazil?
2. Is there migration among the populations?
3. Are there allometric differences among populations from different caves?
4. How are individuals distributed within each cave?

5. Is *Goniosoma* sp. a troglophile or troglomen species?
6. Is there sexual dimorphism?
7. What is the sex ratio and what are the prey, predators, and parasites of this harvestmen?

METHODOLOGY

Study site

This study was conducted in four limestone caves in the Pains district (Minas Gerais, Brazil). The Isaías and Sorvetão caves are located on the city periphery and are 250 m from each other. The Dona Rita and São Lourenço caves are located 10 km from the city, in the opposite direction.

The Isaías cave is the largest of the studied caves, about 250 m in length. Its main entrance is large, with the floor covered by silty sediment and a few rocks, and it opens onto a pasture. In the remaining portions of the cave, depressed blocks constitute the floor. Pains residents frequently visited the Isaías cave. Besides the main entrance, there is a second entrance (narrow) in the median region of the main conduit that connects the cave to a doline bottom surrounded by a small semi-deciduous seasonal forest fragment. The Sorvetão cave measures 60 m in length. Its main conduit shelters many speleothems and a silty floor occurs in some regions at the end of the cave. Its entrance is located within the limestone outcrop, surrounded by a dry forest on limestone outcrops.

The Dona Rita cave measures 160 m in length and there is an old pasture in succession phase in front of it. The floor is rocky at the entrance, becoming sandy in the inner sections, where there are also speleothems. The São Lourenço cave measures 130 m in length. In front of its entrance, there is a pasture with some trees close to the entrance. The cave floor varies from silty to sandy, causing high humidity. At the top of the rocky wall of these two caves there is well-conserved shrubby vegetation (dry forest from limestone outcrops).

Methods

The studied species of *Goniosoma* is being described by Dr Pedro Gnaspini (Instituto de Biociências, Universidade de São Paulo). Since there is no specific name, some photographs of the male and female were added to the manuscript to illustrate the species (Fig. 1).

The study was conducted from April to October 2000, with fortnightly visits to the four caves. The caves were divided, from the main entrance, into linear sections of 15 m length, totaling two sections from the São Lourenço and Sorvetão caves, four sections from the Dona Rita cave and five sections from the Isaías cave. For the Isaías cave, which has two entrances, the internal sections were determined from the two entrances. Thus, this cave was divided into two entrance sections and three internal sections. Temperature and humidity were measured outside the caves and in the sections of each cave with a thermohygrometer.

The harvestmen were captured by hand, marked on the cephalothorax with white corrective liquid and then numbered with Indian ink. The nymphs from the first stages were not used in the population census, since the frequent sheddings would cause the markings to be lost. These nymphs were only marked with spots of acrylic ink of different colors on the cephalothorax and on the base of the legs for identification of possible migrations. To investigate sexual dimorphism and allometric differences among distant populations, four measurements were taken from the specimens captured: cephalothorax width and length, lengths of the right second leg and its femur.

The method of Jolly was used to estimate the population sizes. However, for the Sorvetão cave, the method of Fisher-Ford was used due to the small number of individuals

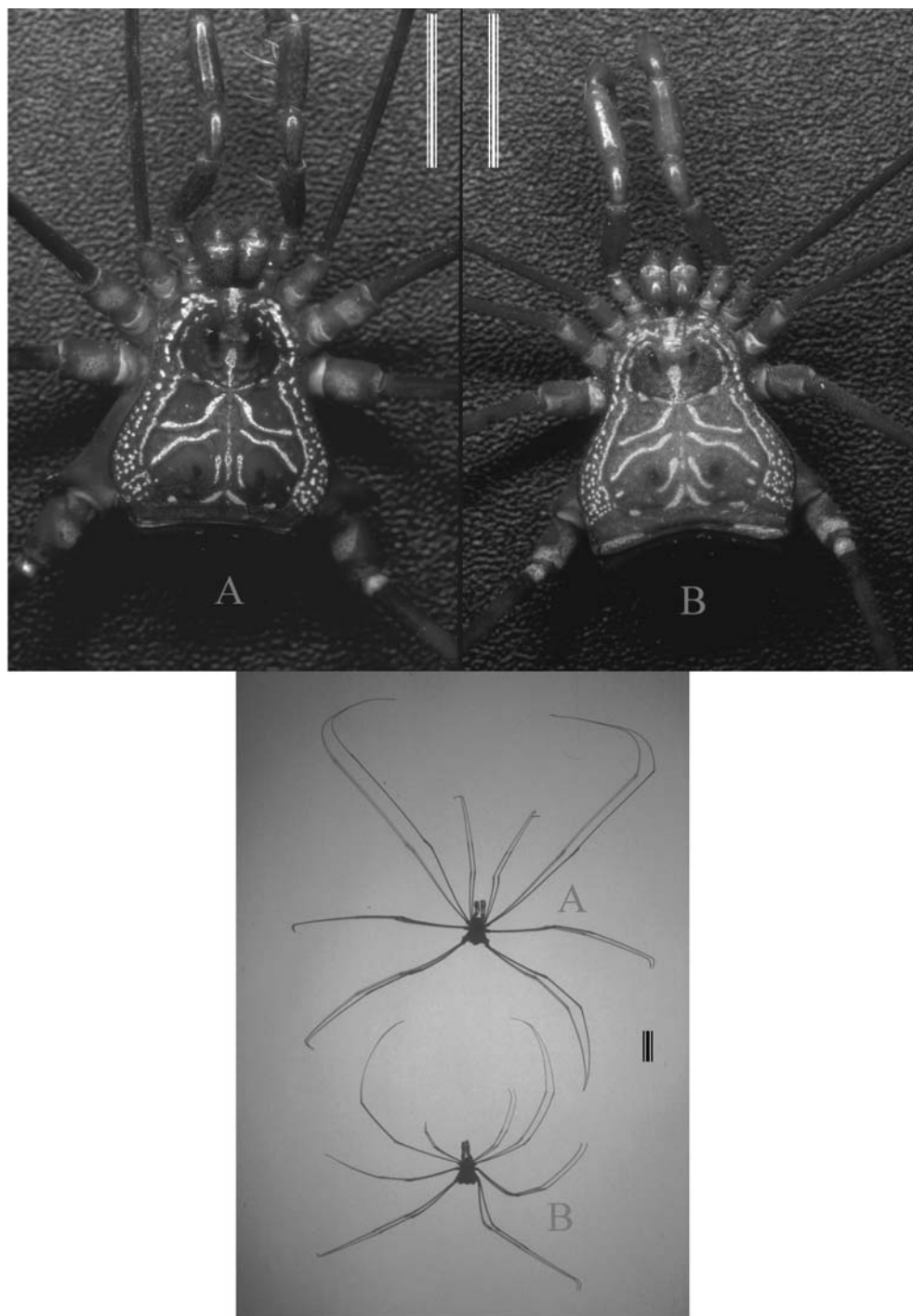


Fig. 1. — General view of individuals of *Goniosoma* sp. (A) dorsal view of the male; (B) dorsal view of the female. White bar: 5 mm; black bar: 10 mm.

observed, especially the recaptured ones (BEGON 1979). In addition to population size, the method of Jolly estimates the survival rate and the recruitment between two visits. The method of Fisher-Ford considers a constant daily survivorship rate during the study and estimates the recruitment and numbers of individuals lost between two visits. Biologically unacceptable results, such as survivorship rates higher than 1.0 and negative recruitment values and numbers of individuals lost may derive from mistakes made during the study. Such values can be assumed as 1.0 and 0.0, respectively (BEGON 1979).

A Principal Components Analysis (PCA) was conducted using the matrix of covariance of the log-transformed variables, a usual procedure in analyses of morphological patterns in populations and communities (MANLY 1986).

During some visits to the Isaias cave, the individuals were marked on the legs with fluorescent powder that shines intensely under UV light. Such markings were used to make crepuscular and nocturnal observations easier (with UV lights) in the vicinity of the entrances of this cave. Such observations aimed to determine the evolutionary status of the species (trogloxen/troglophile).

During the study period, 58 additional caves were also visited in the same region, providing additional observations on the species' biology, as well as information about its distribution.

RESULTS

The species *Goniosoma* sp. is well distributed in the limestone outcrops of the Pains district. Specimens were observed in 55 out of 62 visited caves, including the four studied ones. Thus *Goniosoma* sp. is a common species in the limestone caves of this region of Minas Gerais state, Brazil.

The hypogean systems of the four studied caves have a more constant air temperature and humidity than the external environment (Appendix 1). During the day, the temperatures of the external environment were generally higher. Instead the humidity remained lower outside than inside the cave, except on 2nd and 3rd September which were rainy days.

Population dynamics

For the population size estimations, 552 individuals were marked in Isaias cave, 329 in São Lourenço cave, 206 in Dona Rita cave and 86 in Sorvetão cave. The youngest nymphs, not included in the population size estimates, were relatively few in the populations during the study period, consisting of only 10% of the marked animals in Isaias and São Lourenço, 6% in Sorvetão and 2% in Dona Rita. The sex ratio was 1:1 for all the populations. The rates of recapture were similar for the first three caves, with means of 46% in Isaias, 53% in São Lourenço, and 55% in Dona Rita. The Sorvetão cave was different from the remaining caves, with a mean of only 19% of recaptured individuals. No migration event was observed between the closest caves, Isaias and Sorvetão.

The population size variation in Isaias and São Lourenço was from 93 ± 7 to 509 ± 58 and from 45 ± 11 to 346 ± 62 individuals, respectively (Tables 1-4). In Dona Rita it was from 48 ± 18 to 154 ± 9 individuals, and in Sorvetão from 27 to 125. In spite of their different sizes, the four populations showed very similar oscillation patterns, reaching their maximum numbers in June and July, and then decreasing until October (Fig. 1).

Table 1.

Variation in population size of *Goniosoma* sp. in Isaias cave.

Date	Population size	Survival rate	Recruiting
01/05		0.87	
14/05	287 ± 30	1.02	75
27/05	362 ± 46	0.72	93
10/06	354 ± 38	0.93	83
24/06	413 ± 56	0.92	129
08/07	509 ± 58	0.71	- 66
23/07	295 ± 22	0.84	25
06/08	273 ± 33	0.75	- 11
19/08	193 ± 24	0.95	- 1
03/09	183 ± 21	0.58	24
17/09	130 ± 17	0.48	47
01/10	110 ± 11	1.11	- 17
15/10	93 ± 7		

Table 2.

Variation in population size of *Goniosoma* sp. in São Lourenço cave.

Date	Population size	Survival rate	Recruiting
15/04		0.53	
30/04	64 ± 18	0.95	40
13/05	101 ± 32	0.89	110
26/05	254 ± 46	1.13	92
09/06	346 ± 62	0.75	59
25/06	319 ± 31	1.10	13
08/07	332 ± 18	1.05	6
22/07	338 ± 10	0.82	3
05/08	280 ± 35	0.77	7
18/08	223 ± 44	0.58	25
02/09	155 ± 20	0.86	16
16/09	150 ± 6	0.25	7
30/09	45 ± 11	1.19	42
14/10	87 ± 19		

Distribution patterns, gregariousness and parental care

The distribution of harvestmen varied among caves and in time (Tables 5-8). In Isaias, they occurred preferentially at the second entrance and in the closest sections (Internals 2 and 3). The main entrance of the cave encompasses the Entrance 1 and Internal 1 sections, very frequently visited by the inhabitants of the region and where some harvestmen were occasionally found. In the São Lourenço cave there is a clear preference for the entrance region, in contrast to what happens in the Sorvetão cave, where the most individuals were found in the second section of the cave. In the Dona Rita cave, there was an initial preference

Table 3.

Variation in population size of *Goniosoma* sp. in Dona Rita cave.

Date	Population size	Survival rate	Recruiting
15/04		0.87	
30/04	140 ± 24	0.70	34
13/05	139 ± 14	1.01	- 9
26/05	130 ± 19	0.99	25
09/06	154 ± 9	0.67	11
25/06	114 ± 11	0.90	- 3
08/07	100 ± 4	0.74	9
22/07	83 ± 5	0.92	6
05/08	82 ± 8	0.99	20
18/08	102 ± 18	0.79	- 2
02/09	79 ± 11	0.48	12
16/09	50 ± 14	0.89	4
30/09	48 ± 18	1.00	29
14/10	77 ± 51		

Table 4.

Variation in population size of *Goniosoma* sp. in Sorvetão cave.
(Daily survival rate corresponds to 0.995).

Date	Population size	Survival rate	Recruiting
01/05			
14/05	37	0	17
27/05	54	0	- 27
10/06	27	0	98
24/06	125	1	- 3
08/07	121	1	- 17
23/07	103	1	- 8
06/08	94	0	- 16
19/08	78	0	- 24
03/09	54	0	- 6
17/09	48	0	- 6
01/10	42	0	- 4
15/10	38	0	- 3

for the cave entrance, but in the subsequent visits most individuals occurred in the inner sections.

The aggregations of *Goniosoma* sp. were formed by groups of individuals that remained motionless side by side, very close to each other, with legs overlapping. These groups were formed by males, females and immature individuals. The number of individuals per aggregation varied from a few individuals (10-15) to hundreds of individuals, as observed in Opiliões cave (approximately 250 individuals). The aggregations were observed mainly near the entrances. Inside the caves, most individuals were isolated, while aggregations were quite rare and formed by only a few individuals.

Table 5.

Distribution of individuals of *Goniosoma* sp. in Isaias cave.

Date	Entrance 1	Internal 1	Internal 2	Entrance 2	Internal 3
01/05	0	0	56	72	22
14/05	0	0	49	52	17
27/05	0	0	39	33	15
10/06	0	0	53	42	6
24/06	0	0	26	32	30
08/07	0	0	40	56	31
23/07	0	0	47	49	10
06/08	0	0	34	31	12
19/08	0	7	14	33	10
03/09	0	1	3	17	0
17/09	0	3	4	17	1
01/10	0	3	7	14	0
15/10	0	5	7	4	7
28/10	0	5	12	8	3

Table 6.

Distribution of individuals of *Goniosoma* sp. in São Lourenço cave.

Date	Entrance	Internal
15/04	7	3
30/04	10	2
13/05	29	8
26/05	31	12
09/06	15	5
25/06	41	29
08/07	73	14
22/07	64	21
05/08	66	31
18/08	57	18
02/09	25	12
16/09	7	0
30/09	7	4
14/10	15	8
29/10	10	1

In October, a clutch, containing 103 eggs, was found for the first time in the São Lourenço cave. In November, new clutches were found in four other caves in the region: Curiós cave (Doresópolis, MG) (100 eggs), Massambará cave (83 and 110 eggs), Água Funda cave (105 eggs) and Sede da Ical cave (70 eggs), corresponding to a mean of 95 ± 13 eggs per clutch ($n = 6$). The eggs are laid on the walls and at the roof of the caves. The female exhibits parental care, positioning herself over the eggs till their eclosion. The eclosed nymphs come from the roof of the cave and shelter under rocks on the floor.

Table 7.
Distribution of individuals of *Goniosoma* sp. in Dona Rita cave.

Date	Entrance	Internal 1	Internal 2	Internal 3
15/04	68	1	2	0
30/04	50	5	3	1
13/05	10	8	9	4
26/05	3	9	7	7
09/06	18	17	10	4
25/06	4	8	20	15
08/07	4	9	23	8
22/07	1	3	15	12
05/08	0	6	13	8
18/08	0	3	16	14
02/09	5	6	13	4
16/09	1	1	1	6
30/09	1	1	2	2
14/10	0	2	8	1
29/10	6	1	1	1

Table 8.
Distribution of individuals of *Goniosoma* sp. in Sorvetão cave.

Date	Entrance	Internal
01/05	0	6
14/05	2	5
27/05	2	9
10/06	0	6
24/06	1	11
08/07	2	17
23/07	2	12
06/08	0	13
19/08	1	12
03/09	1	2
17/09	0	0
01/10	0	1
15/10	1	3
28/10	1	1

Defensive behaviour

Two distinct defense strategies were observed in *Goniosoma* sp. The most common was fleeing behaviour, in which the individual runs away from its original location when disturbed. Depending on the degree of disturbance, the individual could fall from the cave wall, and this behaviour was observed many times. The second strategy consists in releasing repugnatory liquid. This was commonly observed when the individuals were manipulated. This liquid is discharged directly

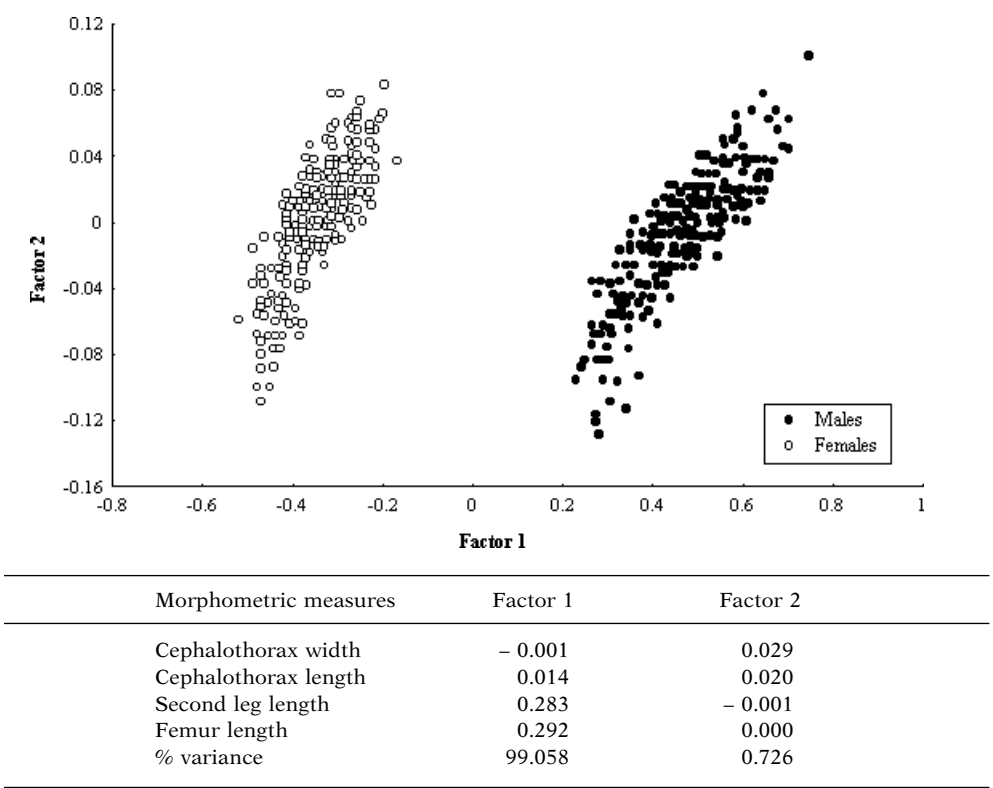


Fig. 2. — Principal Components Analysis (PCA) of the morphometric log-transformed data (Factor 1: Second leg length and Femur length; Factor 2: Cephalothorax width and length).

toward the aggressor as a spray, or it can be eliminated in small drops that remain on the surface of the body. The first discharge consists of a transparent liquid but, if the disturbance persists, a second liquid can be added to the first one, giving the mixture a yellowish coloration. This mixture can form red stains on human skin.

Activity schedule, foraging, predators and parasites

The harvestmen go out regularly at night to feed and come back at morning, which characterizes them as troglaxens. When they go out, they climb the rocky walls, trees and lianas close to the entrance. This behaviour was observed in Isaías where the harvestmen go out through the second entrance. There are no preferential trails when the individuals exit the cave. The harvestmen were observed feeding on adult Lepidoptera (Noctuidae) and being preyed upon, inside the cave, by *Zelus* sp. (Heteroptera Reduviidae), a predator found in almost all the visited caves. Another potential predator is the spider *Enoploctenus* sp. (Araneida Ctenidae), also very common in the Pains region.

Some individuals had Acari as parasites on the abdomen and on the base of the fourth leg. In the Isaías cave a mean of 14% of all individuals had parasites, in

the São Lourenço cave, 28%, and in the Dona Rita cave, 20%. In the Sorvetão cave, no individuals were found with parasites. Individuals with up to 25 Acari were found, the mean corresponding to 1.9 ± 1.5 Acari ($n = 39$) per individual with parasites in the Isaías cave, 3.8 ± 3.9 ($n = 78$) in São Lourenço, and 3.8 ± 3.5 ($n = 27$) in Dona Rita.

Sexual dimorphism and allometric comparisons

The procedures of the Principal Components Analysis (PCA) reduced the four morphological measurements to two axes (Fig. 2). In the first axis the most important variables were second leg length, and length of the femur of the second leg, explaining 99% of the variance observed among individuals. In the second axis the most important variables were cephalothorax width and length, explaining just 0.7% of the variance. Very evident sexual dimorphism was detected for the lengths of the second leg and its femur (Fig. 2). In males the second leg is about 16 cm long, with a femur of 4.5 cm. The females have a much shorter leg, with about 9 cm total length and 2.5 cm femur length (Figs 3-4). However, the means of cephalothorax width and length were very similar in both sexes (Figs 5-6). The populations did not show allometric differences for the variables measured.

DISCUSSION

The population sizes observed for *Goniosoma* sp. are rather similar to those observed for other harvestmen species from caves: the troglobite *Pachylospeleus*

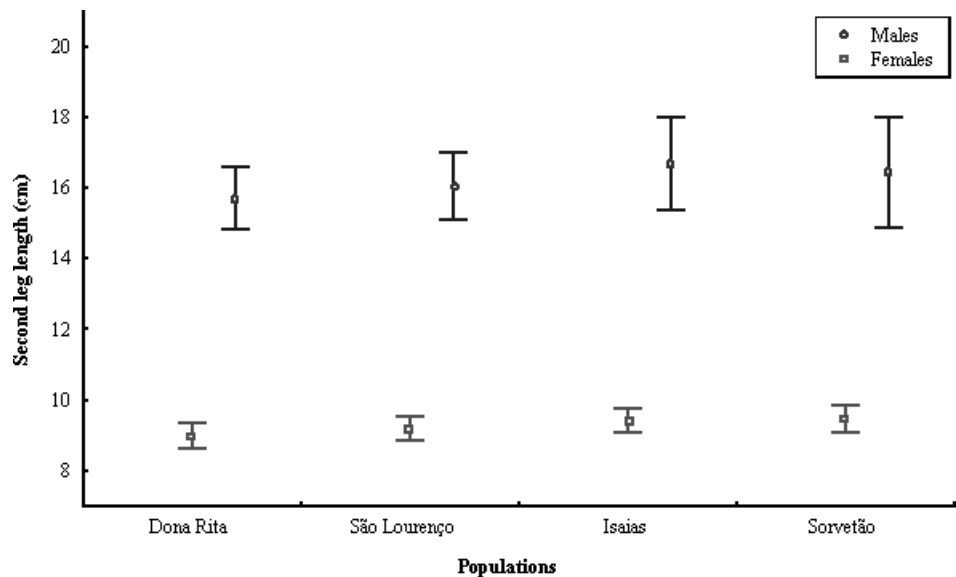


Fig. 3. — Mean second leg length of males and females of the four populations.

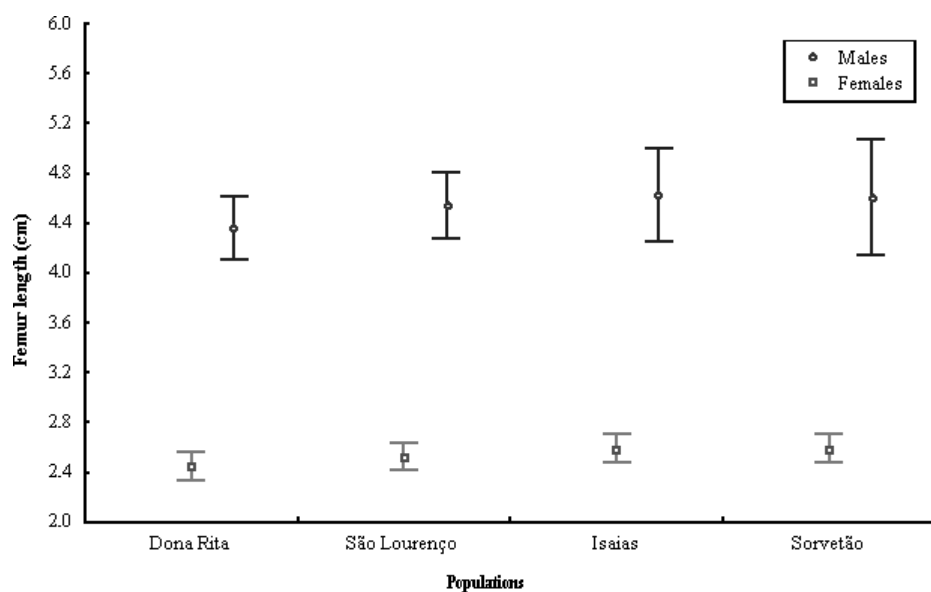


Fig. 4. — Mean femur length of males and females of the four populations.

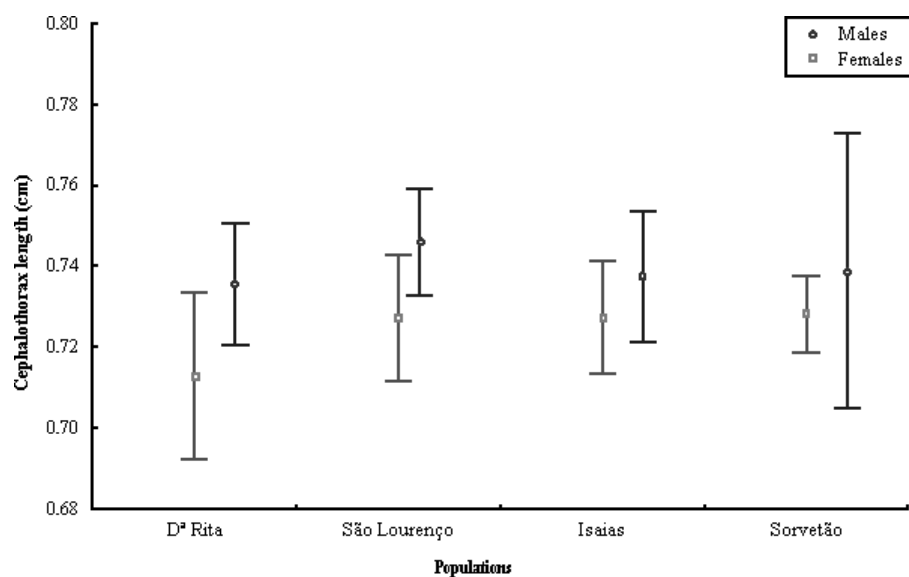


Fig. 5. — Mean cephalothorax length of males and females of the four populations.

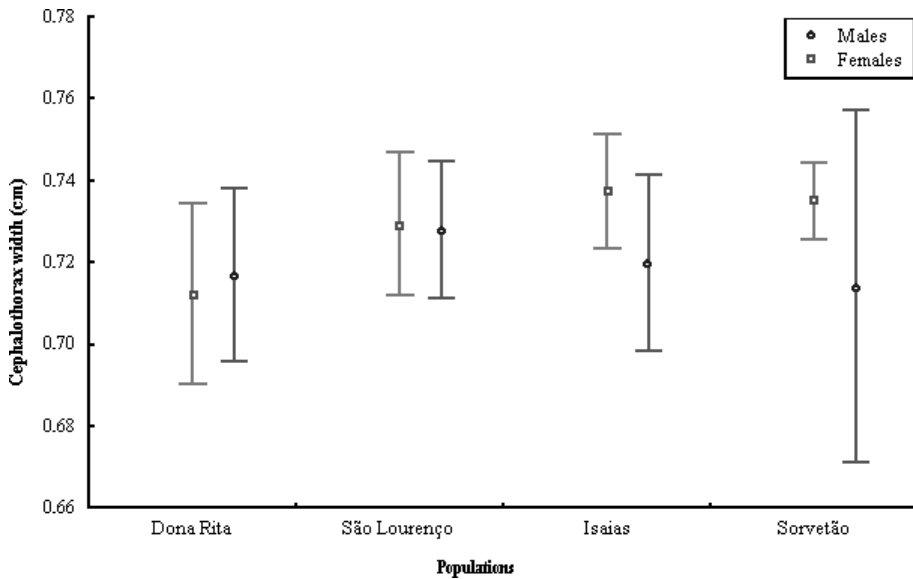


Fig. 6. — Mean cephalothorax width of males and females of the four populations.

strinatii, with a population estimated at 164 to 236 individuals in the Areias de Cima cave, São Paulo state (PINTO-DA-ROCHA 1993); the troglophile *Daguerreia inermis*, with 158 to 610 individuals at the Lancinha cave, Paraná (PINTO-DA-ROCHA 1996a) and the troglaxon *Goniosoma spelaeum* with populations estimated at 6 to 246 individuals in six caves in São Paulo (GNASPINI 1996).

The populations of *Goniosoma* sp. had larger numbers of adults and subadults in the months of June and July but they decreased in the following months. Migration proved to be a rare event among the populations of this *Goniosoma* species, as observed also by GNASPINI (1996) for the troglaxon *Goniosoma spelaeum* in the caves of the Vale do Ribeira (SP). In this case, in a 1-year period, only three specimens were observed to move between two populations located in different entrances of the same cave. Nevertheless, as harvestmen are usually found in moist habitats, dispersions may occur during the rainy season, a period when there were no observations in the present study.

The possibility that the spatial structure of the populations corresponds to that of a metapopulation should be considered, since the caves are relatively isolated habitats and migrations are infrequent. However, since migration events were not looked for during the potentially most suitable period and it is not known whether extinctions are frequent events in these populations, it is too early to initiate a discussion on this subject.

The low number of young nymphs observed from April to October indicates that only a small portion of the hundreds of eggs laid during the reproductive period, starting in October/November, will contribute to the recruitment of adults in the populations. Moreover, during the study period, many carcasses were observed

empty, which may indicate predation by the reduviid *Zelurus* sp., one of the main causes of population decline. The species *Zelurus travassosi* Costa-Lima 1940 is also the most important predator of the trogloden *Goniosoma spelaeum* in São Paulo and the troglophile *Daguerreia inermis* Soares & Soares 1947 in Paraná (GNASPINI 1996, PINTO-DA-ROCHA 1996a).

The section closest to the entrance is usually more strongly influenced by the external environment, while the inner sections had a low temperature and humidity variation during the sampling period. An exception was the Isaías cave, since the second entrance, located in the third section of the cave, allows the climatic conditions of the interior to follow those of the external environment.

The distribution close to the entrance is a characteristic feature of trogloden harvestmen, observed for *Goniosoma spelaeum*, *G. badium*, and *G. longipes* (PINTO-DA-ROCHA 1993, GNASPINI 1996), as it reduces the distance to be covered by the harvestmen to feed. The absence of individuals in the main entrance of the Isaías cave may result from the very altered vegetation (pasture), which provides adverse conditions (high temperature and low humidity) compared to the second entrance, located inside the forest fragment. Moreover, most harvestmen use the trees and lianas to search for food. In the Dona Rita cave, the preference of the harvestmen for the entrance changed at the onset of the dry season, when the trees lose their leaves. The harvestmen then settled in the inner sections of the cave, with more suitable temperature and humidity conditions. In the Sorvetão cave, this choice of the inner section prevailed during the whole study period, in contrast to the São Lourenço cave, where the narrow entrance and very moist soil determined the preferential distribution of the harvestmen at the entrance.

Gregariousness is a common behavior of many Palpatores (COCKERILL 1988, CODDINGTON et al. 1990), but is an apparently rare behavior in individuals of Laniatores. Some Brazilian species such as *Goniosoma badium* (PINTO-DA-ROCHA 1993), *Goniosoma spelaeum* (GNASPINI 1996), *Goniosoma longipes* (MACHADO et al. 2000), *Despirus montanus* and *Holoversia nigra* (MACHADO & VASCONCELOS 1998) can form aggregations. According to HOLMBERG et al. (1984), this behavior can be explained by different hypotheses. The first is related to habitat selection, in which individuals would choose places with low risk of dehydration and with low light exposure. The second suggests that the overlapping legs in compactly aggregated individuals would reduce air movement and consequently decrease evaporation (HOLMBERG et al. 1984). The third suggests that gregariousness increases the defensive ability against predators, by the action of the repulsive fluid secreted concomitantly by all individuals of the aggregation (HOLMBERG et al. 1984). Finally, the gregariousness could decrease individual predation by a dilution effect (MACHADO & VASCONCELOS 1988). In *Goniosoma* sp. the gregariousness seems to be more related to microhabitat selection, since the aggregations were almost always observed near the entrances, where climatic conditions (especially moisture) are more variable. Inside the caves, where moisture is high and there is no light, the individuals do not need to aggregate, since the environment is more stable. Hence, predation apparently does not have a strong influence on gregarious behaviour in this species.

Parental care can be exhibited by several harvestmen species (MORA 1990, GNASPINI 1995, MACHADO et al. 2000). This behaviour seems to be related to protection of the eggs against predation or fungal attack (MORA 1990). In *G. longipes*, the parental care is more related to protection against predators, such as the cricket *Strinatia* sp. (MACHADO et al. 2000). In *Goniosoma* sp., this behavior also seems to prevent egg predation.

Harvestmen can exhibit several defensive strategies when disturbed (DUFFIELD et al. 1981, ACOSTA et al. 1993). For some Palpatores, leg autotomy is considered the most common defensive strategy (ROTH & ROTH 1984). Fleeing behavior is also common for many harvestmen (BRISTOWE 1925, EDGAR 1971) and was recorded for some species of *Goniosoma*, such as *G. longipes* (MACHADO et al. 2000) and *Goniosoma* sp. The repugnatory liquid can be used in many harvestmen both to repel predators (DUFFIELD et al. 1981) and to avoid the establishment of microorganisms that can be their parasites, such as bacteria or fungi (COKENDOLPHER 1993). The actual use of the repugnatory secretion by *Goniosoma* sp. is, however, still unknown and deserves further attention.

Some species of harvestmen exhibit traffic between hypogean and epigean systems (GNASPINI 1996, MACHADO et al. 2000). This traffic may be influenced by the photoperiod, since the individuals leave the cave at the beginning of the night and returning before dawn. Foraging individuals of *Goniosoma longipes* use the same route within the cave, both when entering and leaving the cave (MACHADO et al. 2000), and the same is observed for *Goniosoma spelaeum* (GNASPINI 1996). Individuals of *Goniosoma* sp. do not follow this pattern, leaving the cave by different paths.

Regarding the Acari, the parasitism rates observed in the four populations are relatively low compared to the rates of 90% found in harvestmen from the epigean habitat of the Vale do Ribeira. The cave habitat (unsuitable for the parasites to attack) and the short time spent outside the cave by the harvestmen may be the causes of the low infestation rates (GNASPINI 1996).

There is no reason to think that "facultative" cave organisms would not show allometric differences between populations. One would think that, since they can live in the epigean system, they have no barriers to migration between caves. However, many troglloxenes and troglrophiles are unable to cross some epigean obstacles, such as rivers. Hence, isolation can occur in troglloxes and troglrophiles species as much as in troglobites. The very similar means of cephalothorax length and width and of lengths of the second leg and its femur among individuals of the four populations suggest that these anatomical parts show little variation. No movements between caves were observed, but some individuals might migrate, since the morphologies are quite similar in individuals of different populations, suggesting gene flow between the populations of the area.

The species *Goniosoma* sp. is broadly distributed in the limestone region of Pains, being fundamental to the cave communities and the external environment. In the same way, the remaining troglloxen species represent a connection between these two ecosystems. Acting as a predator only in the epigean habitat, *Goniosoma* sp. contributes organic matter and energy to the interior of the caves while being preyed upon by spiders and reduviids.

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APPENDIX 1

Environmental traits in each section of the studied caves.

Dona Rita	Air moisture (%)						Temperature (°C)					
	Entrance			Internal 1			Entrance			Internal 1		
	External	Entrance	Internal 3	Internal 2	Internal 3	Internal 3	External	Entrance	Internal 3	Internal 2	Internal 3	Internal 3
13-05-2000	44	44	57	75	77	77	27.7	27.2	21	20.3	20.7	20.7
26-05-2000	50	51	57	66	74	74	25	24	20.4	19.7	20.2	20.2
9-06-2000	42	56	72	80	80	80	27.2	20.3	19.8	19.5	20.3	20.3
25-06-2000	35	45	53	64	72	72	24.4	20.3	19.4	19.3	19.8	19.8
7-07-2000	45	47	58	69	75	75	24.8	23.4	20.3	19.7	20	20
22-07-2000	41	45	63	66	76	76	30.4	27	20	20	18.6	18.6
5-08-2000	45	50	55	64	74	74	23.7	22.3	21.2	19.8	19.7	19.7
18-08-2000	49	50	56	67	73	73	22.7	22	20.6	19.3	19.7	19.7
2-09-2000	90	78	77	81	82	82	20.8	20.8	20.4	19.8	20.5	20.5
16-09-2000	48	52	61	70	78	78	30.2	27	22.8	20.7	20.2	20.2
30-09-2000	35	45	53	70	76	76	30	26.5	22.5	20	20.7	20.7
14-10-2000	28	32	47	67	74	74	33.1	29	23	20.4	21.3	21.3
29-10-2000	67	69	71	77	83	83	29.8	27	21.2	20.3	18.6	18.6

São Lourenço	Air moisture (%)						Temperature (°C)					
	Entrance			Internal 1			Entrance			Internal 1		
	External	Entrance	Internal 2	Internal 1	Internal 2	Internal 2	External	Entrance	Internal 2	Internal 1	Internal 2	Internal 2
13-05-2000	49	51	70	80	80	80	26.8	25.9	18	15	15	15
26-05-2000	34	50	70	87	87	87	33	21.8	14.7	16	16	16
9-06-2000	41	64	70	82	82	82	28	19.2	16	18.3	18.3	18.3
25-06-2000	32	58	69	72	72	72	30.6	19.2	14	14.6	14.6	14.6
8-07-2000	41	64	76	81	81	81	29.5	18.5	14.7	17.4	17.4	17.4
22-07-2000	31	44	60	84	84	84	33.7	25.6	15.5	15.6	15.6	15.6
5-08-2000	30	48	59	68	68	68	30.7	20.8	16.7	16.9	16.9	16.9
18-08-2000	31	56	62	70	70	70	32.4	20.5	17.8	16.7	16.7	16.7
2-09-2000	89	88	86	91	91	91	19.8	19.2	16.9	17.6	17.6	17.6
16-09-2000	35	48	63	71	71	71	34	25.7	18.7	18.2	18.2	18.2
30-09-2000	26	35	52	64	64	64	36	27.4	20.2	18.2	18.2	18.2
14-10-2000	25	35	53	62	62	62	36	26	19.5	18.6	18.6	18.6
29-10-2000	70	75	76	84	84	84	26	21.8	19.2	18.2	18.2	18.2

Isaias	Air moisture (%)						Temperature (°C)					
	Entrance			Internal 2			Entrance			Internal 2		
	External	Entrance	Internal 1	Internal 2	Entrance 2	Internal 3	External	Entrance	Internal 1	Internal 2	Entrance 2	Internal 3
14-05-2000	71	73	70	67	75	74	21.5	19.1	20	19.7	19.1	19.3
27-05-2000	64	73	73	74	74	75	26	18.7	19	18.3	18.7	19.1
10-06-2000	72	70	72	75	75	76	15.8	16	16.9	19.6	16	17
24-06-2000	44	50	55	60	66	66	24.2	20	20	18.9	20	19.5
8-07-2000	65	64	65	67	74	76	20	18.9	17.5	18.7	18.9	18.6
23-07-2000	74	71	74	80	81	81	20.6	20.5	17.8	19.2	20.5	18.9
6-08-2000	63	63	63	64	65	68	16.5	16.8	17.3	17.3	16.8	18.6
19-08-2000	65	66	68	71	71	75	19.5	18.7	17.5	19.4	18.7	19.1
3-09-2000	94	90	92	95	92	88	20.3	19.9	18.7	19.5	19.9	20.1
17-09-2000	79	74	76	78	82	81	20.5	20	19.7	20.9	20	20.7
1-10-2000	69	67	69	71	75	79	21.6	19.6	19.3	20.2	19.6	20.7
15-10-2000	43	48	53	59	58	64	26.5	22.9	20.3	22.3	22.9	21.6
28-10-2000	59	58	62	76	72	73	30	27	25	21.8	24.9	24.8

Sorvetão	Air moisture (%)						Temperature (°C)					
	Entrance			Internal 1			Entrance			Internal 1		
	External	Entrance	Internal 1	Internal 1	Entrance 1	Internal 1	External	Entrance	Internal 1	Internal 1	Entrance 1	Internal 1
Date												
14-05-2000	55	70	70	70	70	70	22.1	19.7	19.9	19.9	19.9	19.9
27-05-2000	52	65	76	76	76	76	26	20.6	18.6	18.6	18.6	18.6
10-06-2000	62	67	70	70	70	70	22	19.1	18.8	18.8	18.8	18.8
24-06-2000	53	71	70	70	70	70	20.5	18.2	17.8	17.8	17.8	17.8
8-07-2000	41	59	69	69	69	69	26.7	20	18.3	18.3	18.3	18.3
23-07-2000	70	78	79	79	79	79	20.8	18.2	18.3	18.3	18.3	18.3
6-08-2000	54	61	67	67	67	67	21	18.8	18	18	18	18
19-08-2000	50	69	73	73	73	73	24.2	18.5	18	18	18	18
3-09-2000	89	91	92	92	92	92	21.2	18.8	19.4	19.4	19.4	19.4
16-09-2000	40	56	63	63	63	63	30	23.8	21.6	21.6	21.6	21.6
1-10-2000	70	73	78	78	78	78	22.8	20.6	20	20	20	20
15-10-2000	55	63	70	70	70	70	25.3	21.1	19.7	19.7	19.7	19.7
28-10-2000	68	72	75	75	75	75	27	22.5	22.5	22.5	22.5	22.5