Devoted fathers or selfish lovers? Conflict between mating effort and parental care in a harem-defending arachnid

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Abstract

When there is a temporal trade-off between mating effort and parental care, theoretical models predict that intense sexual selection on males leads to reduced paternal care. Thus, high-quality males should invest more in mating effort because they have higher chances of acquiring mates, whereas low-quality males should bias their investment towards parental care. Once paternal care has evolved, offspring value should also influence males' decisions to invest in offspring attendance. Here, we performed a manipulation under field conditions to investigate the factors that influence male allocation in either mating effort or parental care. We predicted that facultative paternal care in the harem-holding harvestman *Serracutisoma proximum* would be negatively influenced by male attractiveness and positively influenced by offspring value. We found that attractive males were less likely to engage in egg attendance and that the higher the perceived paternity, the higher the caring frequency. Finally, egg mortality was not related to caring frequency by males, but predation pressure was much lower than that recorded in previous studies with the same population. Thus, the benefits of facultative male care may be conditional to temporal variation in the intensity of egg predation. In conclusion, males adjust their investment in either territory defence or egg attendance according to their recent mating history and perceived paternity. Our findings suggest that exclusive paternal care can evolve from facultative paternal care only if the trade-off between mating effort and parental care is circumvented.

Introduction

Since the seminal paper by Trivers (1972), parental investment, defined as any investment by the parent in an individual offspring that increases the offspring's chance of surviving and reproducing at the cost of the parent's ability to invest in other offspring, has been widely used as the theoretical basis for understanding mating and caring patterns (Klug *et al.*, 2012). According to classic parental investment theory, anisogamy promotes marked sexual differences in parental investment to the offspring, leading to competition among individuals of the sex that invest less (usually males)

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for access to individuals of the sex that invest more (usually females). Consequently, male–male competition for access to potential mates selects against paternal care because time, resources and energy allocated to parental activities will not be available to allocation in mating effort (Magrath & Komdeur, 2003). The trade-off between parental and mating effort has been later used in the models proposed by Maynard Smith (1977) and Fromhage *et al.* (2007), which predict that the probability of a male achieving further copulations has a negative effect on the evolution of paternal care.

More recently, the notion that anisogamy generates a bias towards female care when both sexes have identical future reproductive prospects has been challenged. Contrary to previous work, current models predict that male parental care evolved in a scenario in which gamete size is the sole difference between males and females (reviewed in Stiver & Alonzo, 2009). These

models suggest that anisogamy influences parental care indirectly, by providing the conditions for sexual selection on males (Queller, 1997; Kokko & Jennions, 2008). Intense sexual selection on males leads to reduced paternal care because high-quality males, such as those with higher energetic reserves or bearing more elaborated ornaments and weapons, should invest more in mating effort once they have higher chances of acquiring multiple mates. Because high-quality males are those with the highest reproductive success, sexual selection would lead to an evolutionary decrease in male parental care. Low-quality males, in turn, should invest only what is necessary to attract a mate and, once they acquire a mate, bias all further investment towards parental care (Queller, 1997; Kokko & Jennions, 2008). A temporal trade-off between mating effort and parental care is still present in some of these recent models, implying that individuals of both sexes cannot invest simultaneously on both mating effort and parental care (Stiver & Alonzo, 2009).

However, paternal care does not necessarily conflict with male mating effort. For instance, empirical studies with species exhibiting exclusive paternal care have shown that females usually select males that are already caring for offspring, or evaluate males based on traits related to caring ability. Consequently, successful males are expected to accumulate eggs from multiple females (Kvarnemo, 2006; Requena *et al.*, 2013; but see Tazzyman *et al.*, 2012). Trade-offs between mating effort and parental care arise only under particular circumstances, such as (1) when behaviours related to mating and caring activities cannot be performed at the same time; (2) when males have to invest limited resources either to attract and compete for mates or to care for the offspring; and (3) when traits involved in attracting and competing for access to mates are detrimental to offspring care (Stiver & Alonzo, 2009). Temporal trade-offs, in particular, have been more intensively investigated among socially monogamous birds, but results do not show consistent support for a conflict between mating effort and paternal care (see references in Stiver & Alonzo, 2009). On the other hand, in harem-defending species, any time invested by the male in offspring care may improve the risk of harem invasion and reduce mating opportunities with approaching females. Although this type of temporal trade-off has already been demonstrated for a few bird species (e.g. Hoi-Leitner *et al.*, 1993), empirical evidence for other animal groups is scarce, which prevents generalizations.

Once parental care has evolved, factors determining the expected fitness of the current offspring, that is the offspring value, should also influence parents' decisions to invest or not in risky or energetically costly activities related to offspring attendance and provisioning (Clutton-Brock, 1991). Egg number usually shows great interindividual variation, and parents of iteroparous species should invest more in larger rather than smaller clutches because there is a higher probability that more offspring will reach independence and reproduce (e.g. Coleman *et al.*, 1985; Koskela *et al.*, 2000; Rytkönen, 2002). Moreover, parents should invest more in older rather than younger offspring because both the probability of reaching maturity and the parental investment necessary to raise a new offspring to the equivalent developmental stage increase with offspring age (e.g. Thünken *et al.*, 2010). In fact, waterbug males that carry eggs attached to their dorsum are more likely to discard smaller broods with recently laid eggs than larger broods with eggs close to hatch (Kight & Kruse, 1992). Finally, from a male's perspective, paternity certainty is a crucial component of offspring value. Considering that sperm competition promotes paternity uncertainty, a male should be selected to adjust his investment in parental care in relation to how certain he is of being the father of the offspring (reviewed in Sheldon, 2002 and Alonzo, 2010).

Here, we investigate how temporal trade-offs between mating effort and parental care influence male behaviour in a harem-defending invertebrate, the harvestman *Serracutisoma proximum* (Arachnida: Opiliones). The mating system of this species is a resource defence polygyny, in which large territorial males (majors) defend the host plants preferred by females as oviposition sites. After copulating with a territorial male, females lay eggs inside his territory and remain caring for their clutches until nymphal dispersal (Buzatto & Machado, 2008; Fig. 1a). A successful territorial male may have as much as 10 egg-tending females in his harem (Munguía-Steyer *et al.*, 2012). Harems are invaded by small sneaker males (minors) that mate furtively with egg-tending females to fertilize some eggs retained in their reproductive tract after the first oviposition bout with the territorial male (Buzatto *et al.*, 2011). Territorial males may exert facultative paternal care under natural situations, when egg-tending females desert or die, and also when egg-tending females are experimentally removed from their clutches (Buzatto & Machado, 2009; Fig. 1b). Therefore, *S. proximum* is an ideal study system because territorial males cannot acquire further copulations while caring for unattended clutches, contrary to many species of fish and arthropods with exclusive paternal care (see Requena *et al.*, 2013). Moreover, the presence of sneaker males creates paternity uncertainty, which may influence parental decisions of territorial males.

Based on current theoretical models and a solid background on the reproductive biology of *S. proximum* (see Study species below), we predict that facultative paternal care will be negatively influenced by male attractiveness and positively influenced by offspring value, namely egg number, clutch age and perceived paternity. We also predict that egg mortality will be inversely related to the frequency of facultative paternal care because male presence may deter the attack of predators, like egg-tending females do (Buzatto *et al.*, 2007).

Fig. 1 (a) Female and (b) harem-owning male of the harvestman *Serracutisoma proximum* attending eggs in the field (both individuals are marked with enamel ink on their hind legs and carapace). Note that in both cases, the individuals are < 15 cm from the clutches, with the pedipalps and second pair of legs extended frontward in a typical caring position.
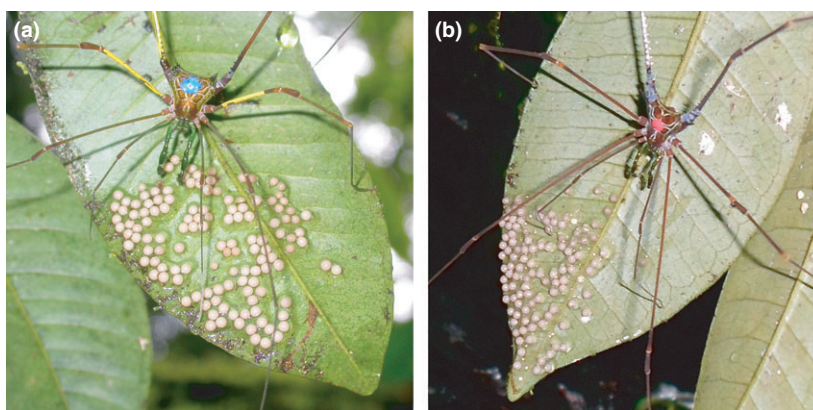
Materials and methods

Study species

The reproductive biology of *S. proximum* has been intensively studied in the field, and here, we provide a brief summary of the main findings. The breeding season usually covers most of the rainy season, starting in the end of September and lasting until the beginning of April (Buzatto & Machado, 2008). Two male morphs are recognized on the basis of the relative length of the second pair of legs, which shows a clearly bimodal distribution (Buzatto *et al.*, 2011). Major males have large body size (6.33–8.89 mm), highly developed weaponry in the form of acuminate spines on their fourth pair of legs and a long second pair of legs, which is 15–20 times longer than male body length. Majors use this long and sexually dimorphic second pair of legs as weapons during contests for territory possession. Minor males, in turn, have small body size (6.11–8.54 mm), poorly developed weaponry on the fourth pair of legs and a short second pair of legs, which is 12–15 times longer than male body length (Buzatto *et al.*, 2011). The relative frequency of minor males in natural populations ranges from 6% to 37%, and their mating tactic is mostly based on harem invasion and sneak copulation with egg-tending females (Munguía-Steyer *et al.*, 2012).

In the beginning of the breeding season, major males establish territories on patches of vegetation at river margins containing the plants used by females as oviposition sites. Territories are visited by females, which copulate with the territorial male, lay their eggs on leaves, and remain caring for the offspring for 25–35 days until the dispersion of the first-instar nymphs (Buzatto & Machado, 2008). Female protection improves offspring survival because unprotected eggs are attacked and consumed by predators, including conspecifics and other arthropods (Buzatto *et al.*, 2007). Under natural field conditions, females live no more than 2 years as adults, and 82% of them lay only one clutch during their lifetime. Females that lay two clutches during their lifetime usually produce one clutch per breeding season, and in both oviposition events, they attend their eggs until nymphal dispersal (Buzatto *et al.*, 2007). Permanent egg desertion by females is very rare, but clutches may be abandoned when females die as a consequence of phorid parasitoid attack (G. Machado, unpublished data).

Egg-tending females inside the territories form harems, which are frequently invaded by minor males seeking sneak copulations. Because approximately 70% of sneaker invasions result in copulation, many clutches probably have mixed paternity (Buzatto *et al.*, 2011; Muniz & Machado, 2015). The degree of female promiscuity varies according to harem size, because the more females in the harem, the less effective is the defence of each egg-tending female by the harem-owning male (Buzatto *et al.*, 2011). Moreover, larger harems are more likely to be invaded by sneaker males (Munguía-Steyer *et al.*, 2012). Finally, given that most of the females in the population lay only one clutch during their lifetime, sperm competition imposed on territorial males is probably restricted to a single set of unfertilized eggs present in the reproductive tract of egg-tending females.

Study site

We conducted the study at Intervales State Park (24°14′S, 48°04′W; 800 m a.s.l.), a large and well-preserved Atlantic Forest fragment in the state of São Paulo, south-eastern Brazil. The locality has high precipitation (2000–3000 mm year^{-1}) and mean annual temperature ranging from 17 to 20 °C. We conducted behavioural observations and the experimental manipulation described below in a 250-m-long transect along both margins of a river following the Caçadinha Track. More details on this area are presented in Requena *et al.* (2012).

Behavioural observations and experimental manipulation

We conducted the study during February 2013, in the peak of the reproductive season (Buzatto & Machado, 2008). We divided data collection into three phases: (1) search for harems in the transect, (2) focal behavioural observations in the harems and (3) experimental removal of egg-tending females. Phase 1 lasted 2 days, during which we searched for egg-tending females on the vegetation flanking both margins of the river along the transect. We individually marked with enamel ink all females found with clutches and all males observed near (up to 1 m) those females. Previous studies with *S. proximum* suggest that the handling and marking procedures do not affect the reproductive behaviour of males and females (e.g. Buzatto *et al.*, 2007, 2011). We also measured all males for dorsal scute (carapace) length and second leg length using callipers (precision 0.01 mm) and a ruler (precision 1 mm), respectively. Based on these measures, we characterized male morph (major or minor) using the same statistical protocol described in Buzatto *et al.* (2011).

In the third day of fieldwork, we started focal behavioural observations in all harems marked in phase 1. This second phase lasted 10 consecutive days, during which we performed daily inspections at regular 2-h intervals (between 10:00 h and 00:00 h) in each harem. During each inspection, we measured the distance (to the nearest 5 cm) between every female inside the harem and the closest major male. If more than one major male was inside the same harem, we measured the distance from each female to both males. In these cases, we defined as harem-owner the major male that we observed more frequently inside the harem during the 10-day period of focal observations. We considered all other males as invaders regardless of their morph because major males may occasionally invade harems to sneak copulations (Muniz *et al.*, 2015). During phase 2, we also counted the number of females that arrived and laid eggs in each harem (hereafter called *newcomer females*).

At the beginning of phase 3, we experimentally removed one egg-tending female from each harem; from now on, we will refer to the clutches whose females were removed as *experimental clutches*. In harems containing more than one female, we selected which female would be removed based on clutch age to distribute all experimental clutches homogeneously in six age classes. Considering that harvestman eggs change in size and colour over the course of embryonic development, these classes can be reliably used as a proxy of clutch age. Following Requena *et al.* (2012), class 1 is composed of recently laid eggs, which are small and cream coloured, and class 6 is composed of eggs about to hatch, which are large (due to water absorption) and black coloured. Classes 2–5 are composed of eggs in intermediate size and colour that can be easily recognized in the field.

After female removal, we carried out inspections to each experimental clutch at regular 1.5-h intervals. In each inspection, we recorded if the harem-owning male was either prostrated on the experimental clutch in a typical resting position or up to 15 cm away from the clutch (Fig. 1). If a harem-owning male was on the experimental clutch consuming eggs or further than 15 cm from the clutch, we did not consider he was caring for the eggs. We also recorded (1) all behavioural interactions between harem-owning males and any organism that approached the experimental clutches, and (2) all predation events on eggs of the experimental clutches. Because of heavy summer rains, seven inspections could not be performed, so that the total number of inspections during phase 3 was 38. Finally, we also photographed and counted the number of eggs in each experimental clutch on three moments: immediately after female removal (day 0), 2 days later (day 2) and 4 days later (day 4), always between 16:00 and 17:00 h. This 4-day period corresponds to nearly 20% of the total duration of egg development in *S. proximum*. Considering that predation pressure on unprotected eggs may be very intense and entire clutches may be consumed in a few hours or days (Buzatto *et al.*, 2007), we used egg survival in phase 3 as a proxy of the efficiency of facultative paternal care in terms of egg protection.

Facultative male care, male attractiveness and offspring value

We quantified facultative male care as the proportion of inspections during phase 3 in which a harem-owning male was observed caring for the experimental clutch. We used the number of newcomer females in each harem during phase 2 as a proxy of the harem-owning male attractiveness. This proxy provides a general measure of attractiveness because it is the result of the attractiveness of both the territory and the male himself, as well the local availability of receptive (ovigerous) females around the harems. Most importantly, the number of newcomer females provides a cue that can be used by harem-owning males to access their own probability of acquiring mates.

To estimate offspring value, we used two descriptors of the clutch and a proxy of perceived paternity. The clutch variables were number of eggs and age (ordinal categories from 1 to 6), both quantified at the time of female removal. As a proxy of perceived paternity, we used the proportion of inspections during phase 2 in which a harem-owning male was recorded within 15 cm of the female we later removed from his harem. Previous studies with *S. proximum* have shown that the presence of a harem-owning male near an egg-tending female is a form of mate guarding that prevents her

from mating with invader males, thus increasing the probability that the harem-owning male will sire most of the eggs in the clutch (Buzatto *et al.*, 2011; Muniz *et al.*, 2015). Although the presence of sneaker males in the harem is also a good predictor of the risk of sperm competition, harvestmen are unable to form images and rely mostly on close-range chemical and tactile stimuli to detect conspecifics (Willemart *et al.*, 2009). Thus, we argue that the frequency of mate guarding is a better descriptor of paternity certainty because it provides information that can be perceived by harem-owning males and can influence their decision to care for unprotected eggs. Moreover, as stated before, sperm competition imposed by sneakers on territorial males is probably restricted to a single set of unfertilized eggs in the reproductive tract egg-tending females. Thus, the higher the frequency of mate guarding by a harem-owning male, the lower the risk and the intensity of sperm competition (Muniz *et al.*, 2015).

Data analysis

To test our first prediction, which posits that the frequency of facultative paternal care should be negatively influenced by male attractiveness and positively influenced by offspring value, we used a generalized linear model. Because we predict that multiple variables may influence the frequency of paternal care, we adopted a model selection approach. The response variable (with binomial distribution) was the number of inspections in which we observed the harem-owning males caring for the offspring. The predictor variables were the number of eggs in the experimental clutches, clutch age, number of newcomer females during phase 2 and frequency of mate guarding in phase 2 (i.e. perceived paternity). We built a saturated model with all predictor variables and competing models with all possible combinations of the variables, including a null model. We did not include interaction terms because we have no biological hypothesis to support models with interactions. We considered the model with the lowest AICc (Akaike information criterion corrected for small samples) as the most plausible and considered as equally plausible all models that differed from the best model by less than two units (Burnham & Anderson, 2002). To compare the effects of each variable and facilitate model interpretation, we centred and standardized all predictor variables prior to model fitting (Schielzeth, 2010).

To test our second prediction, which posits that egg mortality should be inversely related to the frequency of facultative paternal care, we used a generalized linear mixed model. The response variable (with binomial distribution) was the number of surviving eggs per clutch and the predictor variables were the frequency of paternal care and the number of egg-tending females per harem. We included the number of egg-tending females per harem as a predictor in the model because

conspecific females, especially those inside the same harem, are one of the most important sources of egg mortality in *S. proximum* and other harem-defending species (Crespi, 1990; Machado & Oliveira, 1998; Buzatto *et al.*, 2007). Given that we counted the number of eggs in each experimental clutch in three different moments (days 0, 2 and 4), we included clutch identity as a random factor in the analysis (Gelman & Hill, 2006). Again, we centred and standardized all predictor variables prior to the analysis.

We performed all analyses using the software R version 3.2.2 (R Core Team, 2015). Specifically, we used the package *lme4* (Bates *et al.*, 2015) to perform mixed model fitting and the package *MuMIn* (Barton, 2015) to perform model comparison.

Results

During phase 1, we found 35 harems containing from one to five egg-tending females. For all these harems, we were able to unequivocally assign a harem-owning major male. In phase 2, the frequency of inspections in which we recorded harem-owning males inside their respective harems ranged from 1.4% to 100% (median = 40.7%). The number of newcomer females in each harem during phase 2 ranged from zero to three. During this phase, the percentage of inspections in which harem-owning males were mate guarding the females that would be later removed ranged from zero to 100% (median = 2.9%). From the 23 minor males marked during phase 1, 17 were observed invading harems during phase 2. Five of them sneaked copulations with egg-tending females whereas they were not mate-guarded by the harem-owning males.

Of the 35 harem-owning males included in our manipulation, 24 performed facultative paternal care at least once in phase 3. Among these males, the number of inspections in which we observed paternal care ranged from 1 to 26 of a total of 38 inspections (median = 7 or 18.4%). In 18 inspections, we observed harem-owning males cannibalizing eggs from their clutches. The consumed eggs did not show any evidence of fungi infection, which discards the possibility that harem-owning males were selectively removing infected eggs from the clutches as a form of parental care. In most inspections in which we observed harem-owning males close to the experimental clutches, they were not consuming eggs ($n = 220$ inspections). In these cases, they were either prostrated on the clutch ($n = 166$ inspections) or stood on their legs with the pedipalps extended frontward ($n = 54$ inspections), in a posture similar to the egg-caring posture exhibited by females (Fig. 1).

In phase 3, median egg survival of the experimental clutches was 84% (range = 24–100%). The main egg predators were conspecifics, including females from the same harem ($n = 5$ observations), vagrant females

Table 1 Summary of the models built to investigate the factors influencing the frequency of facultative male care in the harvestman *Serracutisoma proximum*.

Competing models	Explanatory variable coefficients					d.f.	AICc	ΔAICc	*w*
	(Intercept)	FA	MG	NE	CA				
FA + MG + NE	−1.73	−0.46	0.52	0.14	–	4	412.41	0	0.4
FA + MG	−1.72	−0.43	0.49	–	–	3	412.53	0.12	0.38
FA + MG + CA	−1.72	−0.42	0.5	–	0.03	4	414.98	2.57	0.11
FA + MG + NE + CA	−1.73	−0.44	0.53	0.14	0.03	5	415.04	2.63	0.11
MG + CA	−1.68	–	0.49	–	0.2	3	428.87	16.46	< 0.01
MG + NE + CA	−1.68	–	0.51	0.08	0.21	4	430.44	18.04	< 0.01
MG	−1.67	–	0.41	–	–	2	431.99	19.58	< 0.01
MG + NE	−1.67	–	0.42	0.07	–	3	433.62	21.21	< 0.01
FA + CA	−1.65	−0.37	–	–	−0.24	3	462.05	49.64	< 0.01
FA + NE + CA	−1.65	−0.37	–	< 0.01	−0.24	4	464.61	52.2	< 0.01
FA	−1.64	−0.24	–	–	–	2	467.21	54.8	< 0.01
FA + NE	−1.64	−0.24	–	−0.03	–	3	469.48	57.08	< 0.01
Null model	−1.62	–	–	–	–	1	473.68	61.28	< 0.01
CA	−1.62	–	–	–	−0.06	2	475.2	62.8	< 0.01
NE	−1.62	–	–	−0.05	–	2	475.46	63.05	< 0.01
NE + CA	−1.62	–	–	−0.05	−0.06	3	477.2	64.79	< 0.01

Predictor variables are coded as follows: FA, female arrival rate in the harem; CA, clutch age; NE, number of eggs in the clutch; MG, frequency of mate guarding before female removal. d.f., degrees of freedom; AICc, Akaike information criterion corrected for small samples; ΔAICc, difference in AICc between each model and the most plausible one; *w*, Akaike weight.

($n = 6$ observations), minor males ($n = 10$ observations) and major males from nearby territories ($n = 10$ observations). Other egg predators included the harvestman *Serracutisoma pseudovarium* ($n = 1$ observation) and an unidentified orthopteran ($n = 1$ observation). We observed harem-owning males aggressively repelling other males while caring for the eggs ($n = 3$). However, harem-owning males allowed the approach of conspecific females to the experimental clutches while caring ($n = 11$). Moreover, these males allowed both females from their harems ($n = 5$ observations) and newcomer females ($n = 3$ observations) to cannibalize eggs of the experimental clutches. In two cases, the harem-owning males copulated with the newcomer females and mate-guarded them while females were consuming eggs.

The two most plausible models to explain the frequency of facultative paternal care in phase 3 included as predictor variables the number of newcomer females, number of eggs per clutch and frequency of mate guarding in phase 2 (Table 1). The third most plausible model (ΔAICc = 2.57) also included clutch age (Table 1). All models with an Akaike weight above 0.01 contained both the number of newcomer females and the frequency of mate guarding as predictor variables (Table 1). The number of newcomer females had a negative relationship with the frequency of facultative paternal care, whereas the frequency of mate guarding in phase 2 had a positive relationship (Table 1; Fig. 2). The number of eggs had a weak positive effect on the frequency of facultative paternal care, and clutch age had an even weaker positive effect in the best ranking

models (Table 1). Egg survival was not affected by the frequency of facultative paternal care, but it was negatively correlated with the number of females in the harem (Table 2).

Discussion

We performed a manipulation under field conditions to investigate the factors that influence male allocation in either mating effort or parental care by males of the harem-holding harvestman *S. proximum*. We predicted that facultative parental care would be negatively influenced by male attractiveness and positively influenced by offspring value. Our findings show that attractive males were indeed less likely to engage in facultative paternal care. The two most plausible models also included number of eggs in the clutch and perceived paternity as important predictors of the frequency of facultative paternal care. As would be expected by theory, males with higher perceived paternity performed facultative care more frequently than males with lower perceived paternity. Egg number and clutch age were included in the most plausible models, but with relatively weak positive effects when compared with other variables. Finally, we rejected the prediction that egg mortality would be inversely related to the frequency of facultative paternal care. In what follows, we integrate these results to understand how trade-offs between mating effort and parental care may influence male reproductive success in harem-holding species. We also discuss how our findings may
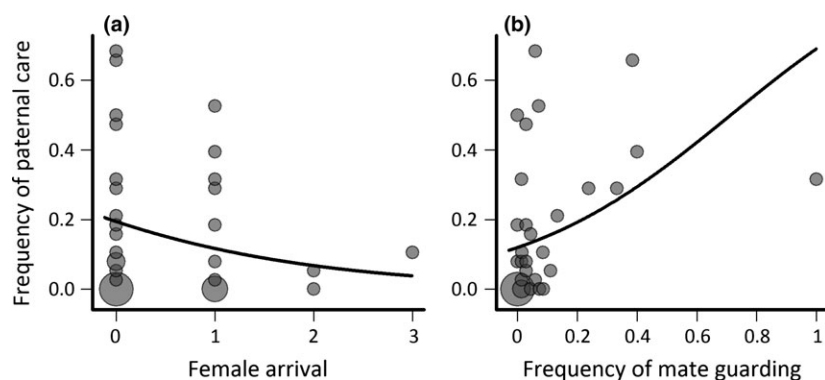
Fig. 2 Factors influencing the frequency of facultative male care in the harvestman *Serracutisoma proximum*. (a) Attractiveness of harem-owning males, estimated as the rate of female arrival in their harems over a period of 10 days before female removal. (b) Perceived paternity, estimated as the proportion of inspections in which the harem-owning male was recorded mate guarding the female we later removed from his harem (see text for details on the methods). In both graphics, the frequency of facultative male care was estimated as the proportion of inspections in which the harem-owning male was close (< 15 cm) to the experimental clutches, without consuming eggs. In both graphics, the area of the circles is proportional to the number of observations, and the black lines represent the prediction of the most plausible model.

shed light on the evolution of exclusive paternal care in arthropods.

In many fish and arthropod species, males with exclusive parental care provide signals of their quality as offspring defenders, so that females usually prefer caring over noncaring males (e.g. Hoelzer, 1989; Jamieson, 1995; Forsgren *et al.*, 1996; Gilbert *et al.*, 2010; Nazareth & Machado, 2010; Requena & Machado, 2015). In these species, there is no temporal trade-off between mating effort and parental care because these activities are synergistic (Stiver & Alonzo, 2009). In harem-holding species, however, even males with high energetic reserves are unable to invest simultaneously in mating effort and parental care because they conflict temporally. In *S. proximum*, successful territorial males spend 58–95% of their time patrolling the territory and the egg-tending females inside it (Buzatto & Machado, 2008). If a harem-owning male invests in egg attendance, he is unable to defend his territory against the invasion of other males and may also decrease the chance of copulation with newcomer females. When there is a trade-off between mating effort and parental care, unattractive males should invest in offspring care, whereas attractive males should invest in female attraction and contests with other males (Kokko & Jennions, 2008). The negative relationship between male attractiveness and frequency of facultative male care reported here supports this hypothesis in a harem-defending arachnid. Although unprotected eggs may be promptly attacked and consumed by predators (Buzatto *et al.*, 2007), attractive males are likely to achieve higher reproductive success investing in territory defence and female patrol to prevent invasions and sneak copulations, as well as to increase the chances of copulating with newcomer females.

Table 2 Summary of generalized linear mixed model of egg survival. The predictive variables are the proportion of inspections in which the harem-owning male was observed performing parental care per 48-h interval and the number of females in the harem. Coefficients were standardized to allow comparison. SE: standard error; d.f. = degree of freedom; number of observations: 60 on 33 clutches (d.f. of the model = 56).

	Coefficient	SE	d.f.	*z*-Value	*P*-value
Intercept	4.73	0.49	1	9.63	< 0.01
Frequency of facultative male care	0.06	0.09	1	0.66	0.51
Number of females in the harem	−0.98	0.46	1	−2.12	0.03

The hypothesis that males adjust the investment in parental care according to their own attractiveness has been tested in many species with exclusive paternal care or biparental care (e.g. Smith, 1995; Duckworth *et al.*, 2003; DeMory *et al.*, 2010). The great majority of these studies have been conducted with vertebrates, mainly fish and birds (reviewed in Stiver & Alonzo, 2009). However, theory should apply to any animal group in which males can perform parental activities, including cases of flexible compensation of parental care – that is when individuals of the noncaring sex assume parental activities if individuals of the caring sex die or desert the offspring. Although relatively rare in nature, flexible compensation of parental care has already been described for several species of amphibians (e.g. Bourne, 1998; Ringler *et al.*, 2015) and arthropods, including *S. proximum* (e.g. Machado & Oliveira, 1998; Willemart & Gnaspini, 2004; Beal & Tallamy, 2006; Buzatto & Machado, 2009). The fact that males of this harvestman species defend a territory that is also an

oviposition site may put them in close proximity to the clutches and improve the chances that they will attend unprotected eggs for at least some time. Additionally, males periodically patrol each egg-tending female inside their harems, so that they can promptly detect whether some of the clutches are unattended (Buzatto & Machado, 2008). In this study, we showed that a male's decision to exhibit facultative paternal care depends mostly on his recent mating rate, which seems to be used as a reliable cue to access his own attractiveness and modulate how much time he will invest in off-spring care.

Paternity certainty is a major determinant of offspring value for males, so that males with low perceived paternity should reduce investment in parental care (Sheldon, 2002; Alonzo, 2010). Mate guarding is a behaviour that may benefit males by reducing the chances of the female accepting copulation with rival males, thus increasing paternity certainty (Alcock, 1994). In *S. proximum*, mate guarding is more intense in the 2–4 days after oviposition, and this behaviour is highly effective in preventing sneak copulations (Buzatto & Machado, 2008). Because females may retain some unfertilized eggs in their reproductive tract after the first oviposition bout, the longer the mate guarding period, the higher the chances of remating and the lower the number of eggs that can be sired by sneakers (Machado *et al.*, 2015). Here, we showed that the frequency of paternal care was positively related to the frequency of mate guarding. This finding suggests that harem-owning males are able to individually recognize females inside their harems (or simply the location of previous matings) and invest more time attending clutches in which perceived paternity is higher due to long mate guarding. Therefore, our data provide one of the first empirical examples supporting the proposed link between perceived paternity and paternal care in arthropods (see also Hunt & Simmons, 2002).

Recently, Kahn *et al.* (2013) proposed that in species with external fertilization and no parental care, the period between sperm release and egg fertilization provides a window of opportunity for other males to release their own sperm on the eggs and steal some paternity from the original male. The risk of cuckoldry would select males to spend some time with the eggs after gamete release to protect paternity. According to the model developed by the authors, protection of paternity provides a spatial and temporal association between the male and his eggs, and it is enough to promote the evolution of exclusive paternal care from an initial state of no care (Kahn *et al.*, 2013). As explained above, males of *S. proximum* are more likely to care for eggs from females with whom they spent more time performing mate guarding. Although fertilization in harvestmen is internal, the model that links protection of paternity to the evolution of paternal care provides an additional explanation to understand why some territorial males care for unprotected eggs. A prolonged period of mate guarding may promote a spatial and temporal association between the harem-owning males and the clutches, which may increase the chances of the males to exhibit facultative parental care if egg-tending females desert or die.

Although nearly 50% of the harem-owning males attended the experimental clutches, we found no positive effect of the frequency of facultative parental care on egg survival. When compared with the results previously reported by Buzatto *et al.* (2007), in which *S. proximum* clutches were left unattended for 14 days, the intensity of predation reported here was surprisingly low. Whereas nearly 42% of the eggs were consumed after 4 days of female removal in the previous experiment, the frequency of eggs consumed during the same time period in this study was only 15%. This finding raises the question: Why do males care for unprotected eggs? Predation pressure is known to vary in both time and space, and a recent meta-analysis with many terrestrial arthropods has shown that the benefits of egg attendance are higher in places where predation is more severe (Santos *et al.*, 2016). Thus, a possible answer to the question raised above is that the benefits of facultative paternal care are conditional to the intensity of predation, so that males improve egg survival only in breeding seasons with high predator activity. Under low predation intensity, facultative paternal care would be selected only if the costs associated with this behaviour were lower than the benefits. We argue that when a harem-owning male is not receiving visits of newcomer females, even a small benefit of staying close to unattended eggs and reducing predation on them may suppress the costs of channelling time and energy to parental care rather than mating effort. Thus, unattractive males that attend eggs are making the best of a bad situation, a strategy already reported for many species in numerous behavioural contexts (e.g. Eberhard, 1982; Nakashima, 1987; Pfennig & Pfennig, 2005). Moreover, by attending unprotected eggs and occasionally consuming some of them, unattractive males could abandon their territories less frequently to feed, which would also reduce the chance of territory usurpation by other males, as reported for some fish species (Manica, 2002).

Harem-owning males clearly defend their clutches against conspecific males, but they do not show any aggressive response towards females, which are allowed to consume a great number of eggs. In two occasions, harem-owning males copulated with newcomer females and mate-guarded them while females were cannibalizing eggs. In other arthropod species with exclusive paternal care, males aggressively repel females that try to cannibalize eggs from their nests (e.g. Mora, 1990; Nazareth & Machado, 2010). Considering that the presence of eggs in these species makes males more

attractive to the females, reductions in the number of eggs may decrease the mating success of caring males, which would explain why they are aggressive against cannibalistic females (Requena *et al.*, 2013). In the case of *S. proximum*, males may allow newcomer females to feed eggs from unattended clutches to increase their chances of achieving copulations. From the females' perspective, conspecific eggs are a rich source of nutrients that may increase their lifetime fecundity (Polis, 1981). We do not suggest, though, that harem-owning males defend unprotected clutches to offer eggs as a nuptial gift to newcomer females because this hypothesis does not explain why the frequency of facultative male care is positively related to perceived paternity. What we suggest is that harem-owning males may increase their reproductive success by trading egg attendance and the reproductive costs associated with this behaviour by the opportunity to acquire new copulations and clutches free of any caring cost.

It has been hypothesized that exclusive parental care is likely to evolve when males defend a territory that is also an oviposition site (Williams, 1975), as it is the case of *S. proximum*. However, our findings suggest that while the trade-off between mating effort and parental care exists, the evolutionary shift between facultative and exclusive paternal care is unlikely. A major step in the evolution of exclusive paternal care from an ancestral state of facultative paternal care is necessary: eggs need to be spatially aggregated so that males can attend all of them at a time without losing additional mating opportunities (Tallamy, 2001). One possible route for the evolution of exclusive paternal care from facultative male care in harem-holding species may occur via male peacekeeping behaviour, a behaviour reported for two harem-holding species, the fish *Lamprologus ocellatus* (Walter & Trillmich, 1994) and the thrips *Elaphothrips tuberculatus* (Crespi, 1990). A peacekeeping male is essentially protecting eggs against other females inside his harem, and this behaviour can be regarded as an initial form of paternal care. If a peacekeeping male is efficient in avoiding egg cannibalism by females, it becomes profitable for a female to abandon her eggs with the harem-owning male and invest in a next clutch. In this moment, egg-tending males should become common in the population and a female with preference for these males would have higher fitness than females that remain with their eggs. As soon as female preference for egg-tending males evolves, the trade-off between caring for eggs and acquiring additional mates no longer exists, and paternal care becomes a form of mating effort (Tallamy, 2001; Stiver & Alonzo, 2009). Subsequently, female preference for egg-tending males should decrease the number of copulations with males that do not attend eggs (i.e. sneakers), which in turn should reduce sperm competition and paternity uncertainty, additionally favouring the evolution of exclusive paternal care (Kokko & Jennions, 2008).

In conclusion, we showed that male's decision to invest in parental care rather than mating effort is negatively influenced by male attractiveness and positively influenced by offspring value, especially paternity certainty. Thus, males are able to adjust their investment in either territory defence or egg attendance according to their recent mating history and perceived paternity. As far as we know, this is the first empirical test of recent theoretical models for the evolution parental care using an invertebrate as study system. The results we present here are in agreement with some previous studies with harem-holding vertebrates (reviewed in Stiver & Alonzo, 2009), which brings generality to the predictions of the models. Although we did not detect any positive effect of facultative male care on egg survival, predation pressure on eggs was much lower than that recorded in previous studies with the same population. Thus, the benefits of facultative male care may be conditional to temporal variation in the intensity of predation. The main implication of our findings is that parental care can evolve from facultative male care only if the trade-off between mating effort and parental care is somehow circumvented. Here, we propose one possible evolutionary route for the transition between facultative paternal care and exclusive paternal care. Considering that facultative paternal care occurs in other taxa, including arthropods and amphibians, future studies should investigate how different species may have solved the problem of temporal trade-offs between mating effort and parental care, allowing the evolution of exclusive paternal care.

Acknowledgments

Data accessibility

All data used in this study will be made publicly available in the Dryad repository upon the acceptance of this manuscript.

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