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Efficiency of uniparental male and female care against egg predators in two closely related syntopic harvestmen

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Although the benefits of maternal care have been investigated in many species, the caring role of males in species with exclusive paternal care has received less attention. We experimentally quantified the protective role of paternal care in the harvestman *Iporangaia pustulosa*. Additionally, we compared the effectiveness of paternal care against predation in this species with a syntopic harvestman with maternal care, *Acutisoma proximum*. We demonstrated that nearly one-third of the unprotected *Iporangaia* clutches disappeared entirely in 12 days, while the other two-thirds suffered a mean reduction of 55% in egg number. Conversely, 50% of the control clutches did not suffer any reduction, and only one was entirely consumed by predators. We also demonstrated that the mucus coat that covers *Iporangaia* clutches has an important deterrent role against predation by conspecifics: 58.3% of the clutches without mucus were attacked and three of them were entirely consumed, whereas only three clutches with mucus were attacked, suffering a reduction of up to three eggs. *Iporangaia* males were as efficient as *Acutisoma* females in protecting eggs. However, unattended *Acutisoma* eggs were attacked 20% more frequently than unattended *Iporangaia* eggs. Unattended *Iporangaia* eggs are protected by a mucus coat that prevents or decreases predation rate, whereas *Acutisoma* eggs are more susceptible to predation, probably because they lack this mucus coat. Thus, besides the fact that *Iporangaia* males efficiently protect the offspring against egg predators, females also contribute to egg protection by providing a mucus coat that deters egg predators.

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Exclusive paternal care is the rarest form of postzygotic investment among animals, occurring only in a few species of birds, amphibians, fish, arthropods and polichaetes (reviewed in: Ridley 1978; Clutton-Brock 1991). The adaptive value of this behavioural trait has traditionally been studied using a cost–benefit approach on the lifetime reproductive success of both females and parental males (Trivers 1972; Maynard Smith 1977; Clutton-Brock 1991). From the males' perspective, parental care is costly because it results in a reduction in their foraging time while allocating energy to parental activities not related to their own growth and maintenance (e.g. Townsend 1986; Jones & Reynolds 1999; Smith & Wootton 1999; Fernandez & Reboreda 2003). Moreover, parental care may diminish males' survival since they are likely to become more exposed to predation while caring for the offspring (e.g. Svensson 1988; Magnhagen 1991; but see Munguía-Steyer & Macías-Ordóñez 2007). Nevertheless, given that males of several species are able to brood multiple clutches of eggs simultaneously, providing parental care and acquiring mates are not mutually exclusive activities, which decreases the costs of egg guarding. At least among some arthropod species, it has been suggested that males that provide care should be preferred by females and obtain a greater number of copulations than males that are unable and/or unwilling to provide care (see review in Tallamy 2000, 2001). According to this hypothesis, females should prefer guarding males because paternal assistance minimizes the fecundity costs related to egg guarding for females, allowing them to forage immediately after oviposition, and also because paternal care may provide an honest signal of a male's quality as offspring defender.

The most important benefits of parental care in arthropods include improving microclimatic conditions such as reducing risk of dehydration and/or increasing egg aeration, protecting the offspring against predators or fungal attack, as well as providing water and food to juveniles (examples in Clutton-Brock 1991). Although these benefits have been investigated in many arthropod species with maternal care (Tallamy & Denno 1982; Fink 1986; Gillespie 1990; Diesel 1992; Kudo & Ishibashi 1995; Gundermann et al. 1997; Machado & Oliveira 1998, 2002; Kudo 2002; Stegmann

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& Linsenmair 2002; Zink 2003; Buzatto et al. 2007), the caring role of males in species with exclusive paternal care has received less attention. In giant water bugs (Belostomatidae), for instance, aeration and moistening of the eggs by guarding males are crucial for offspring survival (Smith 1997). Even though it has been suggested that guarding males of giant water bugs might also protect their eggpads against predators (Cullen 1969; Kraus et al. 1989), no study so far has tested this hypothesis. Actually, there are only two studies that provided experimental demonstration of the effectiveness of male egg-guarding behaviour as a defence against natural enemies in arthropods. In the harvestman *Zygopachylus albomarginis*, guarding males have a crucial protective role, actively defending the clutch against egg predators (such as ants and conspecifics) and fungal attack (Mora 1990). In the assassin bug *Rhinocoris tristis*, guarding males confer protection to eggs against the attack of parasitoids (Thomas & Manica 2003).

While maternal care is widespread among arachnids, exclusive paternal care is found only among some species of the order Opiliones (review in Machado & Macías-Ordóñez 2007). There are several differences in the behavioural patterns shown by parental individuals in harvestman species with uniparental male and female care (discussion in Machado et al. 2004). First, females care for clutches containing eggs in only one stage of embryonic development (references in Buzatto et al. 2007), whereas males care for clutches containing eggs in several stages of embryonic development that come from different oviposition events (references in Machado et al. 2004). Second, the total time spent by females guarding eggs and newly hatched nymphs varies among and within species, but rarely exceeds 40 days (Gnaspini 2007). Among species with exclusive paternal care though, females continually add eggs to the clutches and parental activities can last up to 8 months (e.g. Machado et al. 2004). Finally, females rarely leave the clutch to forage or undertake any other activity during the guarding period, while guarding males frequently leave their clutches and may be found as far as 5 m from the oviposition site (e.g. Machado et al. 2004). These differences probably influence the costs (paid by parental individuals) as well as the benefits (enjoyed by the offspring) of parental care (Manica & Johnstone 2004).

In this paper we experimentally quantified the efficacy of paternal care to prevent egg predation in the Neotropical harvestman *Iporangaia pustulosa* (Gonyleptidae: Progonyleptoidellinae). Additionally, we compared the effectiveness of paternal care in this species with the results previously obtained by our research group for a syntopic harvestman with maternal care, *Acutisoma proximum* (Gonyleptidae: Goniosomatinae), which is closely related to *Iporangaia* and uses the same oviposition sites (i.e. the underside surface of leaves that hang over forest streams; Machado et al. 2004; Buzatto et al. 2007; Buzatto & Machado 2008). More specifically, we tested the following hypotheses: (1) paternal care in *Iporangaia* increases egg survival because of the protective role of guarding males; (2) the thick mucus coat that covers *Iporangaia* clutches (see Model Organism) confers additional protection against egg predators; (3) since *Iporangaia* males frequently abandon their clutches whereas *Acutisoma* females remain close to their eggs most of the time, the benefits of the parental care provided by males, in terms of egg survival, are expected to be less than those provided by females.

METHODS

Model Organism

Iporangaia pustulosa is a colourful, large-bodied harvestman that is endemic to the Brazilian Atlantic forest (Kury 2003) and can be frequently found walking on the vegetation during day and night (Hoenen & Gnaspini 1999). Females of *Iporangaia* lay their eggs exclusively on the underside surface of leaves of shrubs growing at the margin of streams and, after oviposition, abandon the eggs under the males' guard (Machado et al. 2004). Like other species of the subfamily Progonyleptoidellinae, *Iporangaia* eggs are covered by an abundant hygroscopic mucus coat (Machado et al. 2004), which is produced by the female's reproductive tract and deposited on the clutch after oviposition (C. F. Lerche, personal communication). This mucus coat probably protects the clutch against dehydration and may also confer protection to the eggs against certain predators (Machado & Macías-Ordóñez 2007). Several females may visit the same clutch, copulate with the guarding male, and add their eggs to the clutch (Machado et al. 2004). Although eggs last nearly 40 days to hatch in the warm and wet season (C. F. Lerche, personal communication), the guarding period may reach more than 4 months because females continually add eggs to the clutches, which are composed of eggs in different embryonic stages (Machado et al. 2004). Guarding males do not stay close to the eggs all the time and temporarily abandon their clutches, probably to forage or to take shelter from harsh climatic conditions. During the warmer months (October to March), guarding males are found on their clutches throughout the day, although some of them leave their eggs unattended for up to 48 h. During the colder months (April to September), most males are not found on their clutches during the day, and guard their eggs only at night (Machado et al. 2004).

Study Site

We conducted this study in a dense Atlantic forest fragment at Parque Estadual Intervales (24°14′S, 48°04′W; 800 m above sea level), southern São Paulo state, southeastern Brazil. The annual rainfall in the region ranges from 2000 to 3000 mm and the mean annual temperature ranges from 12–20 °C. There is a well-marked seasonality in the region, with a wet and warm season lasting from October to March, and a dry and cold season from April to September, when frosts are common. Between July 2003 and March 2007, we inspected a 200 m transect along a 5 m wide stream that was flanked by abundant vegetation. During the first 2 years, we visited the study site monthly, during 4 consecutive days per month and quantified the number of *Iporangaia* clutches in the transect. In the following years, we concentrated our sampling in the wet and warm season (when the reproductive activity of *Iporangaia* is more intense), spending 10–20 days in the field each month. During all the study period, we inspected the vegetation that flanked the river three times a day (0830–1200 hours, 1430–1800 hours and 2030–0000 hours).

Observational Study

In each sampling day, we identified all clutches found along the transect and visited each of them for 1 min, with regular intervals of 2 h between consecutive inspections. Whenever we encountered predators consuming eggs, we observed the event, continuously recording the predator's behaviour (according to Martin & Bateson 1994). We individually marked every guarding male of *Iporangaia* found with enamel colour paint, a procedure that has been previously used in other studies with harvestmen in the field and has the advantages of not affecting their behaviour and lasting for over 2 years (see Buzatto et al. 2007). After marking, we released the individuals at the same places where they were captured. We photographed all clutches in the first and in the last sampling day of each monthly field trip. With these pictures, we quantified the number of eggs per clutch and the proportion of clutches and eggs per clutch that were attacked by fungus each month.

Effects of Paternal Care on Egg Survival

To evaluate the effect of paternal care on egg survival, we conducted a field experiment that lasted 12 days between December 2006 and January 2007. This 12-day period corresponds to nearly one-third of the development time of *Iporangaia* eggs in the wet and warm season. We designated guarding males of *Iporangaia* to two experimental groups: (1) 'no care', in which we removed the guarding males ($N = 16$) from their respective clutches and maintained them alive in captivity, leaving the eggs unattended in the field and (2) 'care' (or control), in which we individually marked 12 guarding males and released them on their clutches. The initial number of eggs per clutch in the 'no care' group (mean $\pm$ SD $= 66.0 \pm 50.0$ eggs/clutch) was not different from that in the 'care' group (82.9 ± 72.8 eggs/clutch) (two-tailed *t* test: $t_{26} = 0.730$, $P = 0.472$). Since guarding males of *Iporangaia* usually care for clutches that contain eggs in several stages of embryonic development (Machado et al. 2004), we controlled for this variable by designating clutches with eggs in similar stages of development to each experimental group. We did not use clutches containing early hatched nymphs because our main goal was to evaluate the effect of paternal care exclusively on egg predation risk. Moreover, although nymphs are also under the threat of predation, they remain under the male guard for only 3–5 days.

During the experimental period, we inspected all clutches once a day in an attempt to identify egg predators. To avoid disturbing the predation event, whenever we found predators consuming eggs, we took pictures of them for later identification. At the end of the experimental period, we released the guarding males of the 'no care' group on the exact locations previously occupied by their clutches. The number of eggs in each clutch was counted on days 0, 2, 4, 6, 8, 10 and 12 after the beginning of the experiment.

We used a binomial test to compare the proportion of clutches that were attacked by predators in the 'no care' and 'care' groups. Additionally, we used repeated measures ANOVA to compare the number of eggs in clutches over the course of the experiment between the two experimental groups. For this analysis, data were rank-transformed and we did not consider the eggs that were occasionally added to the experimental clutches by ovipositing females.

Protective Role of the Mucus Coat

To investigate the deterrent role of the thick mucus coat that covers *Iporangaia* eggs, we conducted a laboratory experiment. First we collected three clutches containing 100–150 eggs covered by abundant mucus. Then we divided these eggs into two experimental groups: (1) 'no mucus', in which we removed the mucus coat by gently rolling the eggs on a piece of filter paper and (2) 'mucus' (or control), in which we manipulated the eggs, but did not remove the mucus coat. We assembled eggs of each experimental group in 12 artificial clutches containing 10 eggs each, which we placed on individual leaves of the fern *Olfersia cervina* (Dryopteridaceae), a natural host plant of *Iporangaia* (G. S. Requena, personal observation). Finally, we placed each leaf with its 10 eggs inside a plastic cage (17×13 cm base, 10 cm height) containing a small piece of wet cotton (to maintain the moisture), a small branch for perching, and an adult female of *Iporangaia*, which is the main egg predator in the field (see Results). We recorded the number of eggs consumed by the females in each cage once per day during 4 consecutive days. We also conducted ad libitum observations in order to describe the predatory behaviour of the individuals in each experimental group. After the experiment, we released all females in the field and preserved the eggs for future studies.

We evaluated the effect of the mucus coat on the predation suffered by the experimental clutches using a generalized linear model approach. We used a beta-binomial distribution in this model to address overdispersion of our data ($\varphi \pm$ SE $= 0.672 \pm 0.103$). The use of compound probability distributions, such as the beta-binomial or the negative-binomial, is an effective way to address overdispersion in count and proportion data (Bolker 2008; Richards 2008). Finally, we performed a likelihood ratio test comparing the null model with the model that included the effect of the experimental group.

Efficiency of Paternal versus Maternal Care

To compare the efficiency of egg-guarding behaviour in maternal and paternal harvestman species, we calculated egg mortality in 'care' and 'no care' clutches of both maternal *Acutisoma proximum* (experiment described in Buzatto et al. 2007) and paternal *Iporangaia* (experiment described above). Although the field experiment with *Acutisoma* lasted 14 days, we used the number of eggs present on the 12th day for our comparison with *Iporangaia*. Egg mortality was considered as the percentage of the total number of eggs in each clutch that was consumed by predators over the course of the experiments. We chose *Acutisoma* as the basis for our comparison with *Iporangaia* because both species belong to the same family (Gonyleptidae), co-occur in the same environment, use similar host plant species for oviposition, have similar egg predators, and reach their reproductive peak during the wet and warm season (see Machado et al. 2004; Buzatto et al. 2007; Buzatto & Machado 2008; see Table 1). We did not conduct the experiments with the two species simultaneously in the same year, but in the same season, from December to February, which is the period of most intense arthropod activity in our study area. Although we recognize that predation rates may vary among

Table 1
List of arthropods found consuming eggs of the harvestman *Iporangaia pustulosa* and the season when these observations were made in the field

Taxon	Season of observation	
	Dry-cold ($N=141$)*	Warm-wet ($N=237$)*
Opiliones ($N=102$)		
Iporangaia pustulosa†, Gonyleptidae ($N=91$)	4	87
Acutisoma proximum†, Gonyleptidae ($N=5$)	0	5
Longiperna zonata, Gonyleptidae ($N=3$)	0	3
Neosadocus maximus, Gonyleptidae ($N=2$)	2	0
Jussara sp., Sclerosomatidae ($N=1$)	0	1
Araneae ($N=13$)		
Osoriella rubella†, Anyphaenidae ($N=4$)	1	3
Salticidae† ($N=2$)	1	1
Unidentified ($N=7$)	4	3
Orthoptera ($N=2$)		
Gryllacrididae ($N=2$)	0	2
Hymenoptera ($N=2$)		
Agelaia multipicta†, Vespidae ($N=1$)	0	1
Camponotus aff. *abdominalis*, Formicidae ($N=1$)	0	1
Scolopendromorpha ($N=1$)		
Otostigmus sp.†, Scolopendridae ($N=1$)	1	0
Total	13	107

* Dry-cold season: April–September; Warm-wet season: October–March. $N =$ total number of clutches found in the study area.
† Also an egg predator of the syntopic harvestman *Acutisoma proximum*, in which females care for the offspring (see Buzatto et al. 2007).

different years, the comparison we made allowed us to explore, for the first time, the importance of clutch features and behavioural differences between males and females for their efficiency in egg protection (see Discussion).

We evaluated the effect of parental care, harvestman species, and the interaction of both variables on egg mortality using a generalized linear model approach, which considered the general heterogeneity in predation rates between experimental groups. Again, we used a beta-binomial distribution to address overdispersion of our data ($\varphi \pm SE = 0.666 \pm 0.052$), and then performed an analysis of deviance in which we added sequentially to the null model the predictor variables and their interactions in order to quantify the influence of each parameter. Analysis of deviance is a generalization of analysis of variance (McCullagh & Nelder 1989), used for cases in which the residuals are not normally distributed, such as survival data. When this is the case, sums of squares (as used in ANOVA) are no longer useful to measure the discrepancy between the model and the data. Instead, the appropriate measurement is the model's deviance, defined as two times its negative log likelihood (Bolker 2008).

RESULTS

Sources of Egg Mortality

Predation constitutes the main source of mortality for *Iporangaia* eggs in temporarily unattended clutches. During our inspections, we observed 120 predation events on eggs from 65 clutches, and all of them occurred when guarding males were temporarily absent (Table 1, Fig. 1a–c). The majority of the predation events were observed in the warm and wet season (89.2%), although the number of clutches found during this period corresponded to only 63% of the total ($\chi^2_1 = 29.87$, $P < 0.001$). The main egg predators recorded were conspecific adults ($N = 41$ males, $N = 50$ females) and other harvestmen, which were responsible for

more than 85% of the predation events observed in the field. We never found juveniles of *Iporangaia* cannibalizing eggs and, on only two occasions, we observed guarding males eating a few eggs (one and two eggs, respectively) from their own clutches.

We observed 14 aggressive interactions between *Iporangaia* guarding males and potential egg predators (i.e. other harvestmen, mainly conspecifics, in the vicinity of their clutches). Guarding males repelled the intruders by quickly tapping the body or the legs of the intruders using their second pair of legs ($N = 3$), or attacking them with their spiny pedipalps, apparently attempting to bite any limb of the intruders ($N = 8$). On three occasions, guarding males first tapped the intruders with the second pair of legs and then attacked them with the pedipalps. Regardless of the behaviour shown by guarding males, they always repelled the intruders successfully. After all interactions observed, guarding males returned to their respective clutches and inspected the eggs, touching them with the second pair of legs. Although we never observed a male actively taking over another male's clutch, on two occasions we found males taking care of clutches previously guarded by other males, which probably died since they were no longer recaptured in the study site.

Another important source of egg mortality is fungal attack, and 82 of 378 clutches found between 2003 and 2005 were attacked by fungus (Fig. 1d). The frequency of fungal attack on clutches varied throughout the months, ranging from 0 to 26.2% of all clutches, and could not be explained by the average monthly precipitation (Spearman rank correlation: $r_S = 0.100$, $N = 22$, $P = 0.665$). Considering only the attacked clutches, the median number of infected eggs per clutch was 15 eggs (range 1–131 eggs), and the percentage of infected eggs ranged from 0.4% to 100% of the clutch. Although fungus-infected eggs did not develop into juveniles, guarding males did not eat, clean or remove such eggs from their clutches. Since fungal infection cannot be controlled, infected clutches can be entirely destroyed in a few weeks. Eggs in all stages of embryonic development were attacked by fungus and the mucus
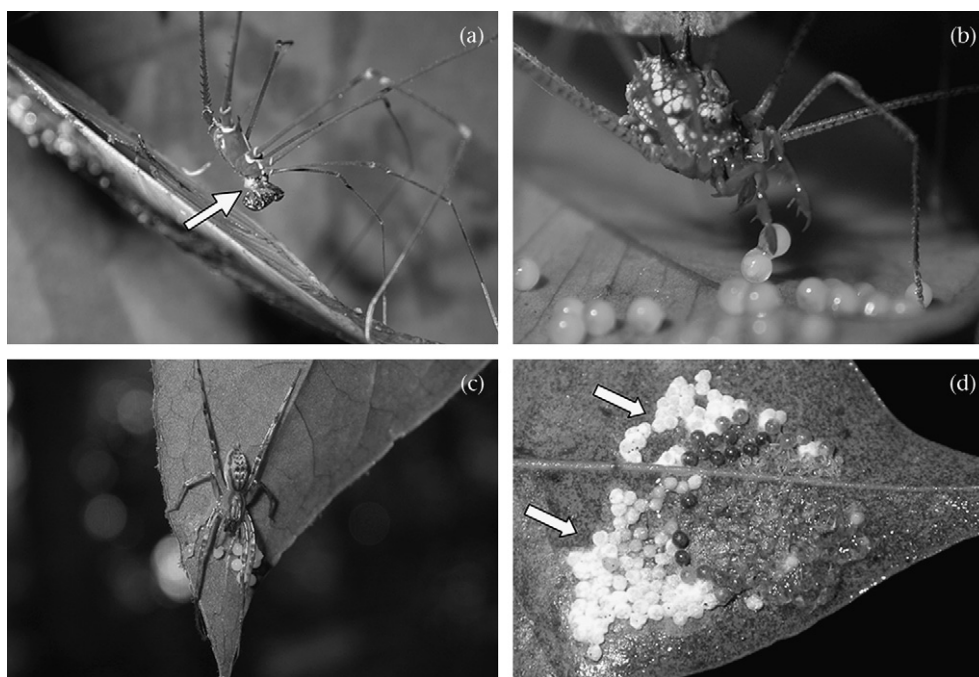

Figure 1. Main sources of egg mortality for the harvestman *Iporangaia pustulosa*: (a) male of the harvestman *Acutisoma proximum* eating an egg (white arrow); (b) *Iporangaia* female cannibalizing an egg; (c) juvenile of the spider *Osoriella rubella* (Anyphaenidae) consuming an egg; and (d) clutch heavily attacked by fungus (white arrows indicate infected eggs). All clutches attacked by egg predators were found unprotected and the guarding males were not found nearby.

coat that surrounds the eggs seems to provide no protection against fungus infection.

Effects of Paternal Care on Egg Survival

The frequency of attacks by egg predators differed between the two experimental groups, being higher in the 'no care' group, in which paternal males were removed ($\chi_1^2 = 4.861$, $P = 0.027$). Almost all clutches (15 of 16) in this group were attacked by egg predators, and six of them completely disappeared during the experiment. In the 'care' group, in which parental males were present, half of the clutches (six of 12) did not suffer any reduction. Only one of the remaining six clutches in this group was entirely consumed by predators and the other five lost only few eggs (1–19 eggs).

There was a strong association between egg loss over time and whether eggs were guarded by males or not ($F_{1,26} = 13.103$, $P = 0.001$; Fig. 2a). Among clutches of the 'care' group, there was no difference between the number of eggs in the first and in the last sampling day ($F_{1,26} = 1.016$, $P = 0.323$; Fig. 2a). On the other hand, the number of eggs in the clutches of the 'no care' group showed a marked decrease throughout the experimental period ($F_{1,26} = 44.801$, $P < 0.001$; Fig. 2a). However, this decrease in the number of eggs among clutches of the 'no care' group was not continuous throughout the experimental period (Fig. 2b). Our field observations indicate that predatory events were episodic and caused by one or a few predators that approached the clutch and consumed many eggs in a short interval between sampling days.
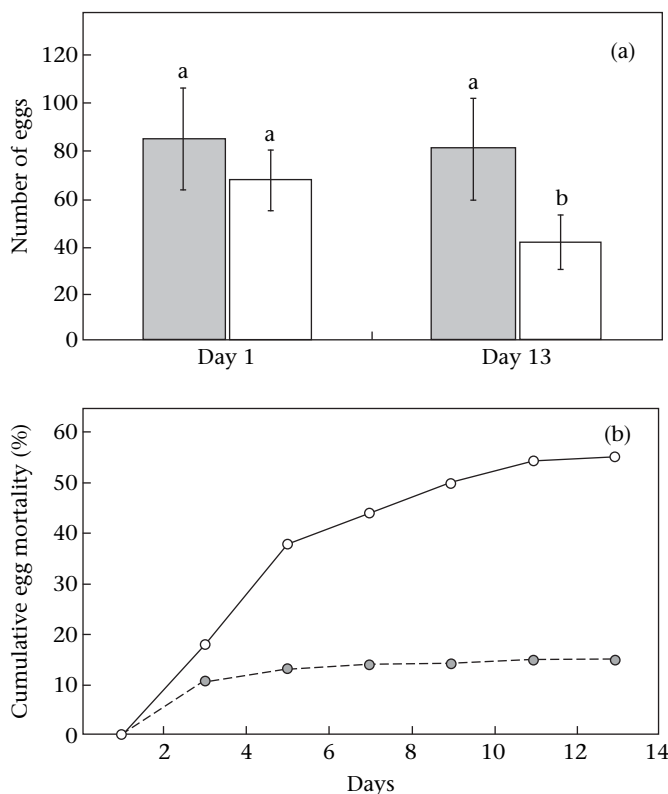
These predatory events occurred both in the beginning and in the final days of the experimental period.

Protective Role of the Mucus Coat

Our laboratory experiment demonstrated that the mucus covering *Iporangaia* clutches is important deterrent against predation by conspecific females ($\chi_1^2 = 4.475$, $P = 0.034$; Fig. 3). Seven clutches (58.3%) in the 'no mucus' group were attacked, and in three of them, all eggs were consumed. In the 'mucus' group, only three clutches were attacked, and in these cases, only two ($N = 2$) or three ($N = 1$) eggs were consumed. Behavioural observations in the laboratory showed that: (1) individuals consumed mucus without preying on the eggs ($N = 5$); (2) individuals tried to remove eggs from clutches of the 'mucus' group, but did not succeed ($N = 2$). We observed similar behaviours in the field, where males and females of *Iporangaia* consumed mucus of unattended clutches ($N > 10$) and were also unable to remove eggs from the mucus coat ($N = 9$).

Efficiency of Paternal versus Maternal Care

Egg mortality caused by predation was higher in clutches without the protection of the parental individual ('no care' group), regardless of the harvestman species (Table 2, Fig. 4). However, there was an interaction between the effects of the experimental group and harvestman species (Table 2, Fig. 4). The mean egg mortality in control clutches of *Iporangaia* did not differ from that for control clutches of *Acutisoma* (Fig. 4). Although clutches of the 'no care' group suffered higher mean egg mortality than the control clutches in both species, this difference was higher in *Acutisoma* than in *Iporangaia* (Fig. 4).

DISCUSSION

Active protection against egg predation is probably the main benefit of parental care in arthropods with maternal care (see examples in Costa 2006). Here we experimentally demonstrated
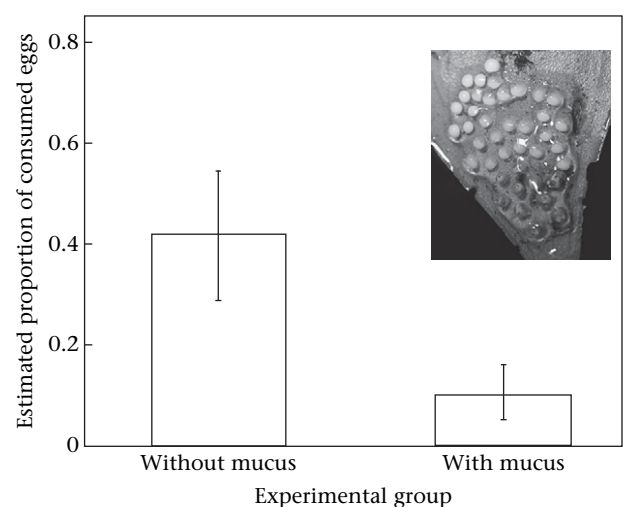
Figure 2. (a) Comparison between the number of eggs of the harvestman *Iporangaia pustulosa* in each experimental group in the first and the last sampling day. Grey bars: 'care' group ($N = 12$), in which guarding males were maintained on their clutches; white bars: 'no care' group ($N = 16$), in which guarding males were removed from their clutches. Different letters indicate significant differences in the number of eggs per clutch ($P < 0.05$). Values are means ± SE. (b) Cumulative mean proportion of *Iporangaia* eggs attacked by predators in each experimental group during the experiment. The dotted line represents the 'care' group and the solid line represents the 'no care' group.

Figure 3. Predation suffered by experimental *Iporangaia* clutches in two experimental groups: eggs without the typical mucus coat (treatment) and eggs with the mucus coat (control). The experiment lasted 4 days and the model predators were conspecific females. Values are means ± SE. The inset shows an *Iporangaia* clutch covered with abundant mucus in the field. Recently laid eggs are white, whereas those close to hatching are dark.

Table 2
Analysis of deviance used to compare the efficiency of parental care against egg predators in two harvestman species: *Iporangaia pustulosa* with exclusive paternal care and *Acutisoma proximum* with maternal care

Model	Deviance	Δ Deviance	df	$P(\chi^2)$
Null	286.1			
Experimental group	244.8	41.30	1	<0.001
Experimental group+ harvestman species	244.8	0.03	1	0.864
Experimental group+harvestman species+Experimental group×harvestman species	240.5	4.24	1	0.039

The null model considered no effect of experimental group (parental individual present versus absent) and harvestman species (*Iporangaia* vs. *Acutisoma*), and no interaction between these two variables.

that exclusive paternal care in the Neotropical harvestman *Iporangaia pustulosa* is also important for egg defence. Almost 38% of the unprotected clutches disappeared entirely during the 12-day experimental period, and the others suffered a mean reduction of approximately 55% in the number of eggs. In another harvestman with exclusive paternal care, *Zygopachylus albomarginis* (Manaosbiidae), male assistance also reduces egg predation (Mora 1990). For both *Iporangaia* and *Zygopachylus*, conspecifics were the main source of egg mortality, causing a great reduction in the number of eggs of unattended clutches. Although there was a high incidence of fungal attack on *Iporangaia* clutches in our study, guarding males seem to be unable to remove fungus from the eggs, as previously recorded for the harvestman *Acutisoma longipes* (Machado & Oliveira 1998). *Zygopachylus* males, on the other hand, are known to

deter fungal attack on eggs (Mora 1990), a unique feature in harvestmen (Machado & Raimundo 2001).

The great majority of predation events occurred in the wet and warm season (see Table 1), which may explain why guarding males are found on their clutches throughout the day during this season, and rarely abandon their eggs (Machado et al. 2004). During the colder months, however, *Iporangaia* males are not found on their clutches during the day (Machado et al. 2004), when the risk of predation is probably reduced. Since the activity of egg predators (mainly conspecific females) is higher at night, when there is a significant increase in air humidity (G. S. Requena, unpublished data), guarding males are found on their clutches only during this period. Remaining close to the eggs during the day would expose guarding males to the stressful climatic conditions of the dry and cold season, and would increase the costs of egg guarding. Moreover, since females are not found walking on the vegetation during the day in the colder months (Machado et al. 2004), there is no opportunity for the guarding males to copulate, which decreases the benefits of egg guarding for them. This seasonal difference in the paternal assistance provides observational evidence that *Iporangaia* males are able to adjust their investment in egg defence according to the costs and benefits they face, as previously recorded for some fish species with exclusive paternal care (e.g. Neff 2003; Manica 2004). Additionally, it suggests that paternal care in this harvestman species is maintained by two selective pressures: natural selection, favouring male decisions that maximize offspring survival, and sexual selection, favouring male decisions that maximize their mating opportunities.

From the females' perspective, paternal care may be favoured by sexual selection because it offers the direct, fitness-enhancing gift of cost-free care of their offspring and the freedom to forage for additional food, which may enhance their lifetime fecundity (Maynard Smith 1982). To select males that are willing to provide care, females should copulate preferentially with guarding males (i.e. with individuals that already have a clutch; Tallamy 2000, 2001). At least for some species with exclusive paternal care, females do prefer to copulate with guarding males (e.g. Pampoulie et al. 2004; Thomas & Manica 2005), and the same is true for *Iporangaia* (G. S. Requena, unpublished data). Besides selecting guarding males that will probably protect the eggs, *Iporangaia* females may further enhance the survival of these eggs by covering them with an abundant mucus coat. In this study, we demonstrated for the first time that this mucus coat has an important protective role. Therefore, the mucus that covers the clutches of all representatives of the subfamily Progonyleptoidellinae with exclusive paternal care (see Machado et al. 2004) may be viewed as a female investment that confers additional protection to the eggs against predation (mainly in the wet and warm season), and perhaps against dehydration (especially during the dry and cold season). Moreover, since filial cannibalism is a common strategy used by guarding males to offset foraging costs of paternal care (e.g. Manica 2002; Thomas & Manica 2003), the mucus coat may also be, at least in part, a maternal investment against paternal predation. Curiously, in other harvestman species with paternal care, females seem to provide alternative forms of egg protection as well, such as the attachment of debris on egg surface, in a process that may last up to 48 h (e.g. Machado 2007; Nazareth & Machado 2009).

The comparison of the benefits in terms of egg survival provided by the uniparental care of *Iporangaia* males and *Acutisoma* females yielded two unexpected results. First, we hypothesized that the mortality of eggs of attended clutches would be higher in *Iporangaia*, because guarding males of this species frequently abandon their clutches, whereas guarding *Acutisoma* females remain close to their eggs most of the time (Machado et al. 2004). Moreover, given that females have sperm receptacles and copulate with several different individuals, males probably have less certainty of their
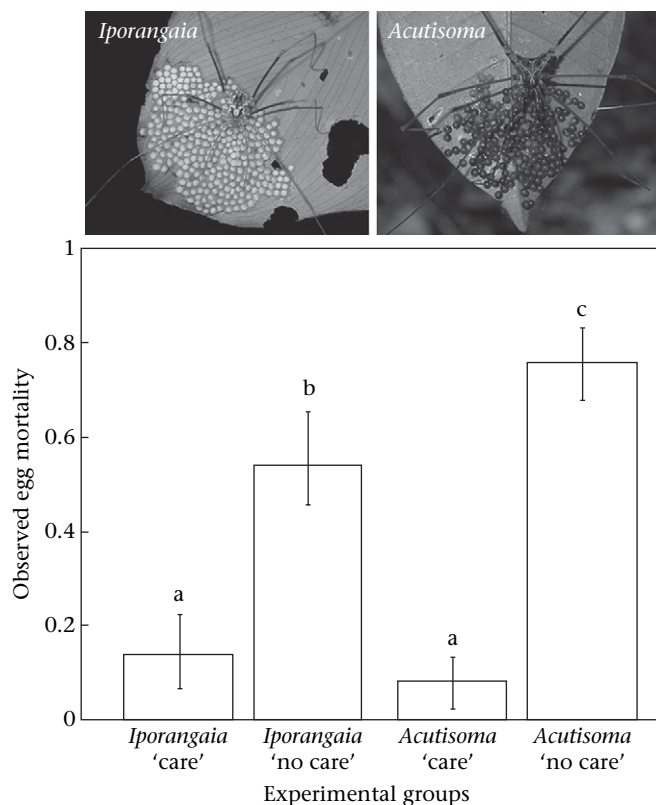

Figure 4. Egg predation in clutches with ('care' group) and without ('no care' group) the parental individual of two harvestman species: *Acutisoma proximum*, with maternal care, and *Iporangaia pustulosa*, with paternal care. Values are means ± SE.

genetic relatedness with the offspring (Macías-Ordóñez et al., in press), and should be reluctant to risk their lives actively defending the eggs. However, egg protection provided by *Iporangaia* males in the 'care' group was as efficient as that provided by *Acutisoma* females. Even though *Iporangaia* males (body size = 5.7 ± 0.2 mm) are smaller than *Acutisoma* females (body size = 7.5 ± 0.3 mm), they always succeeded in repelling potential egg predators, some of which were almost twice as large as *Iporangaia* males.

The second unexpected result was that unattended *Acutisoma* clutches ('no care' group) suffered more egg predation than unattended *Iporangaia* clutches. It is likely that differences in the clutch features between the two species account for the patterns of egg mortality in both experimental groups. When an *Iporangaia* male temporarily abandoned his clutch in the 'care' group or even when he was experimentally removed in the 'no care' group, the unattended eggs were still protected by the thick mucus coat, which prevented or decreased predation rate. Since all predators that consumed eggs also consumed mucus, and many individuals consumed only mucus from the clutches, it is unlikely that this mucus contains unpalatable substances. We think that the mucus coat is simply sticky and mechanically decreases a predator's access to the eggs. *Acutisoma* eggs, on the other hand, are not covered by a mucus coat (Machado 2002; Gnaspini 2007) and are probably more susceptible to predation. In fact, unattended clutches of some *Acutisoma* species may be entirely consumed by predators in a few hours (Machado & Oliveira 1998; Buzzatto et al. 2007).

Comparisons between the efficiency of male and female care in closely related syntopic species are scarce in the literature, probably because of the rarity of this phenomenon in nature. Manica & Johnstone (2004), for instance, compared egg mortality in two assassin bug species of the genus *Rhinocoris*: *R. tristis*, with exclusive paternal care, and *R. carmelita*, with exclusive maternal care. Even though these two bug species do not use the same host plants, they are syntopic and share similar morphology. The presence of the parental individual reduces egg mortality in 30.4% of *R. tristis* clutches and in 34.4% of *R. carmelita* clutches (see Table 2 in Manica & Johnstone 2004), which means that the efficiency of male and female care is nearly the same, as occurs with *Iporangaia* and *Acutisoma*. If males' attractiveness depends on the number of eggs they have in their clutches, even if they have not sired these eggs (Tallamy 2000, 2001), they should care for the offspring as efficiently as females. Additionally, the egg mortality of unattended *Rhinocoris* eggs is higher in the species with maternal care (23.5%) than in the species with paternal care (8.9%) (see Table 2 in Manica & Johnstone 2004). These results are remarkably similar to those obtained here, and we predict that *R. tristis* females also provide an additional form of protection to the eggs that they leave under the guard of males, such as a thick eggshell or some kind of chemical defence. Future comparisons between the efficiency of male and female care in other groups, including fishes and frogs, are needed in order to test the generality of the patterns described here.

In conclusion, paternal care has a crucial protective role preventing egg predation in the harvestman *Iporangaia pustulosa*. Although guarding males confer efficient protection to the offspring, females also contribute to protection of offspring by providing a deterrent mucus coat that covers the clutch. This additional protection is especially important when males temporarily abandon their clutches to forage or take shelter during stressful climatic conditions. Since the relative parental investment between sexes is frequently the subject of sexual conflict (Trivers 1972; Barta et al. 2002), we expect that the amount of maternal investment in egg protection should vary in time and space according to the time that guarding males spend close to their clutches. This is an interesting hypothesis, and both *I. pustulosa* and *R. tristis* are good model organisms with which to test it.

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