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Reproductive biology of the neotropical harvestman (*Goniosoma longipes*) (Arachnida, Opiliones: Gonyleptidae): mating and oviposition behaviour, brood mortality, and parental care

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Abstract

Goniosoma longipes is a neotropical cavernicolous harvestman that exhibits parental care. Reproductive activity in *G. longipes* is more intense during the wet season. Mating lasts up to 3 min, and the whole oviposition process may take over 5 h. During oviposition the female may be reinseminated once or twice by the mating male. Females oviposit 60–210 eggs on the cave wall and guard egg batches for nearly 2 months, until the 1st-instar nymphs disperse. Four main factors can affect egg survival in *G. longipes*: dehydration, fungal attack, cannibalism, and interspecific predation. Frequency of fungal attack on egg batches was greater in the wet season and more intense near the river inside the study cave. Although egg-guarding by females failed to prevent fungal attack on eggs in *G. longipes*, the choice of a suitable oviposition site by the gravid female can reduce fungal attack within the cave habitat of this species. Guarding females successfully repel conspecific egg predators, but unguarded eggs are frequently consumed by adult and juvenile *G. longipes*, as well as cave crickets *Strinatia* sp. Field experiments in which females were removed from egg batches demonstrated that egg-guarding by the mother has an anti-predator role in *G. longipes*, with a significant positive effect on egg survival. Male *G. longipes* actively patrol their egg-guarding mates, and take over brood care for up to 2 weeks if the latter are experimentally removed. The degree to which male assistance can play a relevant role in parental care is still unclear for this species. Damage to the brood is regarded as a major force favouring the evolution of parental care in harvestman species. This field study provides the first experimental demonstration that egg-guarding by females affords protection against egg predation in a harvestman species.

Key words: harvestman, *Goniosoma longipes*, mating, egg-guarding, fungal attack

INTRODUCTION

Parental investment is defined by Trivers (1972: 139) as ‘any investment by the parent in an individual offspring that increases the offspring’s chance of surviving (and hence reproductive success) at the cost of the parent’s ability to invest in other offspring’. This may include investment by females in eggs, as well as incubation and egg-guarding, and the feeding of young by one or both parents (Clutton-Brock, 1991). Parental care is present in all arachnid orders, but there are comparatively few well-documented cases for harvestmen (see Cloudsley-Thompson, 1958; Klingel, 1963; Muma, 1966; Weygoldt, 1969, 1972; Pittard & Mitchell, 1972; Foelix 1982; Polis, 1990; Gnaspini, 1995). Maternal care in harvestmen has been reported for species from different families around the world. In the neotropics, there are several records of maternal care for species in the family Gonyleptidae (reviewed by Gnaspini, 1995). There is no record of biparental care in harvestmen.

Harvestmen are generally nocturnal, vagile, photophobic and solitary omnivores (Savory, 1938; Coddington, Harner & Soderstrom, 1990). The behavioural biology of harvestmen is poorly studied, particularly for neotropical species. Basic data about the natural history are scarce and scattered, and this hampers the formulation of testable hypotheses about their behavioural ecology. Most harvestman species deposit a large number of eggs on a variety of substrates, such as soil, trunk crevices, under stones, wood, foliage and other moist places (Cloudsley-Thompson, 1958). The most common reproductive mode in harvestmen involves copulation, although parthenogenesis may occur in some species (Phillipson, 1959; Tsurusaki, 1986). Mating in harvestmen is usually not preceded by courtship displays, but in some species the males may fight for access to females (Berland, 1949) while in others the courtship is very simple (see Martens, 1969).

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Fertilization is internal and females lay the eggs a few hours or days after mating (Juberthie, 1965).

The harvestman *Goniosoma longipes* (Gonyleptidae) commonly aggregates in sandstone and granitic caves in south-east Brazil (Gnaspini & Trajano, 1994). Foraging takes place outside the caves at night, and during the day many individuals are seen resting on the cave walls, which is also the preferred oviposition site. This paper provides a detailed field account of the behavioural biology of *G. longipes* with special emphasis on reproductive seasonality, mating and oviposition behaviour, sources of brood mortality, and parental care. The study involves descriptions of harvestman behaviour, as well as field experiments designed to assess the relevance of parental care against brood mortality caused by fungal attack, cannibalism, and interspecific predation.

MATERIALS AND METHODS

Study area

Field work was carried out in the Parque Florestal do Itapetinga (23°10′S, 46°25′W; altitude 1000 m), near Atibaia, State of São Paulo, south-east Brazil. The area is a microbasin formed by small perennial streams that flow on granitic and/or sandy beds. In some places the rivers are covered by large granitic rocks that form small caves. The climate has two well-defined seasons. The dry/cold season lasts from April to September, with a mean monthly rainfall of 72 mm and a temperature 17 °C. Winter frosts are frequent, especially in June and July. The wet/warm season lasts from October to March, with a mean monthly rainfall of 182 mm and a temperature 21 °C. The climatic data presented in this study were provided by the meteorological station of the Centro de Ensino e Pesquisa em Agricultura (Cepagri), located 11 km from the study site.

Behavioural observations

The reproductive biology of *G. longipes* was studied in a granitic cave (300 m long) crossed by a river ($\approx$60 cm wide). Field observations were carried out weekly from August to November 1995, and at 7–14 day intervals from March 1996 to August 1997. Egg-guarding females of *G. longipes*, and the number of eggs per batch, were monitored during each census in the cave. Observations inside the cave were made with a flashlight covered by a red filter to avoid disturbing the organisms. Behavioural data on the harvestmen are based on more than 300 h of field work.

Egg-guarding females of *G. longipes* ($n = 69$) were individually marked with coloured dots of enamel paint (Testors Co., Rockford, U.S.A.) on the dorsum of the cephalothorax and on the femur of 1 leg. The behaviour of females was apparently unaffected by this marking procedure (see also Gnaspini 1995, 1996). The behaviour and mobility of marked females was evaluated by checking them, and their egg batches, at 1-h intervals for periods of 3–8 h. Continuous recording was made of all relevant behavioural events, such as a predator attack on eggs or agonistic interactions between individuals, as suggested by Martin & Bateson (1986).

Field experiments

The effect of maternal care on egg survival was evaluated through field experiments in which the mother and/or eggs were kept isolated under 15 × 10 cm perforated plastic cages (3 cm high; 0.5 mm mesh), or the mother was removed from her uncaged brood. Four experimental groups were established ($n = 10$ egg batches per group): (a) guarding females and eggs caged (mean ± SD = 146.3 ± 9.1 eggs/batch); (b) guarding females removed, and eggs caged (142.5 ± 12.3 eggs/batch); (c) guarding females removed, and eggs left uncaged (154.4 ± 9.4 eggs/batch); (d) guarding females and eggs uncaged (139.7 ± 12.8 eggs/batch). There was no significant difference in initial egg numbers between treatments. Experimental egg batches were at initial developmental stages and undamaged, and all under similar light and wind conditions within the cave. Experiments were carried out during the wet season, and lasted 14 days. Fungal attack on experimental batches of groups (a) and (b) was compared by performing Mann–Whitney *U*-tests on the percentages of fungus-infected eggs per batch on the 14th day (percentage values were arcsin transformed). Groups (c) and (d) assessed the efficiency of maternal care against cannibalism by intruding *G. longipes*, and interspecific predation. After square-root transformations on the data, a repeated-measures ANOVA was performed on the number of eggs per batch before (day 1) and after (day 14) treatment.

RESULTS

Reproductive seasonality

Sixty-nine egg batches of *G. longipes* were found in the cave from March 1996 to August 1997. Reproductive activity was much more intense during the wet/warm season (46 egg batches in 24 weeks) than during the dry/cold season (23 egg batches in 24 weeks) (Fig. 1). The average number of eggs per batch also differed between the two seasons (wet/warm season: mean SD = 144.1 ± 33.9 eggs per batch, $n = 42$; dry/cold season: 113.2 ± 32.9 eggs per batch; $n = 23$; *t*-test, $t = -3.74$, d.f. = 63, $P < 0.001$). The number of egg batches per month is significantly correlated with mean monthly day length ($r_s = 0.706$, $P < 0.01$, $n = 12$) and rainfall ($r_s = 0.531$, $P < 0.05$, $n = 12$). During the wet/warm season, however, harvestman reproduction shows two distinct peaks: high in October and medium in March (Fig. 1).

Females oviposit on the cave's granite walls, in cham-

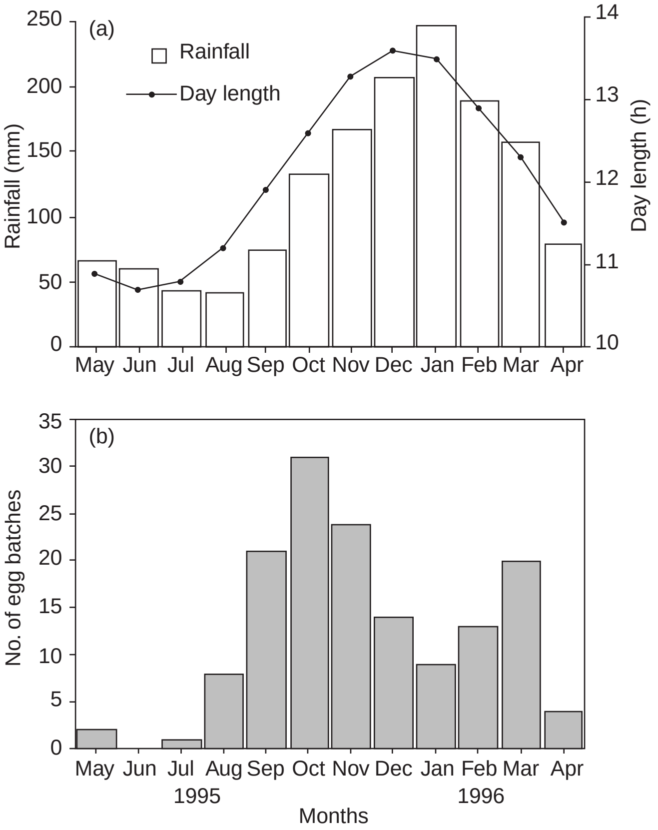

Fig. 1. Climatic data (a) and reproductive activity (b) of *Goniosoma longipes* near Atibaia, south-east Brazil.

bers protected from external wind and light. Oviposition sites were 32–800 cm from the river crossing the cave (mean ± SD = 127.0 ± 95.5 cm; $n = 88$). Six females reproduced twice. The interval between ovipositions varied from 4 to 13 months, with the females laying similar numbers of eggs in the two reproductive events (first oviposition 125.5 ± 25.1 eggs, $n = 4$; second oviposition 129.5 ± 46.3 eggs, $n = 4$).

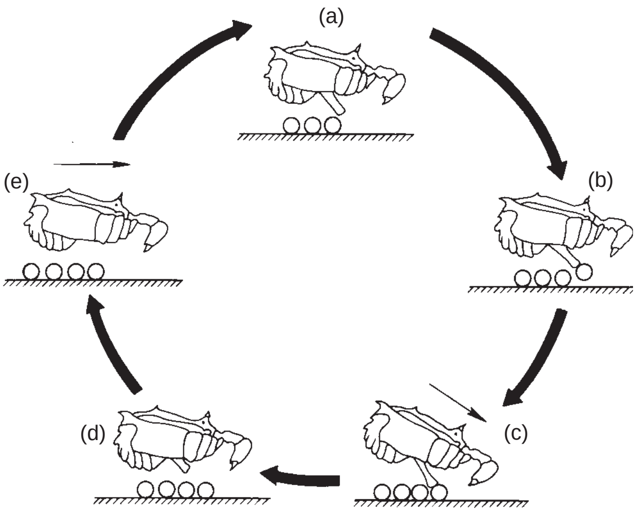

Fig. 2 The oviposition process of *Goniosoma longipes* (legs not drawn). (a) Female everts the ovipositor, (b) lays one egg, (c) lowers the anterior region of the body, (d) retracts the ovipositor, (e) and moves forward to lay another egg.

Mating and oviposition behaviour

Oviposition in *G. longipes* occurs immediately after mating. Before copulation the male approaches the female frontally and grasps her pedipalps with his pedipalps. Subsequently, both raise the anterior portion of the body and mutually approach each other to place their ventral sides in contact. In this position the male everts his penis and penetrates into the female's genital orifice. The copulation process lasts 2–3 min ($n = 2$). Oviposition behaviour is stereotyped and very similar to that described for other laniatorid harvestmen, and may last over 5 h (based on partial observations of seven oviposition events). As the female lays the eggs, the male remains about 2 cm behind her, waving his second pair of legs over her body and tapping her legs occasionally. The eggs are deposited on the substrate at regular intervals of about 3 min (3.2 ± 0.7 min, range = 1.8–4.5 min, $n = 13$; see Fig. 2). Occasionally the female interrupts oviposition and touches the eggs with her second pair of legs. Even during the oviposition process the female may be reinseminated once or twice by her mate. Mating males were observed often ($n = 20$) to remain close to ovipositing females for 1 h to >24 h. One such male copulated with his mate 5 h after the termination of the oviposition process. On one occasion a satellite male approached an ovipositing female, grasped her with his pedipalps and attempted to mate. The female responded by lowering the anterior portion of her body and directing her back towards the satellite male, who walked away as the female resumed oviposition. By end of the oviposition process the resident male walked away, remaining 1.5 m from the female.

Parental care

All observed egg batches ($n = 89$) were guarded by one adult female, who may either sit on the eggs or remain next to the batch (Fig. 3a). Occasionally the guarding female touches the eggs with her second pair of legs and also inspects the periphery of the egg batch. Although many individual *G. longipes* leave the cave at night to forage, guarding females remain with their brood.

Eggs of *G. longipes* change in colour and increase in size with maturation. Recently laid eggs are cream and average 1.44 ± 0.09 mm in diameter ($n = 20$). The eggs darken with development and become black just before hatching, when the average diameter is 1.91 ± 0.12 mm ($n = 20$). Eggs are spaced out by 1–2 mm within the batch (Fig. 3a). Unfertilized eggs make up to 5.3% of the batch, and are easily recognizable by their creamish appearance among the darker fertilized eggs. Unfertilized eggs are not removed by the guarding female. Fertile eggs hatch in 45–64 days (53.1 ± 6.3, $n = 32$

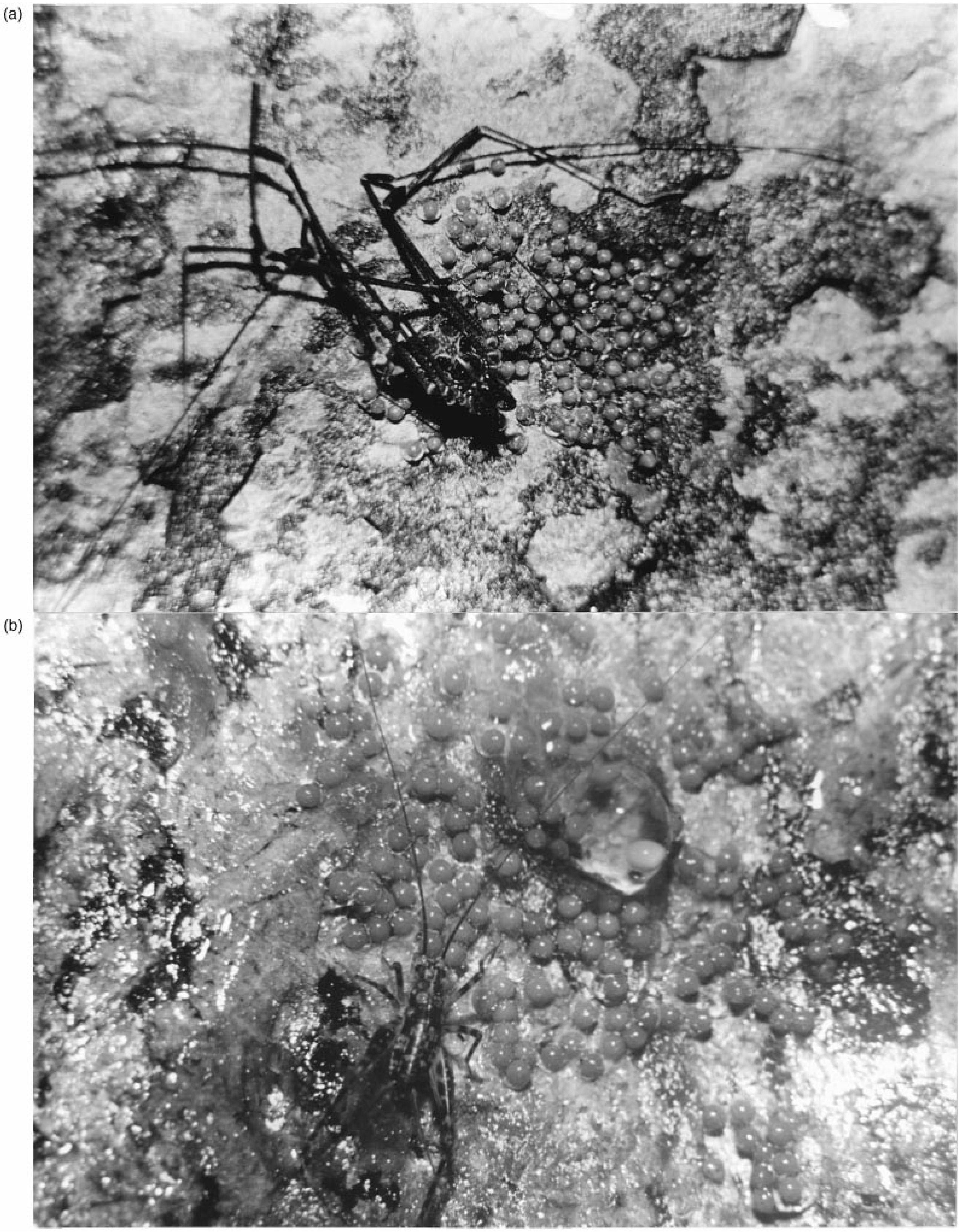

Fig. 3. (a) Female *Goniosoma longipes* (size $\approx$ 1 cm) guarding her eggs on the wall of the study cave. (b) Cave cricket *Strinatia* sp. (size $\approx$ 2 cm) feeding on unguarded eggs of *G. longipes*.

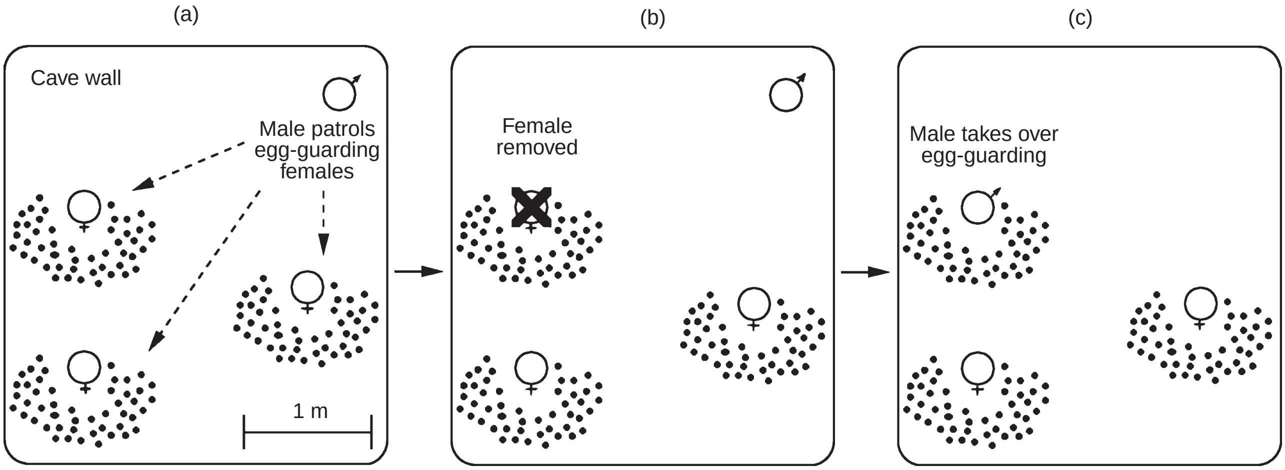

Fig. 4. Male behaviour toward females and eggs within its reproductive area on the cave wall. (a) Patrolling activity (dashed arrows) of a male *Goniosoma longipes* toward egg-guarding females. (b) Experimental removal of one female; eggs left unguarded. (c) Male sits on the egg batch for up to 2 weeks. Organisms are not drawn to scale.

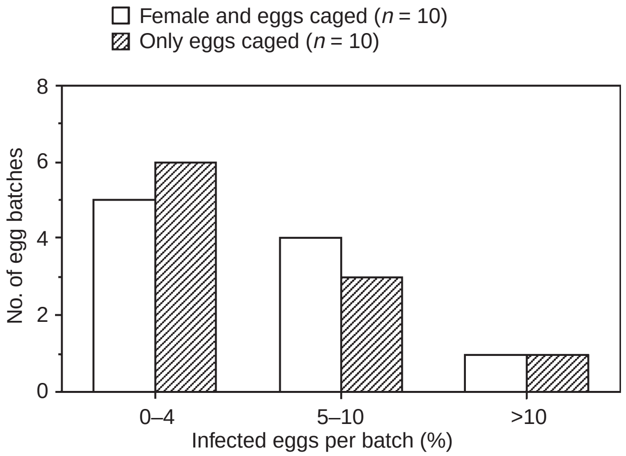

Fig. 5. Intensity of fungal attack on caged egg batches of *Goniosoma longipes* after 2 weeks. Eggs are equally attacked by fungi, irrespective of the presence of the mother (Mann–Whitney *U*-test, $U = 54$, $P = 0.757$).

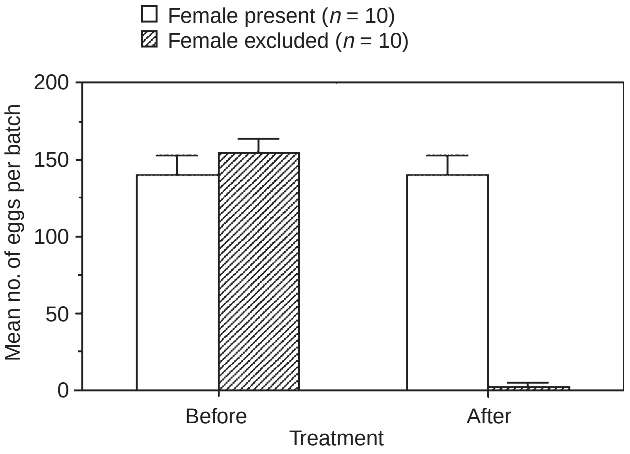

Fig. 6. Effect of maternal care on egg survival in *Goniosoma longipes* after 2 weeks. Egg survivorship is significantly higher when batches are guarded by the female (repeated measures ANOVA, $F_{1,18} = 455.27$, $P = 0.0001$).

batches), and 1st-instar nymphs remain aggregated with their mother for 7–14 days. During this period no egg or juvenile cannibalism has ever been observed within an egg batch. Maternal care towards eggs and nymphs may last 56–78 days (68.0 ± 7.8, $n = 32$ batches); the guarding female only leaves the oviposition site after all 1st-instar nymphs had dispersed.

After copulating with two to five females, a male patrol the area containing his mates and egg batches for up to 2 months (Fig. 4a). On three occasions a male took over egg-guarding activities after the removal of the female from his reproductive area (Fig. 4b, c). In these cases guarding males sit on the egg batch for up to 2 weeks, with no egg mortality being detected during this period. After male desertion, however, egg predators entirely consume the unguarded eggs (see below).

Sources of egg mortality

Four main factors may affect egg survival in *G. longipes*: dehydration, fungal attack, cannibalism, and interspecific predation. One dehydrated egg batch was found in April near the entrance of the cave, 8 m from the river. Although still guarded by the female, nearly 44% (47 of 107) of the eggs in this batch had dried out.

Frequency of fungal attack on egg batches was greater in the wet season (49.5%, $n = 46$) than in the dry season (16.6%, $n = 23$) ($\chi^2 = 22.8$, d.f. = 1, $P < 0.001$). The intensity of attack by fungi within batches ranged from 0.6% to 100% of the eggs, and did not differ between seasons (Mann–Whitney *U*-test, $U = 857.5$, $P = 0.314$). On the other hand, the intensity of fungal attack on egg batches was negatively correlated with the distance between the batch and the river crossing the cave

($r_s = -0.231$, $P < 0.025$, $n = 88$). The average distance of the oviposition site from the river did not differ between the wet and dry season (t-test, $t = 0.74$, d.f. = 86, $P = 0.46$). Although fungus-infected eggs did not develop into juveniles, guarding female *G. longipes* did not eat or remove such eggs from their batches. Fungal attack within batches was apparently the same for fertilized and unfertilized eggs.

Conspecifics may attack eggs, even when these are guarded by females. Attack on eggs by adult *G. longipes* was observed on six different occasions, and in every case the guarding female successfully repelled the intruders. A reduction in the number of eggs of nine guarded batches, however, suggests that the mother may occasionally fail to repel egg predators.

If the guarding female is experimentally removed (see below) the eggs can be cannibalized by adult and juvenile *G. longipes*. Both male and female harvestmen may eat unguarded eggs, and a single individual may consume 7–20 eggs of a batch ($n = 9$). Therefore, depending on the number of attacks by conspecific harvestmen, entire egg batches can be destroyed by cannibalism in a single night. On three occasions cave crickets (*Strinatia* sp., Phalangopsidae) were seen eating eggs from unguarded batches (Fig. 3b; see below).

Field experiments on parental care

The results of the caging experiments revealed that egg-guarding by female *G. longipes* has no effect against fungal attack on the brood after 2 weeks (Fig. 5). Similarly, guarding activity by the mother had no effect on fungal attack to uncaged egg batches (Mann–Whitney U-test, $U = 59.5$, $P > 0.30$). Although some eggs were attacked by fungi in caged batches with and without the mother, no egg disappeared from batches in either experimental group. The experiments in which the mother was removed from uncaged broods, however, revealed that guarding activity has a significant positive effect on egg survival. Less than 2% of the unguarded eggs survived the 2-week experiment (Fig. 6). During this period, adult *G. longipes* ($n = 2$) and *Strinatia* sp. ($n = 1$; Fig. 3b) were seen preying on eggs at unguarded batches.

DISCUSSION

Life-history patterns result from both evolutionary constraints and proximate responses of the organisms to specific environmental conditions (Stearns, 1992). Therefore the biological activities of animal populations, including reproduction, can be closely linked to seasonal parameters such as temperature and rainfall, the latter being particularly important in tropical regions (Opler, Frankie & Baker, 1976; Winemiller, 1989). Harvestman reproduction shows wide seasonal variation across different taxa. Among neotropical laniatorids, some species have one (Juberthie & Muos-Cuevas, 1971; Cokendolpher & Jones, 1991) or two annual reproductive peaks (Goodnight & Goodnight, 1976; Gnaspini, 1995), while others may reproduce steadily throughout the year (Juberthie, 1972; Matthiesen, 1975). Reproductive activity in *G. longipes* is correlated with rainfall, showing two distinct peaks during the wet/warm season. Water absorption during egg maturation accounts for a 43% increase in egg volume. The importance of water for egg survival in *G. longipes* is further enhanced by the females' marked preference for moist oviposition sites within the study cave (see Chapman 1982), despite the increased risk of fungal attack at these locations.

The greater number of ovipositions in the beginning of the wet season (October) may represent a synchronization of the maternal investment in offspring with ideal conditions for hatching and juvenile growth during the peak of rainfall in January, when arthropod prey are more abundant (see Wolda, 1978). The positive correlation between the number of egg batches and day length could suggest that reproductive activity in *G. longipes* is proximately adjusted by variations in the photoperiod, which is a good predictor of more favourable wet/warm conditions (Cloudsley-Thompson, 1978, and citations within). Egg-guarding in *G. longipes* may last as long as 78 days, and during this period the female does not leave her brood to forage for food. As suggested by Gnaspini (1993) for *Goniosoma spelaeum*, however, an increased foraging activity by the ovigerous female before oviposition may be related to the storage of nutrients for the prolonged egg-guarding period, during which she will not feed.

Mating in most harvestmen species is usually fast (1-2 min) and without courtship, after which the mate leaves the site and the female begins oviposition (Juberthie, 1965). In some laniatorid species such as *Zygopachylus albomarginis* (Mora, 1990), *G. spelaeum* (Gnaspini, 1995), and *G. longipes* (present study), however, the male remains close to the ovipositing female while waving his legs over the partner. Gnaspini (1995) speculated that this behaviour in *G. spelaeum* could have a protective role against predators, or function as a signal to promote egg-laying. Edgar (1971) has reported a similar behaviour for palpatorid *Leiobunum* spp. and has suggested that leg-waving and tapping by the resident male could prevent the female from walking away and failing to oviposit. Although an ovipositing female would presumably be more vulnerable to predation, we do not believe that male leg-waving *per se* would protect *Goniosoma* against predators such as marsupials and large arthropods (Pinto-da-Rocha, 1993; Pelegatti-Franco & Gnaspini, 1996). Our observations with *G. longipes* indicate that a male may remain close to his mate for over 24 h after insemination, and that during this period the female may be reinseminated once or twice by the resident male. We also found no evidence that leg-waving by the resident male would deter satellite males from inseminating the ovipositing female. In fact, our behavioural data on *G. longipes* show that the resident male does not interact with approaching males, who are rejected by the ovipositing female herself (see also Edgar, 1971). It is therefore possible that male leg-waving in *G. longipes* functions to prevent female desertion and/or stimulate oviposition, as suggested by Gnaspini (1995) and Edgar (1971). Alternatively, this behaviour in *G. longipes* could simply represent a relict trait that had evolved in different ecological circumstances, with no adaptive significance under the conditions currently faced by this species (see Wanntorp *et al.*, 1990).

The choice of appropriate oviposition sites can be crucial for offspring survival (Clutton-Brock, 1991). Among arthropod species, sites that have low moisture conditions and/or are subject to direct wind may negatively affect egg development and lead to dehydration (Chapman, 1982). Although cave habitats maintain relatively stable temperature and humidity conditions day and night (Gautier, Delaporte & Rivault, 1988), an increase of moisture levels during the wet/warm season make cave organisms considerably more vulnerable to fungal attack during this time of the year (Culver, 1982). Results with *G. longipes* in south-east Brazil support this view since a greater proportion of egg batches was infected during the wet season.

Cannibalism is a common behaviour among many invertebrate taxa (Elgar & Crespi, 1992), and among harvestmen there are some records of egg and juvenile cannibalism (Canals, 1936; Capocasale & Bruno-Trezza, 1964; Edgar, 1971; Mora, 1990). Because eggs are usually energy- and nutrient-rich palatable food items (see Orians & Janzen, 1974), they are the developmental stage particularly susceptible to interspecific predation and cannibalism especially when laid in unprotected sites and/or left unguarded by the parents (Polis, 1981; Clutton-Brock, 1991). Egg cannibalism in *G. longipes* has two main advantages for foraging harvestmen. Firstly, food can be obtained at a lower energetic cost since there is no need to leave the cave for foraging. Secondly, it is probably a safer feeding strategy since outside the cave the foraging individual would be exposed to both an increased risk of predation and less favourable climatic conditions.

Our observations indicate that cave crickets and conspecific adults are the main egg predators of *G. longipes* in the study cave. Other predators known to prey on *Goniosoma* eggs also occur in the study site, and include the predatory reduviid bug *Zelurus travassosi* and the ctenid spider *Ctenus fasciatus* (Gnaspini, 1996). Ants are also reported to consume harvestmen eggs (Mora, 1990) and *Odontomachus* ants (Ponerinae), which are commonly seen in the cave and usually have generalized feeding habits (Brown, 1976), may occasionally feed on *Goniosoma* eggs.

Parental care, and more specifically egg-guarding, is known to reduce mortality of eggs in several arthropod taxa, including the Arachnida (Turnbull, 1973; Clutton-Brock 1991; Castanho & Oliveira, 1997). Mora (1990) has shown that egg-guarding by males in the harvestman *Zygopachylus albomarginis* significantly reduces egg mortality owing to predation and attack by fungi. The current study with *G. longipes* demonstrates that maternal care is crucial for egg survival in this harvestman species. To our knowledge this is the first experimental demonstration of an anti-predator role of female egg-guarding in harvestmen. The caging experiments indicate that the mother does not consume her own eggs, and that egg-guarding prevents brood predation by conspecific harvestmen and *Strinatia* cave crickets. Although egg-guarding activity is known to prevent fungal attack on eggs in insects (Smith, 1976a,b) and harvestmen (Mora, 1990), our field experiments with *G. longipes* demonstrate that the guarding female is unable to protect her eggs against attack by fungi (see also Goodnight & Goodnight, 1976).

Maternal care has already been reported for many harvestman species from different families (see Gnaspini, 1995). Paternal care is extremely rare among arachnids, and the only documented cases come from three harvestman species (Rodriguez & Guerrero, 1976; Mora, 1990; Martens, 1993). There is no record of biparental care in harvestmen. Although Gnaspini (1995) found pairs of *G. spelaeum* near the eggs, male egg-guarding has never been reported for this species. The current study shows that male *G. longipes* actively patrol the area containing their mates and egg batches. By removing one egg-guarding female from a male's reproductive area we also showed that the male can take over egg-guarding activities (Fig. 4), and prevent brood predation for up to 2 weeks ($n = 3$ males). This finding suggests that males can exert brood care in this species if the egg-guarding females deserts or dies. Although egg-guarding by the male lasts only a few days, temporal paternal care can be crucial for brood survival (especially just before hatching), since egg predators can consume entire batches in a single night.

Damage to the brood caused by fungal infection and predation are regarded as major forces favouring the evolution of parental care (Wilson, 1975), especially in harvestmen (Goodnight & Goodnight, 1976; Mora, 1990). Although egg-guarding failed to prevent fungal attack on eggs in *G. longipes*, the field experiments showed that the guarding mother effectively increases offspring survival by deterring potential egg predators. The degree to which male assistance with egg-guarding can play a relevant role in parental care is still to be experimentally assessed for this species.

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