

# Costs and benefits of temporary brood desertion in a Neotropical harvestman (Arachnida: Opiliones)

Marie Claire Chelini · Glauco Machado

Received: 7 May 2012 / Revised: 10 September 2012 / Accepted: 12 September 2012 / Published online: 25 September 2012  
© Springer-Verlag Berlin Heidelberg 2012

**Abstract** Brood desertion is a life history strategy that allows parents to minimize costs related to parental care and increase their future fecundity. The harvestman *Neosadocus maximus* is an interesting model organism to study costs and benefits of temporary brood desertion because females abandon their clutches periodically and keep adding eggs to their clutches for some weeks. In this study, we tested if temporary brood desertion (a) imposes a cost to caring females by increasing the risk of egg predation and (b) offers a benefit to caring females by increasing fecundity as a result of increased foraging opportunities. With intensive field observations followed by a model selection approach, we showed that the proportion of consumed eggs was very low during the day and it was not influenced by the frequency of brood desertion. The proportion of consumed eggs was higher at night and it was negatively related to the frequency of brood desertion. However, frequent brood desertion did not result in higher fecundity, measured both as the number of eggs added to the current clutch and the

probability of laying a second clutch over the course of the reproductive season. Considering that harvestmen are sensitive to dehydration, brood desertion during the day may attenuate the physiological stress of remaining exposed on the vegetation. Moreover, since brood desertion is higher during the day, when egg predation pressure is lower, caring females could be adjusting their maternal effort to the temporal variation in predation risk, which is regarded as the main cost of brood desertion in ectotherms.

**Keywords** Brood size · Brood success · Egg protection · Fecundity · Maternal care · Parental effort

## Introduction

Parents are expected to maximize their fitness by adjusting their investment in parental care in relation to two main components: the benefits provided by increased survival of the current brood and the costs paid in terms of reduction of subsequent reproductive success (Trivers 1972; Gross 2005). Given that any investment in the current brood may reduce future reproduction of the parents, most theoretical models on the evolution of parental care assume a trade-off between these two components (e.g., Trivers 1972; Winkler 1987; Kokko and Jennions 2008). Experimental evidence for numerous taxa exhibiting post-zygotic maternal care has indeed shown that while offspring clearly benefit from female assistance, parental care in the form of egg guarding and offspring provisioning may compromise females' lifetime fecundity (e.g., Balshine-Earn 1995; Zink 2003; Agrawal et al. 2005; Hanssen et al. 2005; Buzatto et al. 2007, reviewed in Stiver and Alonzo 2009; Gilbert and Manica 2010).

Females of several species exhibit strategies that keep their eggs protected against predation without the fecundity

---

Communicated by N. Wedell

M. C. Chelini  
Programa de Pós-graduação em Ecologia, Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, Brazil

G. Machado (✉)  
Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo,  
Rua do Matão, trav. 14, no 321, Cidade Universitária,  
05508-900, São Paulo, SP, Brazil  
e-mail: glaucom@ib.usp.br

*Present Address:*  
M. C. Chelini  
Department of Ecology, Evolution and Behavior, University of Nebraska–Lincoln,  
348 Manter Hall,  
Lincoln, NE 68588-0118, USA

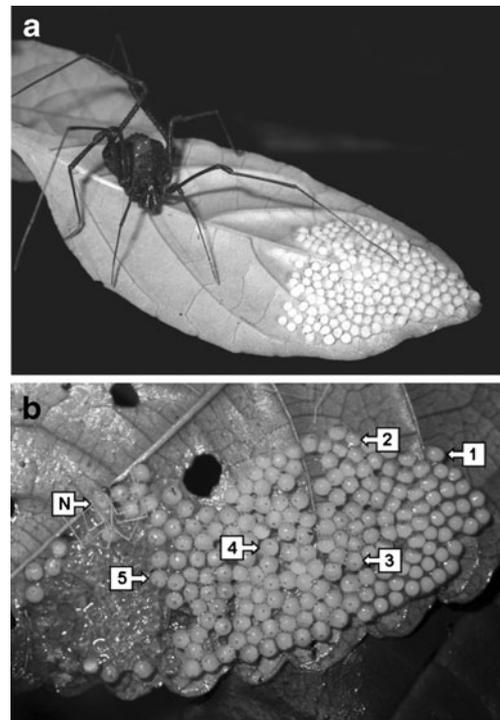
costs related to post-zygotic parental care (Tallamy and Schaefer 1997). These strategies include, for instance, egg dumping in the nests of conspecific or heterospecific females (e.g., Zink 2005; Tallamy 2005), egg hiding (e.g., Machado and Raimundo 2001), egg coating with protective substances (e.g., Ang et al. 2008), and brood desertion, which occurs when a parent or parents leave the brood either temporally or permanently before offspring are fully independent of care (e.g., Balshine-Earn 1995; Ackerman and Eadie 2003; Zink 2003). Brood desertion, in particular, may be beneficial for lifetime reproductive success when (1) parent's chances to raise another brood in the same reproductive season are high, (2) raising broods has a negative impact on the parent's residual reproductive value, and (3) the reproductive value of the current brood is low (Clutton-Brock 1991; Stiver and Alonzo 2009). In such situations, the avoidance of costly parental care in the current brood may allow increased investment in future broods and thus increase lifetime reproductive fitness.

In this study, we investigated the costs and benefits of temporary brood desertion using the harvestman *Neosadocus maximus* (Gonyleptidae) as a model system. Post-zygotic maternal care is widely distributed among arachnids of the order Opiliones, in which guarding females usually remain close to their clutches until nymphs hatch and disperse (Machado and Macías-Ordóñez 2007). The main benefit of maternal care in these species is the protection of eggs from predation (Machado and Oliveira 1998, 2002; Buzatto et al. 2007). However, such care may be costly to females because females do not forage, potentially compromising the production of additional eggs (Machado and Macías-Ordóñez 2007). Although food deprivation does not result in higher mortality of caring females, maternal care does lead to a reduction in female lifetime fecundity (Buzatto et al. 2007). Unlike all other harvestman species exhibiting maternal care studied so far, females of *N. maximus* periodically abandon their clutches (Chelini 2011).

Given that predation pressure on harvestman eggs laid on the vegetation is intense (Machado and Oliveira 2002), temporary brood desertion could impose a cost to *N. maximus* females, reducing their reproductive success by means of offspring loss. Temporary brood desertion, however, could also provide a benefit to females, increasing their foraging opportunities and consequently the amount of energy and resources that could be converted to eggs (Wheeler 1996; Boggs 2009). It is possible because contrary to other harvestman species exhibiting maternal care, in which females undergo discrete gonadotrophic cycles culminating in oviposition of a single large clutch (e.g., Machado and Macías-Ordóñez 2007), *N. maximus* females produce eggs continuously, maturing and laying them in small batches of 20 to 50 eggs (Chelini 2011). The gonadotrophic cycle extends through the caring period resulting in clutches

containing eggs in several stages of embryonic development coming from different oviposition bouts (Fig. 1). In addition, considering that harvestmen are particularly sensitive to dehydration (Santos 2007), brood desertion may also decrease the physiological stress of remaining exposed on the vegetation for a long period.

The unique natural history of maternal care in *N. maximus* allowed us to test two hypotheses directly related to the theoretical trade-off between parental effort and reproductive effort. According to our first hypothesis, female presence is important in the protection of eggs against predation, especially at night, when conspecific egg predators are more active (Osses et al. 2008). Therefore, eggs are expected to be more exposed to predator attacks during temporary brood desertion, imposing a cost to the guarding female that should be directly proportional to the time females spend away from their eggs. Our second hypothesis postulates that brood desertion benefits females through an increase in fecundity. Therefore, the number of eggs added to the current clutch after the beginning of the oviposition and the probability of laying a second clutch over the course of the reproductive season would be both inversely related to the caring frequency.



**Fig. 1** **a** *N. maximus* female caring for her eggs on the undersurface of a leaf. **b** Clutch containing eggs in different stages of embryonic development and recently hatched nymphs. Numbers indicate eggs in each one of the five age classes (see text for definition) and “N” indicates an early hatched nymph. In both pictures, note the presence of a mucus coat around the eggs

## Materials and methods

### Study system

*N. maximus* is a large-bodied Neotropical harvestman (carapace length measuring nearly 1 cm), whose females care for their eggs until all nymphs have hatched and dispersed (Fig. 1), comprising a caring period of nearly 40 days. After oviposition, females cover their eggs with a hygroscopic mucus coat (Fig. 1), similar to the one described for the harvestman *Iporangaia pustulosa* (Requena et al. 2009). The reproductive season is restricted to the warmer months, more specifically from October to March, just as recorded for several other local harvestman species (Gnaspini 1995; Buzatto et al. 2007; Zatz et al. 2011). Ecophysiological experiments demonstrated that *N. maximus* has high negative phototaxis and prefer mild temperatures when compared to other syntopic species from the same family (Santos 2003), which may explain why individuals of *N. maximus* exhibit most intense activity at night year round (Osses et al. 2008).

### Behavioral observations

We conducted this study at Intervales State Park (24° 14'S, 48° 04'W, altitude of approximately 750 m), an Atlantic Forest fragment in the state of São Paulo, southeastern Brazil. This region has a subtropical weather, with two well-marked seasons (Chelini et al. 2011). We gathered our data in seven field trips regularly spread between October 2009 and February 2010, during the warm and wet season. These field trips lasted from 8 to 14 days each, and were spaced out by 2- to 3-week intervals. We conducted our behavioral observations along a 450 m long transect flanked by abundant vegetation and at a distance ranging from 5 to 50 m to a stream. We individually marked all caring females with enamel paint, which lasts for several years and does not interfere with harvestmen fitness (e.g., Gnaspini 1996; Buzatto et al. 2007).

We monitored each clutch once per hour, throughout 24 h spread during three consecutive days (8 h per day). In the first day of observations, we monitored the clutches between 2200 and 0600 hours. In the second day of observations, we monitored the clutches between 1400 and 2200 hours. Finally, in the third day of observations, we monitored the clutches between 0600 and 1400 hours. In each one of these periods, we recorded once per hour if caring females were present or absent from their clutches. We considered that a female was caring for her eggs when she was up to 5 cm from her clutch, otherwise she was considered absent.

Given that each field trip lasted between 8 and 14 days, we obtained two to four full 24-h sets of observations for each clutch. For analytical purposes, we divided each set of

24 h into two blocks: observations made between 0700 and 1800 hours were considered as diurnal and those made between 1900 and 0600 hours were considered as nocturnal. We calculated the caring frequency for diurnal and nocturnal observations for each clutch dividing the number of times we saw a female caring for her eggs in each period by the total of 12 observations per period. We discarded from our analysis clutches that had already begun to hatch, since this made it difficult to calculate the total number of eggs laid by each female. From a total of 52 clutches we found during the study period, we included 40 of them in our analyses, discarding those with signs of egg hatching and those that were followed for less than 24 h.

To determine how many eggs were consumed and/or added to each clutch during the day and at night, we photographed each clutch at 0700 hours (beginning of the diurnal observations) and at 1900 hours (beginning of the nocturnal observations). We used these photographs to count the eggs at the beginning of each day and night. Comparing and superimposing subsequent photos of the same clutch, we were able to identify which eggs were added or consumed. Additionally, we classified the clutches in five age classes based on the stage of embryonic development of the oldest eggs (loosely based on Gnaspini and Lerche 2010). From younger to older clutches, the age classes were (Fig. 1b): (1) clutches containing only recently laid eggs, which are uniformly white; (2) clutches containing at least some cream colored eggs and with the germ band clearly distinguishable as a conjunct of cells at one side of the egg; (3) same as before, but with embryo's eyes visible; (4) same as before, but with intestinal cecum clearly distinguishable as a darker line in the center of the egg; (5) clutches containing at least some grayish eggs with embryos clearly pigmented. We used these age classes as a proxy for the time females had already invested in parental activities and used them as an ordinal variable in our analyses.

### Predictions and statistical analyses

To investigate the costs of brood desertion, we built five models relating female caring frequency and period of the day to the proportion of eggs consumed in each clutch (Table 1). We predicted that: (1) the proportion of eggs consumed would be higher during the night, when conspecifics and other important egg predators are more active (Buzatto et al. 2007; Cokendolpher and Mitov 2007; Osses et al. 2008) and (2) the proportion of eggs consumed in each clutch would be inversely proportional to the caring frequency. We also compared the fit of an additive and interactive effect between caring frequency and period of the day, and a null model in which the proportion of eggs consumed is not influenced by any of the predictor variables.

Regarding the benefits of brood desertion, we first built four models to investigate the effect of the caring frequency

**Table 1** Second order Akaike's Information Criteria table for the GLMMs of costs and benefits of temporary brood desertion in the harvestman *N. maximus*

Models	Predictions	AICc	k	$\Delta$ AIC	AIC weight
Costs of brood desertion: egg mortality					
M~CF*P	M is inversely proportional to CF and is influenced by P	1,257.9	5	0	1
M~CF+P	M is influenced by the additive effect of CF and P	1,338.9	4	81.0	<0.0001
M~P	M is higher at night	1,385.8	3	127.9	<0.0001
M~CF	M is inversely proportional to CF	1,655.3	3	397.4	<0.0001
M~1	M is not influenced by P or CF (null model)	1,686.0	2	428.1	<0.0001
Benefits of brood desertion: increased female fecundity					
F~CF*A	F is influenced by the interaction between A and CF	1,094.7	5	0	1
F~CF+A	F is influenced by the additive effect of A and CF	1,125.9	4	31.3	<0.0001
F~CF	F is inversely proportional to CF	1,127.7	3	33.0	<0.0001
F~A	F is inversely proportional to A	1,310.6	3	215.9	<0.0001
F~S+NT	F is influenced only by the additive effect of S and NT	1,312.1	4	217.4	<0.0001
F~1	F is not influenced by CF or A (null model)	1,312.5	2	217.8	<0.0001

*k* number of parameters of the models,  $\Delta$ AIC difference between the current model and the better-adjusted model, *M* egg mortality (measured as the proportion of eggs consumed in a 12-h period), *P* period of the day (day or night), *CF* caring frequency (measured as the proportion of observations a caring females was found on the clutch in a 24-h period, then categorized), *F* fecundity (measured as the number of eggs added to the clutch in a 24-h period), *A* brood age, *S* female size, *NT* total number of eggs laid in a clutch

on the number of eggs added to the current clutch (Table 1). We predicted that: (3) immediate fecundity, measured as the number of eggs added to the current clutch in consecutive oviposition bouts, would be inversely proportional to the caring frequency and (4) the number of eggs added to the clutches would decrease throughout the caring period. This pattern would be a consequence of either a limited number of mature eggs in the female ovaries or a female strategy to avoid an excessively long caring period, which could reduce her residual fecundity. In addition, we compared the fit of a model with additive and interactive effect of caring frequency and clutch age, and a null model in which the number of added eggs is not influenced by any of the predictor variables. We added the size of the caring female and the total number of eggs of each clutch as co-variables in all these models because female size in many arthropod species may have an effect on its fecundity (Gilbert and Manica 2010) and the total number of eggs present in a clutch may have an effect on the number of eggs that can be added to this clutch.

In our second analysis regarding the benefits of brood desertion, we investigated the effect of the caring frequency of the first clutch on the probability of laying a second clutch over the course of the reproductive season. We predicted that: (5) the probability of laying a second clutch would be higher in females with low caring frequency in the first clutch. Again, we added the size of the caring females as covariable in the model. Given that we followed some females for more than 24 h, we estimated the total caring frequency of their first clutch as the number of times these females were seen close to their eggs divided by the total number of observations.

To test predictions 1–4, we used a generalized linear mixed model (GLMM) approach, using clutches as sampling units and female identity as a random variable to account for repeated measures on the same individuals. We selected the most plausible model of each set of competing models selecting the one with the lowest second order Akaike's Information Criteria value. GLMMs are a recently developed statistical tool that provides a more flexible approach for analyzing non-normally distributed data when random effects are present, extending the analytical power of generalized linear models (GLMs) for analysis of blocked data with count or proportional responses (Bolker et al. 2009).

For the models related to the costs of brood desertion (predictions 1–2), we fitted the error distribution to a binomial, which is the most appropriate distribution for proportion data. Due to a great variance in the proportion of eggs consumed when the caring frequency was low (<25 %) and a high frequency of zeros when the caring frequency was high (>25 %; see “Results” section), we categorized the caring frequency into four classes: (1) 0–25 %, (2) 26–50 %, (3) 51–75 %, and (4) 76–100 %. This categorization considerably increased the fit of the models, without loss of information.

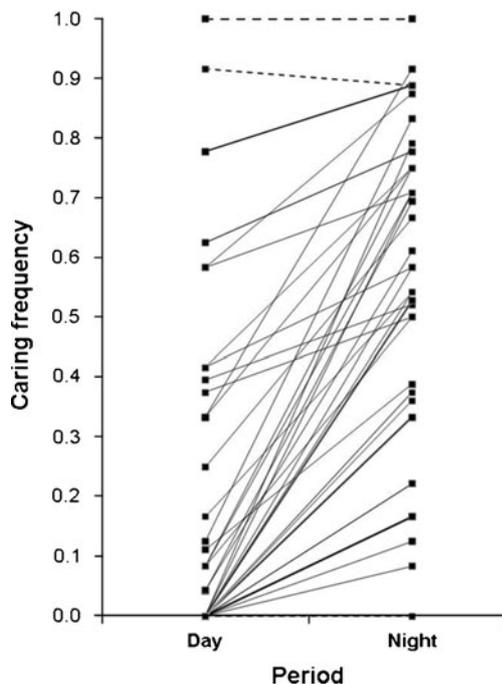
For the models related to the benefits of brood desertion (predictions 3–4), we used absolute numbers of eggs added to the clutch (instead of proportions), and fitted the errors to a Poisson distribution. The patterns obtained using absolute numbers and proportions were qualitatively similar, and thus we report only the former in the results. Finally, we

tested prediction 5 using a GLM approach with errors following a binomial distribution. In this case, we used females as our sampling unit and then performed an analysis of deviance. We ran all analyses with the software R (R Development Core Team 2009), using the function *glmer* of the *lme4* library package (Bates and Maechler 2010).

## Results

### Caring frequency

The time spent by individual females guarding their eggs was extremely variable, ranging from 2 to 98 % of our observations (Fig. 2). The caring frequency was higher during the night (median=52 %, min–max=0–98 %) than during the day (median=5 %, min–max=0–80 %). When caring for their eggs, females were seen adding eggs to their clutches ( $N=5$ ), copulating or interacting with males ( $N=5$ ), actively defending their clutches against egg predators (*Jussara* sp.,  $N=1$ ; *Promitobates ornatus*,  $N=2$ ; cricket,  $N=1$ ), eating close to the clutch ( $N=1$ ), or standing close to the eggs ( $N=1,600$ ). When not caring for their eggs, females were seen walking on the ground up to 1.5 m away from their eggs ( $N=62$ ), sheltered in natural cavities or under dead leaves close (up to 50 cm) to their clutches ( $N=35$ ) or eating at the vicinity of



**Fig. 2** Caring frequency of the harvestman *N. maximus* during the day and at night. Lines connect observation on the same caring female. Note that for the great majority of the females, caring frequency increases at night (solid lines). Only for a small number of females, caring frequency decreases or remains equal between day and night (dashed lines)

their clutches ( $N=6$ ). Most of the time, though, females were away from their clutches and we were unable to find them because they easily hide on the vegetation or among the leaf litter ( $N=2,370$ ).

### Costs of brood desertion: egg mortality

Comparing diurnal and nocturnal photographs of all observed clutches, we identified 68 events of egg predation on 35 clutches—25 events occurring during the day and 43 occurring at night. The number of eggs consumed per clutch varied between 1 and 43 (mean $\pm$ SD=1.94 $\pm$ 6.47 eggs) during the day, and between 1 and 135 (mean $\pm$ SD=6.07 $\pm$ 19.07 eggs) at night. Our analysis indicates that the most plausible model to explain the proportion of consumed eggs was the one that incorporates the effect of the interaction between period of the day and caring frequency (Table 1). During the day, the proportion of consumed eggs was very low and did not seem to be influenced by the frequency of brood desertion (Fig. 3a). The proportion of consumed eggs was higher at night and it was negatively related to the frequency of brood desertion (Fig. 3b).

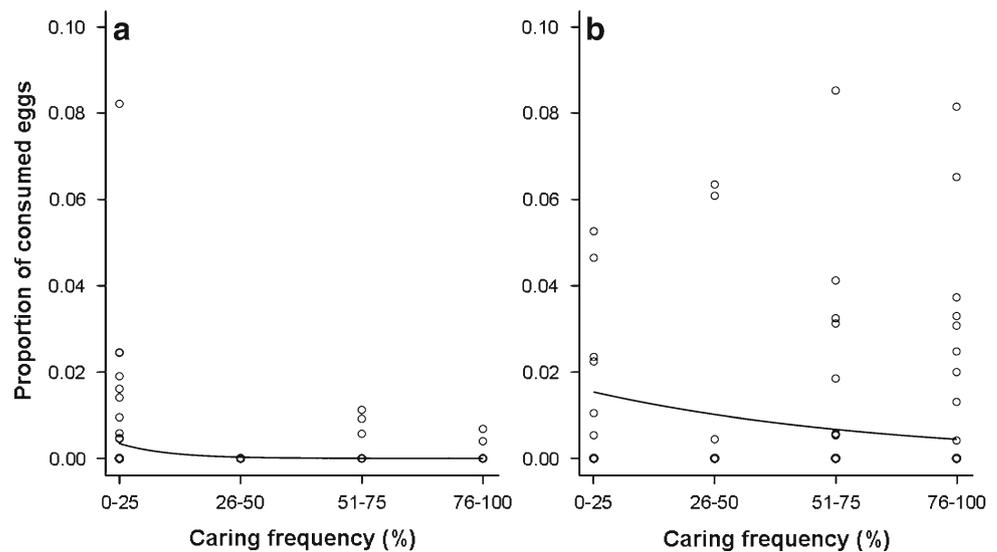
### Benefits of brood desertion: increased female fecundity

Thirty-two of the 52 females that we marked added eggs to their clutches during the caring period. Recently laid clutches (age 1) contained from 9 to 295 eggs (mean $\pm$ SD=118.6 $\pm$ 68.1 eggs). Among females that added eggs to their current clutches, the number of eggs added in a single day varied between 2 and 73 (mean $\pm$ SD=3.2 $\pm$ 8.2 eggs), and the interval between two oviposition events of the same female varied from 1 and nearly 20 days. We observed up to eight different oviposition events in a clutch, spaced out by 2- to 3-day intervals.

The most plausible model to explain the addition of eggs to the clutches was the one associating female immediate fecundity to the interaction between caring frequency and clutch age (Table 1). Contrarily to our prediction, however, the number of eggs added to a clutch was positively associated with the caring frequency (estimate=3.87; Table 1). This pattern is especially evident in young clutches of age 1, in which most of the oviposition events occurred (Fig. 4a). In fact, the age of the clutch had a negative effect on the number of eggs added to the clutch (estimate=0.48; Table 1), and only few eggs were added to old clutches of ages 2–5 (Fig. 4b). The best fitted model did not include the control variables, i.e., female size and total number of eggs in the clutch (Table 1).

We found only five females producing an additional clutch during the same reproductive season. The estimated caring frequency of the first clutch in these cases ranged from 0 to 100 %. Despite of this great variation, the

**Fig. 3** Relation between the caring frequency of the harvestman *N. maximus* and the proportion of eggs consumed during (a) the day and (b) at night. Lines represent predicted values by the best fitted model in Table 1. To better visualize the trends of these two lines, we removed from the graphics (but not from the analysis) values of proportion of consumed eggs higher than 0.10 ( $N=4$  values in a and  $N=9$  values in b), and we are not showing the points of each period paired by female identity



probability of laying a second clutch in the same reproductive season was not influenced by the caring frequency of the first clutch ( $\Delta$  deviance=0.0001,  $df=1$ ,  $p(\chi^2)=0.992$ ).

## Discussion

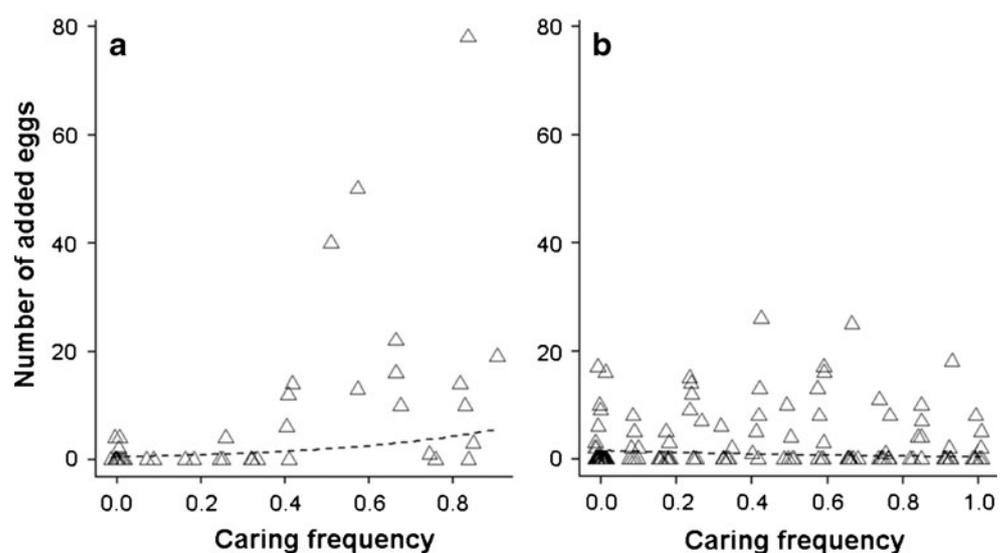
### Costs of brood desertion: egg mortality

Our results demonstrate that the costs of brood desertion in *N. maximus* depend on the period of the day. During the day, the proportion of consumed eggs was generally low, and even clutches with high frequency of desertion did not suffer intense predation (Fig. 3a). On the other hand, predation was more intense at night, but clutches with lower frequency of desertion suffered lower egg mortality (Fig. 3b). We suppose this difference is related to the identity of the most important egg predators, which changes from day to night.

Our field observations indicate that the most common species observed attacking the eggs during the day were the harvestmen *P. ornatus* (Gonyleptidae) and *Jussara* sp. (Sclerosomatidae; Chelini 2011). Individuals of these two species are considerably smaller than individuals of *N. maximus* and are unable to consume a high proportion of eggs. In fact, they were frequently observed consuming the mucus coat around the eggs, but not the eggs of unattended clutches (personal observation). At night, egg predation was caused by a wider range of predators including large-bodied arthropods, such as centipedes (Chilopoda: Scolopendridae) and wetas (Orthoptera: Anostostomatidae), which can consume a high proportion of eggs, especially when caring females are absent (Chelini 2011).

Considering that *N. maximus* caring frequency is higher at night, when predation pressure is also higher, caring females could be adjusting their maternal effort to the temporal variation in predation risk, which is regarded as the

**Fig. 4** Relation between the number of eggs added to a single clutch and the caring frequency in a clutches of age 1 and b clutches of ages 2, 3, 4, and 5. The fitted lines represent the values predicted by the most plausible model (see Table 1). Given that fitted lines for clutches of ages 2, 3, 4, and 5 are nearly indistinguishable, we are showing only one of them



main cost of brood desertion in ectotherms (Clutton-Brock 1991). Such adjustment has already been reported for some arthropod and fish species exhibiting maternal care. In the membracid *Publilia concava* (Hemiptera), for instance, females decide whether to care for a brood or abandon it permanently depending on food availability, presence of shelters against predators, and presence of tending ants that adopt and protect the membracid eggs (Zink 2003). In the cichlid fish *Cichlasoma nigrofasciatum*, parents decrease their foraging activities and increase their defensive behavior in the presence of a predator (Rangeley and Godin 1992). In our case, however, despite intensive maternal presence on the clutches at night, eggs loss is higher during this period, probably because caring females are ineffective in repelling the most important nocturnal egg predators. Experimental results with other arthropods species exhibiting maternal care have also shown that the effectiveness of female protection depends on the species of the natural enemies. Whereas parasitoids generally impose a great mortality to the eggs of bugs and beetles, pedestrian predators are successfully repelled by caring females (e.g., Eberhard 1975; Kudo 1996; Kudo and Ishibashi 1996).

Differences in the frequency of brood desertion between day and night may also occur because caring females are constrained to abandon their clutches during daylight hours to attenuate stressful climatic conditions and decrease the physiological costs of parental care. Ecophysiological studies have shown that *N. maximus* has particularly negative phototaxy and prefer milder temperatures than other syntopic harvestmen exhibiting maternal care, such as *Serracutisoma proximum* (Santos 2003), in which females remain on their clutches during most of the day for more than 30 days (Buzatto et al. 2007). In addition, *N. maximus* individuals show lower diurnal than nocturnal activity year round (Osses et al. 2008). Thus, the activity pattern of the caring females may be a consequence of heat and/or light intolerance, which may explain more frequent desertions during the day. Diurnal desertion has also been reported in the frog *Thoropa miliaris*, in which males care for eggs laid on shaded places in rocky shores (Giaretta and Facure 2004), a stressful environment that probably constrains parental activities only to the nocturnal period.

#### Benefits of brood desertion: increased female fecundity

In many predatory or detritivorous arthropods, parental care generally prevents foraging activities of parents (Tallamy 1994). In some species, however, parents perform filial cannibalism, which attenuate the costs of parental care without leaving the offspring unattended (e.g., Manica 2002; Thomas and Manica 2003). Instead of frequently cannibalizing eggs, *N. maximus* females temporarily desert their offspring. The fact that females were seen up to 1.5 m from

their clutches supports the assumption that at least some of the wandering females were foraging. In accordance to this suggestion, we witnessed few caring females eating close to their clutches. However, females that do not wander far from their clutches have their foraging activity limited to a small area on the leaf litter around the clutches where dead arthropods, an unpredictable food source, are likely to be scarce or promptly consumed by ants. Therefore, it is unlikely that the continuous gonadotrophic cycle of *N. maximus* can be explained by high food intake, like has been proposed for several insect species (Wheeler 1996).

Contrary to our prediction, an increased frequency of brood desertion in *N. maximus* did not increase immediate fecundity. Females that invested more in parental care were also those that added more eggs to their clutches. It is worth noting, however, that females only added eggs to their clutches for a period of up to 3 weeks after the first oviposition bout, which explains the negative relation between clutch age and number of added eggs. This also explains why most of the oviposition events occurred in clutches of age 1 (Fig. 4). We suggest that fecundity and caring frequency are both influenced by female nutritional state prior to oviposition. Well-fed females in good body condition are probably able to invest more energy in egg production and maturation, thus adding more eggs to their clutches than poorly-fed females—a pattern that has already been reported for many arthropod species (reviewed in Fox and Czesak 2000). Moreover, well-fed females may also be able to invest more time in parental activities, whereas poorly-fed females may benefit from or be constrained to more frequent foraging bouts. In fact, food-deprived parents in several taxa shorten the duration of brood care (e.g., Scott and Traniello 1990; Steinegger and Taborsky 2007) or invest less in egg assistance (e.g., Townshend and Wootton 1985; Segers et al. 2011).

In this study, we also investigated if temporary desertion of the current brood has long-term benefits to *N. maximus* females. In many species, fecundity benefits of brood desertion are only detected when analyzing female's lifetime reproductive success (see example with harvestmen in Buzatto et al. 2007). Given that the reproductive season of *N. maximus* lasts up to 6 months, females with low parental effort in a first clutch could have a higher probability to produce another clutch than females with high parental effort in a first clutch. However, less than 10 % of the females laid an additional clutch over the course of the same reproductive season. If there was a trade-off between current maternal effort and future fecundity, we would expect a higher number of females producing a second clutch, especially among those exhibiting high frequency of brood desertion, which we did not observe. Moreover, the probability of laying an additional clutch was not influenced by the caring frequency of the first clutch. We propose, therefore, that brood desertion also does not imply in fecundity benefits measurable in a single reproductive season.

In accordance to our findings, data on parental care modes across a phylogeny of 287 insect species indicate that only provisioning parental care has a negative effect on lifetime fecundity, contrarily to no care and care by egg-guarding (Gilbert and Manica 2010).

#### Concluding remarks

If brood desertion does not increase fecundity and if females' ability to raise another brood in the same reproductive season is very low, why would *N. maximus* females leave their eggs exposed to predators so frequently, especially during the day? Although temporary desertion does impose a cost associated with egg loss, this cost is markedly smaller than for other harvestmen with maternal care—including syntopic species that oviposit in similar microhabitats and whose eggs are exposed to similar predators (see Fig. 2 in Buzatto et al. 2007). We suggest that the mucus coat deposited by *N. maximus* females after oviposition (Fig. 1) may keep their eggs physically protected against predators during temporary brood desertion. Eggs of the harvestman *I. pustulosa* are also covered by a hygroscopic mucus coat deposited by females before abandoning them to the males' care (Requena et al. 2009; Gnaspini and Lerche 2010). Using both field and laboratory experiments, Requena et al. (2009) demonstrated that this mucus coat hampers egg consumption by potential predators during temporary male desertion, attributing to the mucus the lower susceptibility to predation when compared to clutches of the syntopic *S. proximum*, whose eggs lack the mucus coat. Although we do not know if the presence of mucus around the eggs evolved before or after temporary brood desertion in *N. maximus*, the potential physical protection provided by the mucus could attenuate both the costs related to egg loss during female absence, and the physiological costs of maternal care, allowing females to shelter when climatic conditions are stressful or to occasionally search for food during the day.

**Acknowledgments** We thank the staff of the Intervales State Park for logistical support; AA Baceti, LE Costa-Schmidt, and GS Requena for helping in the fieldwork; PIKL Prado, R Munguía-Steyer, and GS Requena for statistical advices to implement optimization routines in R language; JP Gibert for helping with the model averaging; and GS Requena, LEC Schmidt, DS Caetano, RH Willemart, MO Gonzaga, AS Mello, and two anonymous reviewers for useful comments on early versions of the manuscript. The study was supported by fellowships from Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP, 02/00381-0, 08/55867-0, 08/06604-7) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq).

**Conflicts of interest** The authors declare that they have no conflicts of interest.

#### References

- Ackerman JT, Eadie JM (2003) Current versus future reproduction: an experimental test of parental investment decisions using nest desertion by mallards (*Anas platyrhynchos*). Behav Ecol Sociobiol 54:264–273
- Agrawal AF, Combs N, Brodie ED (2005) Insights into the costs of complex maternal care behavior in the burrower bug (*Sehirus cinctus*). Behav Ecol Sociobiol 57:566–574
- Ang TZ, Oluanaigh C, Rands SA, Balmford A, Manica A (2008) Quantifying the costs and benefits of protective egg coating in a chrysomelid beetle. Ecol Entomol 33:484–487
- Balshine-Earn S (1995) The costs of parental care in Galilee St Peter's fish, *Sarotherodon galilaeus*. Anim Behav 50:1–7
- Bates D, Maechler M (2010) lme4: Linear mixed-effects models using Eigen and S4. R package version 0.999375-35. <http://CRAN.R-project.org/package=lme4>
- Boggs CL (2009) Understanding insect life histories and senescence through a resource allocation lens. Funct Ecol 23:27–37
- Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol Evol 24:127–135
- Buzatto BA, Requena GS, Martins EG, Machado G (2007) Effects of maternal care on the lifetime reproductive success of females in a neotropical harvestman. J Anim Ecol 76:937–945
- Chelini MC (2011) Cuidado maternal no opilião *Neosadocus maximus* (Arachnida: Opiliones). Master thesis, Instituto de Biociências, Universidade de São Paulo, São Paulo, Brazil, p 62
- Chelini MC, Willemart RH, Gnaspini P (2011) Caves as a winter refuge by a neotropical harvestman (Arachnida, Opiliones). J Insect Behav 24:393–398
- Clutton-Brock TH (1991) The evolution of parental care. Princeton University Press, Princeton
- Cokendolpher JC, Mitov PG (2007) Natural enemies. In: Pinto-da-Rocha R, Machado G, Giribet G (eds) Harvestmen: the biology of Opiliones. Harvard University Press, Cambridge, pp 339–373
- Eberhard WG (1975) The ecology and behavior of a subsocial pentatomid bug and two scelionid wasps: strategy and counterstrategy in a host and its parasites. Smithson Contrib Zool 205:1–39
- Fox CW, Czesak ME (2000) Evolutionary ecology of progeny size in arthropods. Annu Rev Entomol 45:341–369
- Giaretta AA, Facure KG (2004) Reproductive ecology and behavior of *Thoropa miliaris* (Spix, 1824) (Anura, Leptodactylidae, Telmatobiinae). Biota Neotropica 4:1–10
- Gilbert JDJ, Manica A (2010) Parental care trade-offs and life-history relationships in insects. Am Nat 176:212–226
- Gnaspini P (1995) Reproduction and postembryonic development of *Goniosoma spelaum*, a cavernicolous harvestman from southeastern Brazil (Arachnida: Opiliones: Gonyleptidae). Invertebr Reprod Dev 28:137–151
- Gnaspini P (1996) Population ecology of *Goniosoma spelaum*, a cavernicolous harvestman from southeastern Brazil (Arachnida: Opiliones: Gonyleptidae). J Zool 239:417–435
- Gnaspini P, Lerche CF (2010) Embryonic development of *Ampheres leucopheus* and *Iporangaia pustulosa* (Arachnida: Opiliones: Gonyleptidae). J Exp Biol 314:489–502
- Gross MR (2005) The evolution of parental care. Quart Rev Biol 80:37–46
- Hanssen SA, Hasselquist D, Folstad I, Erikstad KE (2005) Cost of reproduction in a long-lived bird: incubation effort reduces immune function and future reproduction. Proc R Soc London 272:1039–1046
- Kokko H, Jennions MD (2008) Parental investment, sexual selection and sex ratios. J Evol Biol 21:919–948

- Kudo S (1996) Ineffective maternal care of a subsocial bug against a nymphal parasitoid—a possible consequence of specialization to predators. *Ethology* 102:227–235
- Kudo S, Ishibashi E (1996) Maternal defence of a leaf beetle is not effective against parasitoids but is against pedestrian predators. *Ethology* 102:560–567
- Machado G, Macías-Ordóñez R (2007) Reproduction. In: Pinto-da-Rocha R, Machado G, Giribet G (eds) *Harvestmen: the biology of Opiliones*. Harvard University Press, Cambridge, pp 414–454
- Machado G, Oliveira PS (1998) Reproductive biology of the neotropical harvestman *Goniosoma longipes* (Arachnida, Opiliones: Gonyleptidae): mating and oviposition behaviour, brood mortality, and parental care. *J Zool* 246:359–367
- Machado G, Oliveira PS (2002) Maternal care in the Neotropical harvestman *Bourguyia albiornata* (Arachnida: Opiliones): oviposition site selection and egg protection. *Behaviour* 139:1509–1524
- Machado G, Raimundo RLG (2001) Parental investment and the evolution of subsocial behaviour in harvestmen (Arachnida Opiliones). *Ethol Ecol Evol* 13:133–150
- Manica A (2002) Filial cannibalism in teleost fish. *Biol Rev* 77:261–277
- Osses F, Nazareth TM, Machado G (2008) Sexual and seasonal variation in the behavioral repertory of the neotropical harvestman *Neosadocus maximus* (Opiliones: Gonyleptidae). *J Arachnol* 36:518–526
- R Development Core Team (2009) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>
- Rangeley RW, Godin JG (1992) The effects of a trade-off between foraging and brood defense on parental behaviour in the convict cichlid fish, *Cichlasoma nigrofasciatum*. *Behaviour* 120:123–138
- Requena GS, Buzatto BA, Munguía-Steyer R, Machado G (2009) Efficiency of uniparental male and female care against egg predators in two closely related syntopic harvestmen. *Anim Behav* 78:1169–1176
- Santos FH (2003) Estudo de parâmetros fisiológicos relacionados ao modo de vida cavernícola em Goniosomatinae (Opiliones, Gonyleptidae). PhD dissertation, Instituto de Biociências, Universidade de São Paulo, São Paulo, Brazil, p 140
- Santos FH (2007) Ecophysiology. In: Pinto-da-Rocha R, Machado G, Giribet G (eds) *Harvestmen: the biology of Opiliones*. Harvard University Press, Cambridge, pp 473–488
- Scott MP, Traniello JFA (1990) Behavioural and ecological correlates of male and female parental care and reproductive success in burying beetles (*Nicrophorus* spp.). *Anim Behav* 39:274–283
- Segers FHID, Gerber B, Taborsky B (2011) Do maternal food deprivation and offspring predator cues interactively affect maternal effort in fish? *Ethology* 117:708–721
- Steinegger M, Taborsky B (2007) Assymmetric sexual conflict over parental care in a biparental cichlid. *Behav Ecol Sociobiol* 61:933–941
- Stiver KA, Alonzo SH (2009) Parental and mating effort: is there necessarily a trade-off? *Ethology* 115:1101–1126
- Tallamy DW (1994) Nourishment and the evolution of paternal investment in subsocial arthropods. In: Hunt JH, Nalepa CA (eds) *Nourishment and evolution in insect societies*. Westview, Boulder, pp 21–56
- Tallamy DW (2005) Egg dumping in insects. *Annu Rev Entomol* 50:347–370
- Tallamy DW, Schaeffer C (1997) Maternal care in the Hemiptera: ancestry, alternatives, and current adaptive value. In: Choe JC, Crespi BJ (eds) *The evolution of social behavior in insects and arachnids*. Cambridge University Press, Cambridge, pp 94–115
- Thomas LK, Manica A (2003) Filial cannibalism in an assassin bug. *Anim Behav* 66:205–210
- Townshend TJ, Wootton RJ (1985) Adjusting parental investment to changing environmental conditions: the effect of food ration on parental behaviour of the convict cichlid, *Cichlasoma nigrofasciatum*. *Anim Behav* 33:494–501
- Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) *Sexual selection and the descent of man 1871–1971*. Aldine, Chicago, pp 136–179
- Wheeler D (1996) The role of nourishment in oogenesis. *Annu Rev Entomol* 41:407–431
- Winkler DW (1987) A general model for parental care. *Am Nat* 130:526–543
- Zatz C, Werneck RM, Macías-Ordóñez R, Machado G (2011) Alternative mating tactics in dimorphic males of the harvestman *Longiperna concolor* (Arachnida: Opiliones). *Behav Ecol Sociobiol* 65:995–1005
- Zink AG (2003) Quantifying the costs and benefits of parental care in female treehoppers. *Behav Ecol* 14:687–693
- Zink AG (2005) The dynamics of brood desertion among communally breeding females in the treehopper, *Publilia concava*. *Behav Ecol Sociobiol* 58:466–473