

Effects of maternal care on the lifetime reproductive success of females in a neotropical harvestman

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Summary

1. Few studies have experimentally quantified the costs and benefits of female egg-guarding behaviour in arthropods under field conditions. Moreover, there is also a lack of studies assessing separately the survival and fecundity costs associated with this behavioural trait.
2. Here we employ field experimental manipulations and capture–mark–recapture methods to identify and quantify the costs and benefits of egg-guarding behaviour for females of the harvestman *Acutisoma proximum* Mello-Leitão, a maternal species from south-eastern Brazil.
3. In a female removal experiment that lasted 14 days, eggs left unattended under natural conditions survived 75·6% less than guarded eggs, revealing the importance of female presence preventing egg predation.
4. By monitoring females' reproductive success for 2 years, we show that females experimentally prevented from guarding their eggs produced new clutches more frequently and had mean lifetime fecundity 18% higher than that of control guarding females.
5. Regarding survival, our capture–mark–recapture study does not show any difference between the survival rates of females prevented from caring and that of control guarding females.
6. We found that experimentally females prevented from guarding their eggs have a greater probability to produce another clutch (0·41) than females that cared for the offspring (0·34), regardless of their probability of surviving long enough to do that.
7. Our approach isolates the ecological costs of egg-guarding that would affect survival, such as increased risk of predation, and suggests that maternal egg-guarding also constrains fecundity through physiological costs of egg production.
8. Weighting costs and benefits of egg-guarding we demonstrate that the female's decision to desert would imply an average reduction of 73·3% in their lifetime fitness. Despite the verified fecundity costs of egg-guarding, this behaviour increases female fitness due to the crucial importance of female presence aimed to prevent egg predation.

Key-words: *Acutisoma*, costs of reproduction, Gonyleptidae, Opiliones, parental investment

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Introduction

In iteroparous species, parents are expected to decide how much they should invest in each brood, weighing the benefits of investing in current offspring against

the costs of investing in future reproduction (Williams 1966; Trivers 1972; Clutton-Brock 1991). Even simple forms of parental care, such as the physical protection of eggs from predators and parasites (Tallamy & Wood 1986), should include both benefits (usually enjoyed directly by the offspring) and costs (invariably paid by one or both parents). In arthropods, the benefits of egg-guarding, without the occurrence of extended maternal care, have been investigated in several lineages of

insects (e.g. Tallamy & Denno 1981; Kudo & Ishibashi 1995; Kudo 2002; Stegmann & Linsenmair 2002; Zink 2003) and spiders (e.g. Fink 1986; Gillespie 1990; Gundermann, Horel & Roland 1997), as well as in two species of harvestmen (Machado & Oliveira 1998, 2002) and one species of bromeliad-dweller crab (Diesel 1992). These studies have found that the female presence enhances the survival of the brood by reducing predation on eggs and/or early instars. On the other hand, the fitness costs paid by the female for defending her eggs are far from being that well documented in arthropods.

Maternal care is costly as females reduce their foraging time while allocating energy on parental activities not related to their own growth and maintenance, an unbalance that may negatively affect future reproduction (reviewed by Clutton-Brock 1991). To date, only few studies have managed to quantify experimentally the costs of egg-guarding in arthropods and all of them have dealt with species of the orders Araneae (Fink 1986; Gundermann *et al.* 1997) and Hemiptera (Tallamy & Denno 1982; Stegmann & Linsenmair 2002; Zink 2003). In these cases, females that were prevented from guarding their eggs had an increase in subsequent fecundity. Nevertheless, two of these studies were conducted under laboratory conditions (Tallamy & Denno 1982; Gundermann *et al.* 1997) while a third used caged individuals (Fink 1986). As far as we know, the studies by Stegmann & Linsenmair (2002) and Zink (2003) are the only experimental quantifications of the costs of egg-guarding in arthropods conducted in the field, where predation pressure and environmental harshness may influence the performance of guarding females in a more realistic way.

Despite a number of methodological differences, all studies mentioned above have demonstrated that egg-guarding behaviour compromises future reproduction. If egg-guarding behaviour is costly for females, one might predict that this behaviour diminishes parental survival as well. Paradoxically, the only study aimed to evaluate the effects of egg-guarding on survival in arthropods found exactly the opposite, i.e. as investment in maternal behaviour increased, so did female life span (Tallamy & Denno 1982). The authors argued that females whose maternal care was prevented experimentally, spent all their reproductive life in egg production and thus were subjected to physiological hardships more often than females that replaced egg production with some period of maternal care. Contrasting this suggestion with the widely accepted theory of parental investment (Trivers 1972) leads to two entirely opposite predictions: (1) maternal egg-guarding is costly and therefore diminishes female survival, and (2) maternal egg-guarding prevents females from the costly overproduction of eggs and therefore increases female survival. Therefore, the remaining question is: Does egg-guarding increase or decrease parental survival?

Opiliones, commonly known as harvestmen, are suitable organisms for addressing questions about the costs and benefits of maternal care as this behavioural

trait is widespread in the order and has evolved at least six times independently (reviewed in Machado & Macías-Ordóñez 2007). Field experiments have demonstrated that maternal care is crucial for preventing egg predation: entire clutches may be consumed by predators, including ants, crickets and conspecifics, in a few hours when left unprotected (Machado & Oliveira 1998, 2002). In one of these species, *A. longipes*, eggs are also attacked by fungi, especially during the wet and warm season, when nearly 50% of the clutches may be infected. Although fungus-infected eggs do not develop, guarding females do not eat or remove such eggs. Furthermore, field experiments with this species have shown that females are unable to protect their eggs against fungal attack (Machado & Oliveira 1998).

The main goal of this paper is both to identify and quantify the costs and benefits of egg-guarding for female *Acutisoma proximum* Mello-Leitão (Gonyleptidae: Gonyosomatinae), a neotropical harvestman that exhibits maternal care (Ramires & Giaretta 1994). We estimated the fitness of female egg-guarding by comparing its lifetime reproductive success with that of a simulated alternative strategy, the desertion by the mother. The methods used here have been already used to study the adaptiveness of maternal care in the lace bug *Gargaphia solani* (Tallamy & Denno 1982) and in the lynx spider *Peucetia viridans* (Fink 1986). However, and unlike these studies, the present study is the first one to use this experimental approach in the field. Finally, the study also addresses the question on the effects of egg-guarding behaviour on female life span. We expect female care in *A. proximum* to have a positive and crucial effect on egg survival, but a detrimental effect on female fecundity and life span as parental individuals are prevented to forage and are more exposed to predators, parasites and climatic harshness.

Materials and methods

STUDY SITE

The study was conducted in a dense ombrophyle Atlantic Forest fragment at the Intervalles State Park, southern São Paulo state, south-eastern Brazil. The annual rainfall in the region ranges from 2000 to 3000 mm and the mean annual temperature ranges from 12 °C to 20 °C. There is a well marked seasonality, with a wet and warm period lasting from October to March and a dry and cold period from April to September, when frosts are common. Both experiments and naturalistic observations were done on the vegetation flanking the river that follows the Caçadinha track (24°14'S; 48°04'W; 800 m a.s.l.). The river is approximately 5 m wide at the location and is flanked by abundant vegetation that sometimes partially covers the river's bed. Two transects spaced by 50 m were established alongside this river: one with 200 m length (named T1) and another with 500 m length (named T2).

REPRODUCTIVE BIOLOGY OF *A. PROXIMUM*

The reproduction of *Acutisoma proximum* has been briefly studied by Ramires & Giaretta (1994) in Paranaipacaba, São Paulo state, south-eastern Brazil. The authors found that *A. proximum* females lay their eggs among gaps in granitic stones on river margins and remain guarding eggs and first instar nymphs. During the guarding period, females were always seen on the clutches, frequently monitoring their eggs using the first and second pairs of legs and pedipalps. The authors suggested that the maternal egg-guarding behaviour in *A. proximum* may protect the clutches from infection attacks by pathogenic microorganisms or parasites and also reduce egg and young predation.

Previous unpublished data indicates that females from Intervales population lay their eggs primarily on the underside of leaves (81.4% of clutches found on leaves against 16.6% found on rocky surfaces, $n = 350$), using mainly the vegetation hanging above the river (Fig. 1a). Following oviposition, females guard their eggs until they hatch nearly 30 days later, remaining with nymphs until these disperse, usually 7 days after hatching. Contrary to other goniosomatine species previously studied (review in Machado 2002), a female

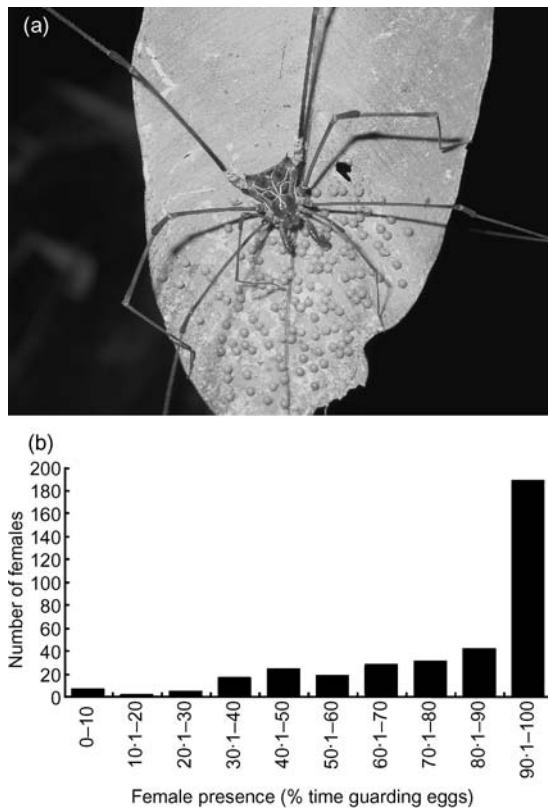


Fig. 1. (a) Female *Acutisoma proximum* guarding her recently laid eggs on the underside of a leaf. (b) The majority of the 363 guarding females monitored in the field spent more than 90% of their time with their clutches. However, the frequency of female presence on their clutches showed great variation, and some females did not spend more than 10% of their time guarding the offspring.

A. proximum does not stay close to the offspring all the time (see Fig. 1b). Guarding females stay on average 73.3% (range 9–100%) of the time above their eggs or young (Fig. 1b) and the frequency of female attendance is marginally correlated with monthly temperature taken *in loco* ($r_s = 0.461$; $n = 17$; $P = 0.062$). This relationship probably occurs because harvestmen are very sensitive to low temperatures (Santos 2007), and during the coldest hours of the day some guarding females are commonly found sheltered among the moss that grows on tree trunks close (from 0.1 to 1.0 m) to their clutches.

The Intervales population shows a marked seasonal reproduction, with females concentrating their egg-laying activities exclusively from September to April. Although there are no data on the life span of *A. proximum*, adults possibly live at least 2 years, as recorded for other goniosomatine species (Gnaspini 1995). With this relatively long life span, females are capable of surviving as adults for up to three reproductive seasons, then potentially producing multiple clutches during their lifetime (see Results).

BENEFITS OF EGG-GUARDING

To quantify the effectiveness of female egg-guarding against egg predators and parasites, a field experiment was conducted using 40 guarding females found on T2 during February 2004. Whenever a clutch with eggs in an early stage of embryonic development was found, the number of eggs was counted and the guarding female was randomly allocated to one of two experimental groups. In the treatment group, females were removed from their clutches and maintained alive in captivity, while their eggs were left unattended in the field for 14 days (cf. Machado & Oliveira 1998, 2002). At the end of the experiment, the experimental females were set free on the exact locations previously occupied by their clutches. In the control group, females were individually marked with enamel paint (Gnaspini 1996; Machado & Oliveira 1998) and then released again on their original clutches. During this period, all clutches were inspected four times a day (01.00, 07.00, 13.00 and 19.00 h) as an attempt to identify egg predators. Whenever predators were encountered consuming eggs, the event was observed along with a continuous record of the predator's behaviour. Pictures of predators were also taken for later identification, to avoid disturbing the predator. The number of eggs on each clutch was counted on days 0, 4, 8 and 14, and the number of eggs was compared between experimental groups through a Friedman's ANOVA.

COSTS OF EGG-GUARDING

To quantify the costs of female egg-guarding behaviour, an almost 2-year capture–mark–recapture study was conducted on T1. A set of 144 females found guarding recently laid eggs on the first reproductive season of our study, between September 2003 and April 2004, were used. All of these females were measured for the

dorsal scute length and width and individually marked with enamel paint. This marking procedure has been previously used in other studies with harvestmen and has the advantages of not affecting egg-laying or egg-guarding behaviour (Machado & Oliveira 1998), and the paint remains for over 2 years (Gnaspini 1996). After marking, females were then randomly allocated to one of two experimental groups. In the first experimental group ('no care'), the clutches were removed and the guarding females were released on the location previously occupied by the eggs. This procedure was done 5 days after each experimental female was found in order to ensure that they had already completed their oviposition by the time of our manipulation (in *A. proximum* all eggs are laid within 3 days, B.A. Buzatto unpub. data). In the second group ('care'), females were released on their intact clutches. In both groups, the number of eggs per clutch was counted before the experimental manipulation.

The reproductive activity of experimental females of both groups was followed for 2 years (comprising the reproductive seasons of 2003–04 and 2004–05) in which T1 was inspected three times a day (from 08.30 to 12.00 h, from 14.00 to 17.30 h and from 20.30 to 00.00 h) during four consecutive days per month. Whenever a female from the 'no care' group was found guarding a new clutch, the eggs were removed in the same way described before. Females that were never found guarding new clutches on T1 were considered incapable of reproducing again (following Stegmann & Linsenmair 2002). This procedure underestimates the number of females reproducing more than once and gives us a conservative estimation of iteroparity in the species. It is important to notice, however, that this bias occurs in both experimental groups.

MODELLING SURVIVAL AND RECAPTURE RATES

To assess whether the egg-guarding behaviour influences the survival of females, the survival (ϕ) and recapture (p) rates were modelled using a statistical modelling approach (Lebreton *et al.* 1992), applying program MARK (White & Burnham 1999). The capture–recapture history data used in this analysis were obtained from 55 females assigned to the 'care' group and 55 assigned to the 'no care' group between January and March 2004 and followed monthly from September 2004 to May 2005. To test the effect of the experimental group on the survival and recapture rates of females, the following models were fitted to the capture–recapture history data (notation within parentheses): (1) with no effects (.); (2) with experimental group effects (group); (3) with temperature effects (temperature); and (4) with temperature and experimental group effects (temperature + group). Therefore, the set of candidate models formulated included a total of 16 models.

We assessed the fit of the global model, which is the fully parameterized model $\{\phi_{(\text{temperature+group})}$,

$p_{(\text{temperature+group})}\}$, to the data using the median \hat{c} approach implemented in program MARK (White & Burnham 1999). This approach is based on the assumption that the best estimate of the overdispersion parameter of the global model, \hat{c} , is the value for which the observed deviance \hat{c} (i.e. the model deviance divided by the model degrees of freedom) falls at the median of the distribution of all possible deviance \hat{c} simulated under the hypothesis that a given value of c is the true value. Data are simulated and replicated for a range of c -values and a deviance \hat{c} is estimated for each of the simulated data sets. A logistic regression between the c -values and the simulated deviance \hat{c} values is then performed to estimate the value of c for which the observed deviance \hat{c} falls at the median of the distribution of all simulated deviance \hat{c} . The global model is considered to fit the data if the estimated value of c is between 1 and 3 (Lebreton *et al.* 1992). We simulated data for 10 evenly spaced values of c ranging from 1 to 3, with 100 replications for each value.

To select the most parsimonious model to describe the survival and recapture rates of the experimental groups, we used the bias-corrected version of the Akaike Information Criterion, AIC_c (Burnham & Anderson 1998), which is computed as

$$AIC_c = -2(\ln L) + 2k \left(\frac{n}{n-k-1} \right), \quad \text{eqn 1}$$

where $\ln L$ is the natural logarithm of the likelihood function evaluated at the maximum likelihood estimate for a given model, k is the number of parameters and n is the sample size (Burnham & Anderson 1998; Johnson & Omland 2004). The model with the lowest AIC_c value was selected as the most parsimonious model to describe the survival and recapture rates of female *A. proximum*.

Results

BENEFITS OF EGG-GUARDING

There was a reduction in egg number in the clutches that were left unattended experimentally (Fig. 2a), with 12 of the initial 20 clutches in this experimental group disappearing entirely during the 14-day experiment. In the control group, however, there was no significant reduction in the number of eggs in the clutches and only one of them was attacked and suffered high predation (96.1%). In this only case, the female was missing since the second day of the experiment, suggesting that she naturally deserted or was preyed on. The difference in survival of eggs between experimental groups already first detected 4 days after female removal with such difference increasing over time (Fig. 2b).

During the experiment, we recorded 45 predation events, all of them on unprotected clutches. The main source of egg mortality was cannibalism, both by conspecific males ($n = 12$ clutches) and females ($n = 4$). On

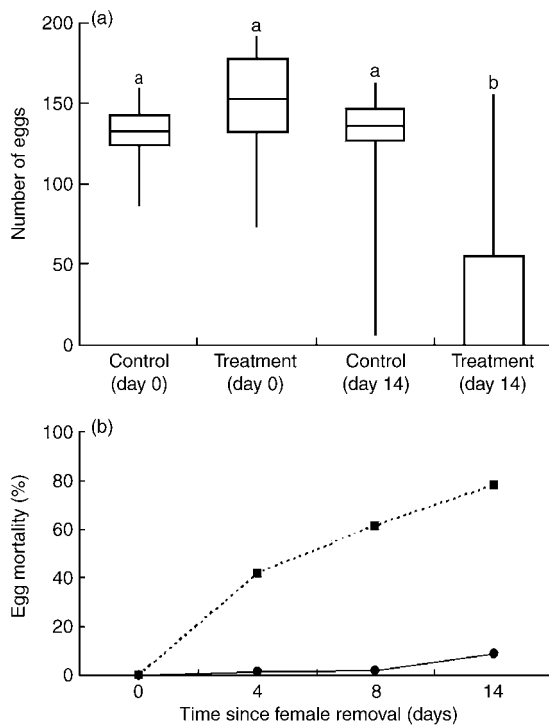


Fig. 2. Predation on *Acutisoma proximum* eggs during the experiment concerning the benefits of egg-guarding. (A) There was no difference in the initial number of eggs between experimental groups, or between the initial and final number of eggs in the control group. However, there was a significant difference between the initial and final number of eggs in the treatment group and in the final number of eggs between groups (Friedman ANOVA = 28.36, d.f. = 3, $P < 0.001$). The horizontal lines represent the median, the boxes represent the upper and lower quartiles, and the vertical lines represent the range (minimum and maximum values in each sample). Different letters above the box-plots indicate significant difference with $P < 0.05$. (B) Mean percentage of consumed eggs on both experimental groups along the experiment. Treatment group = dashed line; control group = solid line.

one occasion we observed a guarding female next to her clutch repelling a conspecific female through an attack using pedipalps and chelicerae. Other sources of mortality for *A. proximum* eggs were: other harvestman species, such as the gonyleptids *Discocyrtus* sp. ($n = 1$), *Iporangaia pustulosa* Mello-Leitão ($n = 4$) and *Promitobates ornatus* (Mello-Leitão) ($n = 9$); the anyphaenid spider *Osoriella rubella* Keyserling ($n = 7$, Fig. 3a); an unidentified jumping spider ($n = 2$); the scolopendrid centipede *Otostigmus* sp. ($n = 1$); a katydid nymph and the vespid wasp *Agelaisia multipicta* (Haliday) ($n = 4$, Fig. 3b).

FECUNDITY COSTS OF EGG-GUARDING

Between September 2003 and April 2005, we found a total of 144 females guarding eggs on T1 and half of them were assigned to the 'care' group ($n = 72$), whereas the other half were assigned to the 'no care' group ($n = 72$). From January 2004 to April 2005, we found 35 females

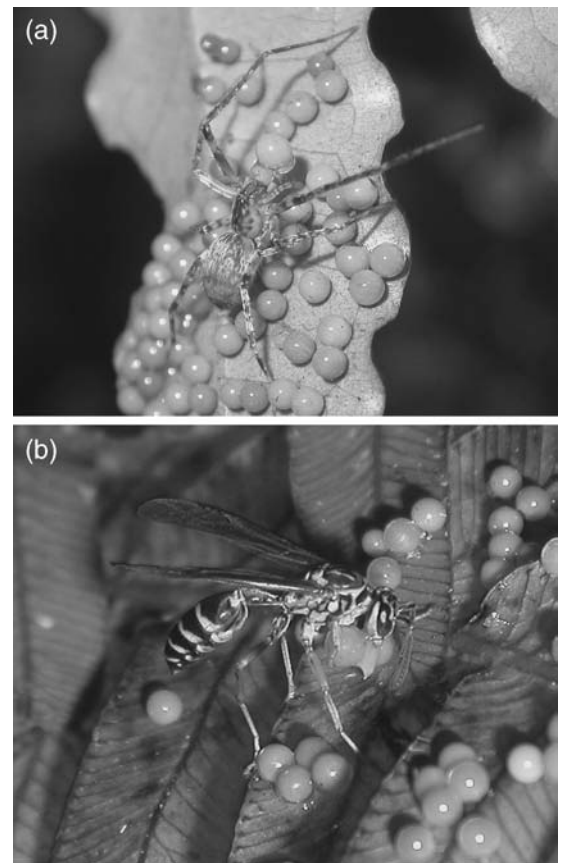


Fig. 3. Two of the major predators of *Acutisoma proximum* eggs. (a) The spider *Osoriella rubella* (Anyphaenidae), and (b) the wasp *Agelaisia multipicta* (Vespidae).

reproducing for a second time, 13 of them belonging to the 'care' group and 22 to the 'no care' group. Six females from the 'no care' group produced a third clutch after the experimental removal of their second one and, remarkably, 3 months after the experimental removal of the third clutch, one female was capable of producing a fourth batch containing 62 eggs (Table 1). This frequency of egg production was significantly different between experimental groups (G -test = 10.67; d.f. = 3; $P = 0.014$). There was no difference in the body size measures of females that produced a single clutch and females that reproduced more than once (Table 2). Additionally, the time between two consecutive reproductive events in the 'no care' group was shorter than in the 'care' group (Mann-Whitney test, $U = 118.50$; $P = 0.057$; Table 1). Finally, females of the 'no care' group laid more eggs than did females of the 'care' group over the study period ($t = 2.26$; d.f. = 142; $P = 0.013$; Table 1).

SURVIVAL COSTS OF EGG-GUARDING

The global model, $\{\phi_{(\text{temperature}+\text{group})} P_{(\text{temperature}+\text{group})}\}$, fitted well to the data as the overdispersion parameter was close to 1 ($\hat{c} = 1.13 \pm 0.02$ SE), as estimated by the median \hat{c} approach. The most parsimonious model among those in the set of candidate models did not

Table 1. Quantitative features associated with female fecundity obtained in the field experiment on costs of egg-guarding in *Acutisoma proximum*. For categories related to ‘number of eggs’, the mean ± SD is shown; for the category related to the interval between clutches, the median is shown with the range in parentheses

Reproductive parameters	‘Care’ group (n = 72)	‘No care’ group (n = 72)
Females that produced two clutches	13	22
Females that produced three clutches	0	6
Females that produced four clutches	0	1
Eggs in the first clutch	124.53 ± 28.9 (n = 72)	127.08 ± 30.0 (n = 72)
Eggs in the second clutch	107.00 ± 35.4 (n = 13)	110.05 ± 32.8 (n = 22)
Eggs in the third clutch	–	106.50 ± 31.5 (n = 6)
Eggs in the fourth clutch	–	62 (n = 1)
Lifetime fecundity (number of eggs laid)	143.85 ± 51.9 (n = 72)	170.44 ± 85.4 (n = 72)
Time between first and second clutch (months)	4 (2–13, n = 13)	2 (1–11, n = 22)
Time between second and third clutch (months)	–	2.5 (1–10, n = 6)
Time between third and fourth clutch (months)	–	3 (n = 1)

Table 2. Comparison of two body size features of *Acutisoma proximum* females that produced one or more clutches in the ‘care’ group (females that guarded eggs) and in the ‘no care’ group (females experimentally prevented from egg-guarding)

Size features	Females that produced a single clutch	Females that produced more than one clutch	Statistics
‘Care’ group			
Dorsal scute length	7.58 ± 0.23 (n = 59)	7.54 ± 0.33 (n = 13)	<i>t</i> = 0.451; <i>P</i> = 0.330
Dorsal scute width	8.30 ± 0.36 (n = 59)	8.25 ± 0.39 (n = 13)	<i>U</i> = 311.0; <i>P</i> = 0.289
‘No care’ group			
Dorsal scute length	7.55 ± 0.25 (n = 50)	7.57 ± 0.34 (n = 22)	<i>U</i> = 491.0; <i>P</i> = 0.471
Dorsal scute width	8.36 ± 0.39 (n = 50)	8.24 ± 0.39 (n = 22)	<i>t</i> = 0.945; <i>P</i> = 0.175

include the effect of the experimental group and temperature on the survival rate of female *A. proximum* (Table 3). As for recapture rates, the most parsimonious model included only the effect of temperature (Table 3). The monthly survival rate estimate obtained by the best model, $\{\phi_{(.)} P_{(temperature)}\}$, was 0.857 ± 0.022 for

females in both experimental groups. Although we cannot determine directly from this analysis whether the estimated survival rate was biased by emigration out of the sampled area, we have quantitative evidence that this source of bias in our estimates may affect both experimental groups in a similar way. The frequency of females that were captured only once was similar between the ‘care’ (70.8%) and ‘no care’ (65.3%) group (chi-square test, $\chi^2 = 0.511$; *P* = 0.475). Additionally, the total displacement of females captured more than once in each experimental group did not differ significantly (mean ± SD, ‘care’ = 9.0 ± 11.3 m; ‘no care’ = 10.9 ± 16.9 m; *t* = 0.08; d.f. = 44; *P* = 0.939).

Table 3. Summary of the model selection statistics for models describing survival and recapture rates of *Acutisoma proximum* females. Models are ranked by increasing order of their AIC_c values, which is the bias-corrected modified Akaike Information Criterion. ΔAIC_c is the difference between the AIC_c value of model *i* and the AIC_c value of the most parsimonious model, *w_i* is the Akaike weight of model *i*, *K* is the number of estimable parameters in the model and Dev is the deviance. The best model is indicated in bold

Model	AIC _c	ΔAIC _c	<i>w_i</i>	<i>K</i>	Dev
$\{\phi_{(.)} P_{(temperature)}\}$	271.09	0.00	0.28	3	73.82
$\{\phi_{(.)} P_{(temperature+group)}\}$	272.73	1.64	0.12	4	73.34
$\{\phi_{(group)} P_{(temperature)}\}$	272.88	1.79	0.12	4	73.49
$\{\phi_{(temperature)} P_{(temperature)}\}$	273.36	2.27	0.09	4	73.98
$\{\phi_{(.)} P_{(.)}\}$	273.58	2.49	0.08	2	78.40
$\{\phi_{(temperature)} P_{(temperature+group)}\}$	274.42	3.33	0.05	5	72.89
$\{\phi_{(group)} P_{(temperature+group)}\}$	274.84	3.75	0.04	5	73.31
$\{\phi_{(.)} P_{(group)}\}$	275.10	4.01	0.04	3	77.84
$\{\phi_{(group)} P_{(.)}\}$	275.34	4.25	0.03	3	78.07
$\{\phi_{(temperature)} P_{(.)}\}$	275.36	4.27	0.03	3	78.10
$\{\phi_{(temperature+group)} P_{(temperature)}\}$	275.37	4.28	0.03	5	73.84
$\{\phi_{(temperature)} P_{(group)}\}$	276.41	5.32	0.02	4	77.03
$\{\phi_{(temperature+group)} P_{(temperature+group)}\}$	276.51	5.42	0.02	6	72.80
$\{\phi_{(group)} P_{(group)}\}$	277.21	6.12	0.01	4	77.82
$\{\phi_{(temperature+group)} P_{(.)}\}$	277.35	6.25	0.01	4	77.96
$\{\phi_{(temperature+group)} P_{(group)}\}$	278.47	7.38	0.01	5	76.94

Discussion

BENEFITS OF EGG-GUARDING

Maternal care is widespread among terrestrial arthropods and the benefits of this behaviour may include feeding facilitation or food provisioning as well as protection of the offspring against biotic (such as predators, pathogens and parasites) and abiotic (such as temperature, dehydration and flooding) factors (references in Clutton-Brock 1991). Among harvestmen, there is no evidence that females can benefit their offspring by enhancing the feeding efficiency of the nymphs, or that parents are able to actively protect offspring against environmental stress, such as dehydration (Machado & Oliveira 1998).

Nevertheless, field experiments with two neotropical species, the cavernicolous *Acutisoma longipes* and the bromelicolous *Bourguyia albiornata*, have demonstrated that maternal care is crucial for preventing egg predation (Machado & Oliveira 1998, 2002). In our female removal experiment, the majority of clutches left unattended were entirely consumed by predators within a few days, demonstrating the importance of female presence preventing egg predation in *A. proximum*.

The main detected sources of egg mortality were conspecifics (especially males) and other harvestman species, which together totalled almost 65% of observed predation events. Contrary to what was found for the neotropical harvestman *B. albiornata* (Machado & Oliveira 2002), another maternal species that also reproduces on vegetation, ants were not the most important egg predators. Furthermore, our results indicated several novel egg predators, such as centipedes, wasps and katydids. The latter two were capable of causing great egg mortality on short periods of time (sometimes less than 30 min). Predatory wasps, for instance, attacked the same clutch repeatedly, always leaving with groups of two to three eggs (Fig. 3b). These predators kept returning until all eggs of the clutch were taken, probably to provision of the wasps nests. It is also worth mentioning that predation events took place both during day and night, suggesting that unattended clutches are constantly under high predation risk.

Given that predation on unattended eggs seems high, the benefit of guarding is certainly enormous in *A. proximum*. However, to estimate the net benefit of this behaviour it is also crucial to calculate the cost of guarding. Additionally, both the costs and the benefits must be measured in terms of lifetime reproductive success, rather than the success of a single brood. In the following sections we discuss the costs of egg-guarding behaviour in the studied species and then we integrate costs and benefits in order to quantify the lifetime output of two hypothetical alternatives: female care and female desertion.

COSTS OF EGG-GUARDING

The reproductive costs associated with maternal care can be classified into two major categories: (1) ecological costs, which are related to an increased exposure to predation while searching for oviposition sites, laying or guarding the offspring, and (2) physiological costs, related to the allocation of resources to egg production and other parental activities rather than to individual growth or somatic maintenance (Clutton-Brock 1991). In relation to ecological costs, our results show that female survival in *A. proximum* was not influenced by egg-guarding behaviour, given that the most parsimonious model describing female survival did not include the effect of the experimental group ('care' vs. 'no care') on the survival rate of females (Table 3). Our study is the first to assess the effects of egg-guarding behaviour on the survival of a female arthropod by modelling

survival and recapture rates of marked individuals monitored in the field. Our findings contrast with those obtained by Tallamy & Denno (1982) for the hemipteran *Gargaphia solani*, in which females that guarded their brood produced fewer clutches, but survived longer than females that had been experimentally prevented from guarding eggs. However, Tallamy and Denno's study was conducted with captive individuals, which may have not faced ecological hazards and predation risk. Our study was conducted in the field and the ecological costs of maternal care in *A. proximum*, if any, may be regarded as minimal. There are at least two nonexcluding reasons for that: (1) all known predators of Goniosomatinae harvestmen, including opossums, wandering spiders, and toads (Cokendolpher & Mitov 2007), are active at night, when females of both experimental groups are found exposed on the vegetation, and (2) females of the 'care' group temporarily abandon their clutches during the coldest hours of the day and shelter in places where they get protection from climatic harshness (see section 'Reproductive biology of *A. proximum*'), which possibly attenuate their physiological stress.

Concerning the physiological costs of reproduction in *A. proximum*, females are known to invest a considerable amount of energy to produce large and nutritionally rich eggs, which may reach 2.0 mm in diameter each (Ramires & Giaretta 1994). In other Goniosomatinae species, the total volume of a single clutch may correspond to 50% of the female body volume (Machado & Macías-Ordóñez 2007). After oviposition, maternal care reduces foraging activities and probably decreases the intake of energy to produce additional eggs in *A. proximum* females, a critical issue in iteroparous species (Tallamy & Brown 1999). In fact, our experimental manipulations in the field indicate that egg-guarding behaviour reduces the probability of females to oviposit again. When considering exclusively the probability of producing new clutches, females of the 'no care' group were much more likely to do so than were females of the 'care' group (40.3% vs. 18.1%, respectively; $\chi^2 = 15.02$; $P < 0.001$). Additionally, the mean fecundity of the females in the 'no care' group during the study was nearly 18% higher than that of females of the 'care' group. These results provide additional support to a pattern previously described for hemipterans (Tallamy & Denno 1982; Zink 2003) and spiders (Fink 1986; Gundermann *et al.* 1997) in which future reproduction is negatively affected by present reproductive investment.

Females of the great majority of maternal harvestmen seem limited to a single oviposition event per breeding season or even during their entire lives (Machado & Macías-Ordóñez 2007). This is also the case of *A. proximum*, in which nearly 82% of the females that were allowed to care for the offspring produced only one clutch during 2 years. If environmental constraints, such as food and/or nest site shortage, reduce the success of subsequent ovipositions during a breeding season, the fecundity-related costs of maternal care are

Table 4. Variables used to estimate the fitness (W) of guarding and deserting females of *Acutisoma proximum*. Unless otherwise stated, the values are presented as means. See text for equations and explanation on the meaning of each variable

Term	Explanation	'Care' group	'No care' group
S	Egg survival (assayed for 14 days)	0.911	0.222
N_k	Number of eggs in the clutch k	124.5 ($k = 1$)	127.1 ($k = 1$)
		107.0 ($k = 2$)	110.0 ($k = 2$)
		–	106.5 ($k = 3$)
		–	62 ($k = 4$)
P_k	Probability of having the reproductive event number k	0.181 ($k = 2$)	0.306 ($k = 2$)
		0 ($k = 3$)	0.273 ($k = 3$)
		0 ($k = 4$)	0.167 ($k = 4$)
		–	–
ϕ	Monthly survival probability	0.857	0.857
t	Median number of months elapsed between two reproductive events	4 months	2 months
d_k	Probability of producing the k -th clutch	0.336 ($k = 2$)	0.417 ($k = 2$)
		–	0.372 ($k = 3$)
		–	0.227 ($k = 4$)
W	Lifetime fitness	125.12	33.46

minimized, regardless of whether the female lives to produce another clutch in the following breeding season (Tallamy & Brown 1999). Females constrained to produce only one clutch in a given breeding season could increase their lifetime reproductive success by guarding the eggs that they have already laid, especially in environments with high egg and juvenile predation, as seems to be the case in *A. proximum*.

COMBINING COSTS AND BENEFITS

Once the costs and benefits of egg-guarding were identified and quantified, we used a simple equation that quantifies the lifetime fitness (W) of female *A. proximum*. This W refers to the lifetime number of eggs produced that survive at least two-thirds of the embryonic development, and not overall reproductive success as we do not have information about nymph mortality. In this way, W is calculated as follows:

$$W = S \left(N_1 + \sum_{k=2}^n N_k P_k \right), \quad \text{eqn 2}$$

where S is the mean survival of eggs for the first 14 days after oviposition (empirically estimated in the field experiment described in the section 'Benefits of egg-guarding'), N_k is the mean number of eggs per batch produced in reproductive event k , and P_k is the probability of having the reproductive event k (P_k was empirically estimated in the field experiment described in the section 'Costs of egg-guarding', based on the assumption that the probability of capturing a guarding female is 1). P_k is comprised of two probability terms:

$$P_k = \phi^t \times d_k \quad \text{eqn 3}$$

where ϕ is the monthly survival rate obtained from the best model, exponent t is the median number of months

elapsed between two reproductive events (see values in Table 4), and d_k is the probability of producing the k -th clutch given that the female survived from reproductive event $k - 1$ to k . We can rearrange eqn 3 to compute d_k as

$$d_k = \frac{P_k}{\phi^t}. \quad \text{eqn 4}$$

Solving eqn 4 for values of P_k and ϕ^t (see values in Table 4), we find that females that choose to desert clutches have a slightly greater probability of producing a second clutch (0.417) than do females that choose to care for the offspring (0.372). Moreover, the probability of producing additional clutches in females of the 'no care' group decreases over time (Table 4). The parameter d_k has never been estimated in any previous field study that we are aware of, which makes our work the first attempt to investigate the effect of maternal care on the physiological ability of producing new clutches. Our approach disentangles the ecological costs of egg-guarding that would affect survival, and suggests that maternal egg-guarding also constrains fecundity through physiological costs of spending the whole guarding period (until 37 days) without actively foraging. The low food intake during this period probably prevents females from producing eggs in the next months.

To assess the net benefit of egg-guarding behaviour, we used eqn 1 to contrast the mean fitness of guarding females with that of females that were experimentally prevented from guarding. This approach was modified from Fink (1986), with the considerable advantage that in the present study we were able to quantify female fecundity and estimate their life span under more natural conditions, without caging females. Solving eqn 1 for the values of S , N_k and P_k estimated for both experimental groups ('care' and 'no care', see values in Table 4) we demonstrate that the hypothetical female decision to desert causes a reduction of 73.3% in lifetime fitness (33.46 surviving eggs produced by females of the 'no care' group against 125.12 surviving eggs produced by females of the 'care' group).

Although guarding behaviour diminishes the females' future fecundity, the great improvement in egg survival more than compensates the costs of care in *A. proximum*. Among arthropods with the capacity to enhance the survival of their young, maternal care will only evolve when the benefits of such behaviour exceed the costs (Clutton-Brock 1991). This can occur either when the benefits of care are extraordinarily large in relation to moderate costs, or when the costs are exceptionally low in relation to moderate benefits. The first option seems to be the case not only for *A. proximum* but also for all the other maternal arthropods studied so far.

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