



Original Article

Effects of egg attendance on male mating success in a harvestman with exclusive paternal care

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The expected quality of paternal behavior can influence female mating decisions and determine male mating success. We evaluated the importance of oviposition site quality, male body size, parental status (presence vs. absence of eggs under males' protection), and time invested in care (less vs. more than 1 month) for male mating success in the harvestman *Iporangaia pustulosa*. The chances of acquiring a clutch are relatively small for noncaring males but increase nearly 4 times once males start caring for eggs. After 1 month of caring, the chances of acquiring an additional clutch show a marked decline, probably because the cumulative energetic costs imposed by paternal care decreases males' attractiveness or their ability to replenish gametes throughout the caring period. Therefore, male mating success seems to be affected by a combination of presence of eggs and body condition while caring. Because the presence of eggs increases male attractiveness, we also conducted a field experiment removing caring males from their broods and expected that noncaring males would adopt unattended broods as a deceptive strategy to acquire matings. However, noncaring males cannibalized eggs and no brood adoption was recorded. Because well-fed males stay stationary on the vegetation waiting for mating opportunities, unattended broods may have been found more often by vagrant and poorly fed males. We argue that detailed comprehension of the costs and the benefits of paternal activities, as well as the direct benefits of female preference, is fundamental to better understand the interaction between male care and female mate choice.

Key words: body condition, egg adoption, energetic costs, mate choice, oviposition site selection, sexual selection.

INTRODUCTION

One central question in sexual selection is what determines male attractiveness to females. Numerous empirical studies with a wide variety of organisms have already demonstrated that males possessing certain phenotypic attributes have mating advantages arising from female mate choice (Andersson and Simmons 2006; Clutton-Brock and McAuliffe 2009). The underlying processes why females prefer some male attributes rather than others is still subject of intense debate, and there are 2 main hypotheses to explain the evolution of female mate choice (Kotiaho and Puurtinen 2007). Females may select mates based on traits that indicate the genetic quality of their potential partners, which may increase offspring viability and/or attractiveness, or may select males that provide direct material

benefits, which may enhance female fecundity and offspring survival (Price et al. 1993; Kokko et al. 2006; Gwynne 2008; Wagner 2011).

In species with exclusive male care, females are predicted to take into account not only traits that indicate the genetic quality of potential partners but also the quality of the paternal activities, which are expected to be directly linked with the survival chances of the offspring (Sargent 1988; Hoelzer 1989; Tallamy 2001; Kvarnemo 2006; Klug et al. 2012). For instance, females of some species prefer to mate and lay eggs with males associated with already established broods (fishes: Kraak and Groothuis 1994; Matsumoto et al. 2011; arthropods: Gilbert et al. 2010; Nazareth and Machado 2010). Moreover, females may evaluate the prospects of offspring survival based on the quality of paternal behavior and leave their eggs preferentially with males that provide better care (e.g., Östlund and Ahnesjö 1998; Lindström et al. 2006; Hale 2008). In both fishes and arthropods, it has been suggested that female preferences for parental individuals would have favored

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the evolution of specific morphological and behavioral traits on males. Examples include marks on males' fins that resemble eggs in size and coloration (egg mimicry) and male deliberate care of unrelated offspring, either in the form of stealing eggs from competitors' territories (egg thievery) or invading nests containing eggs (nest takeover) (e.g., Porter et al. 2002; Thomas and Manica 2005; Nazareth and Machado 2010). By laying eggs with males that are already associated with a brood, females may benefit from increasing offspring survival because eggs would be protected either by the dilution effect during a predation event or by the high quality of male care (e.g., Sargent 1988; Hoelzer 1989; Forsgren et al. 1996; Kvarnemo 2006).

When deciding where to lay eggs, the quality of the oviposition site defended by the males is also important to the females' reproductive success because it will determine the biotic and abiotic conditions for the early developmental stages of the offspring (Refsnider and Janzen 2010). Female preference for limited oviposition sites promotes strong male–male competition, with dominant males monopolizing the reproductive resource and excluding inferior competitors from the preferred sites (e.g., Forsgren et al. 1996; Lehtonen and Lindström 2008; Reichard et al. 2009). Size-related traits generally influence the outcome of male–male agonistic interactions (Emlen 2008; Arnott and Elwood 2009) and, considering that the maintenance of these traits is costly, they are argued to honestly indicate male condition and/or genetic quality (Zahavi and Zahavi 1997; Andersson and Simmons 2006). Therefore, by selecting partners based on size-related traits, females may experience fitness advantages because their offspring would be raised inside suitable territories and sired by good competitors (Andersson and Simmons 2006; Emlen 2008). Moreover, in some species with exclusive paternal care, male size is positively correlated with aggressiveness against rivals that attempt to usurp the nest and negatively correlated with egg loss due to predation (e.g., Lindström and Hellström 1993; Fujii et al. 2005; Natsumeda et al. 2012).

Females of the Neotropical harvestman *Iporangaia pustulosa* lay eggs on the underside surface of leaves of different plant species growing at the margin of streams and abandon the offspring under males' protection after oviposition (Machado et al. 2004). Paternal care consists of egg attendance (sensu Smiseth et al. 2012), which prevents predation by conspecifics and other arthropods (Requena et al. 2009). Successful males may attend multiple clutches composed of eggs laid asynchronously by different females (hereafter called "brood"), which may extend the caring period for as much as 4 months (Requena et al. 2009). The long lasting period of parental care erodes male body condition because foraging activities are greatly reduced during egg attendance. After 1 month of parental activities, for instance, males of the same size may present a decrease between 10.8% and 15.2% of their body volume when compared with their condition in the beginning of the caring period (Requena et al. 2012). In response to these energetic costs imposed by prolonged egg attendance, males are likely to intensify their foraging activity, leaving their broods unattended more frequently over the course of the caring period, instead of cannibalizing eggs, a rare behavior only observed twice during more than 3000 h of field observations (Requena et al. 2012). Therefore, the quality of paternal care (i.e., frequency of egg attendance) is expected to decrease during the caring period as male body condition deteriorates. Because egg attendance is essential for offspring survival, females should base their mating decisions on males' commitment to perform costly parental behavior.

The first goal of this study was to evaluate the relative importance of oviposition site quality, male body size, and paternal care to male mating success in *I. pustulosa*. We expected that the probability of a male acquiring a new clutch of eggs, as well as the total number of clutches and the number of eggs per clutch received, should be positively related to male body size and to the quality of the plants where males take care of the offspring. Additionally, we investigated the effects of paternal care on male mating success, focusing on how the probability of acquiring a new clutch, the number of clutches received, and the number of eggs per clutch would be affected by the presence versus absence of previous eggs under male's protection and by the time already spent in paternal activities (hereafter called "previous paternal investment"). We expected positive effects of egg presence and negative effects of previous paternal investment on male mating success. If the presence of eggs honestly indicates high prospects of egg survival, we expected that caring males should achieve higher mating success than noncaring males. On the other hand, if male parental performance depends on his body condition, we expected the highest success when males are in good conditions, that is, as noncaring males that have had not invested in care recently. However, given that male body condition decays over the course of the caring period, male mating success should monotonically decrease with previous paternal investment.

Our second goal was to test for sexual divergence in the adoption of unrelated offspring. Given that female cannibalistic attacks are an important source of egg mortality in *I. pustulosa* (Requena et al. 2009), we expected that females would consume experimentally unattended eggs as soon as they find a brood in the field. In fact, cannibalism of unattended eggs represents the typical conduct of males and females in many harvestman species, probably because eggs are a high-quality food resource (Machado and Raimundo 2001). However, in species with exclusive paternal care, males associated with eggs are likely to be more attractive to females (e.g., Kraak and Groothuis 1994; Gilbert et al. 2010; Nazareth and Machado 2010; Matsumoto et al. 2011), and noncaring males should adopt experimentally unattended broods because the prospects of future mating opportunities would overcome the costs of caring for unrelated offspring (Tallamy 2001) and losing a high-quality meal. If this is the case in *I. pustulosa*, we expect divergent behavioral responses between males and females toward unattended eggs. The observational and experimental results reported here provide complementary information to understand not only the factors that determine male mating success in a species with exclusive paternal care but also the interaction between paternal care and female mate choice in general.

MATERIALS AND METHODS

Study site and marking procedure

We carried out fieldwork in an Atlantic Forest fragment at Intervales State Park (24°14'S; 48°04'W; 800 m of altitude), located in the state of São Paulo, southeastern Brazil. The region has high precipitation levels, with average annual rainfall ranging from 2000 to 3000 mm/year and mean annual temperature ranging from 12 to 20 °C. To collect our observational data, we visited the study site monthly during 4 consecutive days per month between August 2003 and July 2004, inspecting a 200-m-long transect along the vegetation flanking both margins of a stream 3 times a day (from 08:30 to 12:00 h, from 14:30 to 18:00 h, and from 20:30 to 00:00 h).

In each daily survey, we actively searched for *I. pustulosa* adults on the marginal vegetation at a maximum distance of 1 m from the water and from the ground to the height of 2 m. We marked all new adults individually with enamel color paint and released them at the site of capture, recording the recapture of previously marked individuals. We also exhaustively searched for broods, photographing every one twice a month and flagging their position in the transect.

Measuring male and paternal care quality

The first time we captured a male, we measured his dorsal scute (= carapace) length using an electronic caliper (precision of 0.01 mm). Given that dorsal scute length in harvestmen does not increase in size after individuals reach adulthood, we used this measure as proxy for male body size in the analyses (see below). Furthermore, every time we captured males, we classified them according to their parental status as either *caring males* (if they were attending a single clutch or a brood) or *noncaring males* (if they did not have any clutch). Parental status is a fluctuating condition that may change at any time over the year because caring males may become noncaring males after the dispersion of all nymphs, whereas noncaring males (either virgins or males that have already mated before) may obtain a clutch, thus becoming caring males.

Broods always show a regular arrangement of eggs, so that the first clutch received is laid close to the leaf apex and the subsequent clutches are laid toward the leaf base (Machado et al. 2004). Under typical conditions, *I. pustulosa* embryos take nearly 1 month to develop completely and hatch (Gnaspini and Lerche 2010). Instead of placing subsequent eggs in the empty space previously occupied by the offspring after they have hatched and dispersed, newcomer females keep ovipositing toward the leaf base. Therefore, we used characteristics of the broods to classify caring males into 2 categories related to the time they have had already invested in parental behavior (i.e., previous paternal investment): 1) *long-term caring males*, if they were attending a brood with an empty space and, therefore, had been in the caring status for at least 1 month (Figure 1A), and 2) *short-term caring males*, if they were attending a brood without an empty space and, therefore, had been in the caring status for less than 1 month (Figure 1B). Given that *I. pustulosa* reproduces continuously all year long (Requena et al. 2012), we observed noncaring males, as well as long-term and short-term caring males, in every month during the study period (Supplementary Figure S1).

Measuring oviposition site quality

We identified 36 plant species (hereafter called “host plants”) that were used at least once as an oviposition site by *I. pustulosa* in the transect between August 2003 and July 2004 (Supplementary Table S1). We quantified the availability of these host plants by counting the number of individuals of each species in the study area (two 200-m-long and 1-m-wide plots, one at each margin of the stream). We calculated a selection index for each host plant according to the formula $w_i = u_i/a_i$, where u_i is the proportion of the total 300 broods observed that were laid on the host plant i and a_i is the proportion of the total 2534 available plants in the transect that corresponds to the host plant i . Finally, we calculated the standardized plant quality index for each host plant i , according to the following formula $(w_i / \sum_{x=1}^n w_x) \times 100$, where n represents the total 36 host plant species (modified from Manly et al. 1993).

Given that the list of host plants comprises great taxonomic diversity, including herbs, shrubs, treelets, and trees (Supplementary

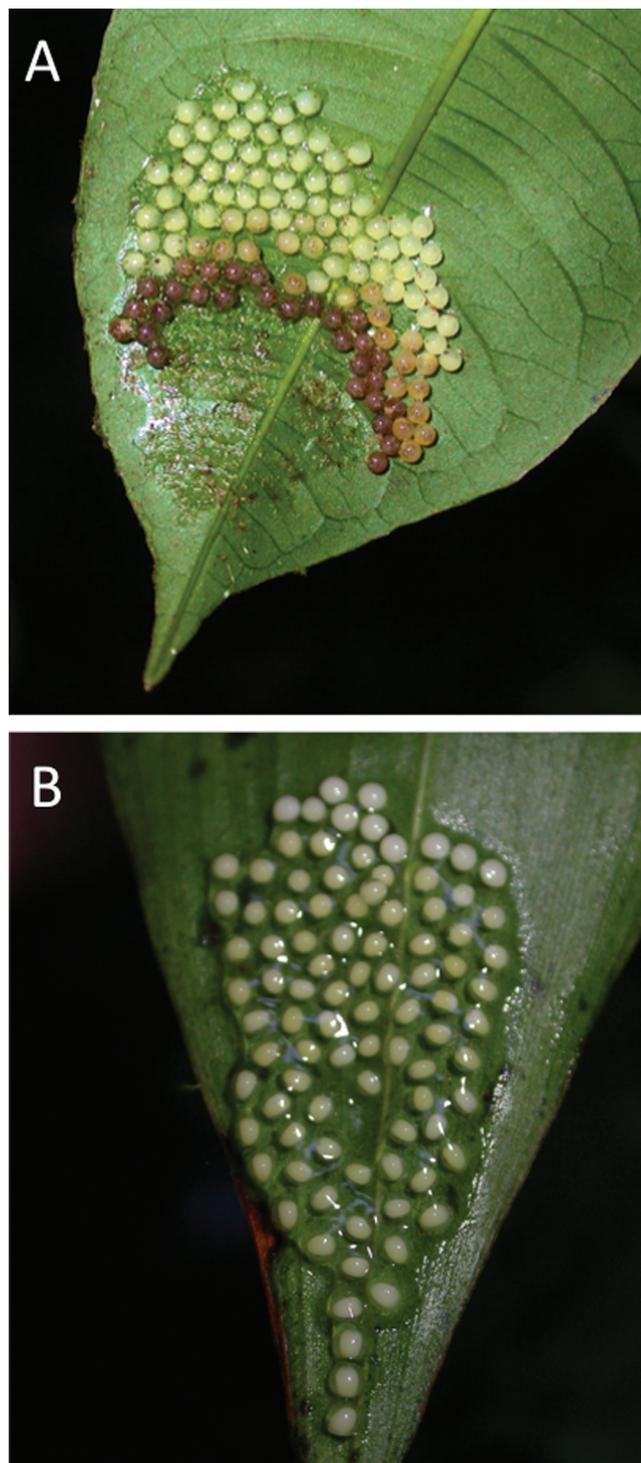


Figure 1

Broods of the harvestman *Iporangaia pustulosa*. (A) When some eggs have already hatched after nearly 1 month of embryonic development, there is an easily recognizable empty space at the leaf apex, which we used to classify the individuals as long-term caring males. (B) When there was no empty space at the leaf apex, we classified the individuals as short-term caring males.

Table S1), we also calculated other version of the plant quality index using the number of leaves as proxy for host plant availability. First, we estimated the median number of leaves of the host plants

based on a sample of 3–10 individuals of each species. Then, we estimated the availability of leaves of each host plant multiplying the total number of individuals of the species i by its estimated median number of leaves. Finally, we calculated the standardized plant quality index for each host plant following the same procedure described above. In this case, however, a_i is the proportion of the total number of leaves estimated in the transect that corresponds to the host plant i . To assess the sensitivity of our results to different proxies of host plant availability, we performed all the analyses described below using both versions of the plant quality index. Details on the identity of the host plants as well as their availability (both in terms of individuals and number of leaves), frequency of use as oviposition site, and their plant quality indexes are presented in [Supplementary Table S1](#).

The list of host plants includes species with long-lived leaves, which may decrease the risk of losing a brood due to leaf abscission, and also species with chemically defended leaves, which may decrease the risk of herbivory in leaves bearing a brood. Regardless of the criteria of oviposition site selection, the underlying assumption of our proxy is that preferred host plants would somehow represent high-quality oviposition sites. It is important to stress, however, that we have no behavioral evidence suggesting that *I. pustulosa* males defend the preferred host plants, as in a typical resource defense polygyny exhibited by other harvestman species (e.g., [Buzatto and Machado 2008](#)). In more than 3 years of fieldwork, we never observed caring males exhibiting agonistic behaviors toward conspecifics (either males or females) beyond the leaf where the brood was laid ([Requena et al. 2009](#)), which we interpret solely as a case of offspring protection. Moreover, noncaring males are constantly moving on the vegetation and usually do not stay on a specific area for a long period ([Requena et al. 2012](#)). Therefore, we cannot attribute a host plant to noncaring males and used the plant quality index only in the analyses about the number of clutches and the number of eggs per clutch received by males already caring for eggs, but not in the analysis about the probability of acquiring a new clutch (see details below).

Measuring male mating success

In every month, we classified males as 1) *successful*, if they were noncaring males in the $(i - 1)$ th month and were observed caring for eggs in the i th month or if they were caring males in the $(i - 1)$ th month and had new eggs added to their broods in the i th month or 2) *unsuccessful*, if they were found as noncaring males both in the $(i - 1)$ th and the i th months or if there was no addition of eggs to their broods between the $(i - 1)$ th and the i th months. We excluded from our data set individuals that were recaptured in only one of the months as well as males associated with broods that were attacked by fungi ($n = 8$; 2.7% of all broods) during the interval between the $(i - 1)$ th and the i th months because we were unable to count accurately the number of eggs of these broods. We used the photographs of the broods to assess whether or not a male received new eggs and to quantify how many clutches and eggs per clutch each male received between consecutive months.

Given that eggs of *I. pustulosa* change in size and coloration over the course of the embryonic development ([Machado et al. 2004](#); [Gnaspini and Lerche 2010](#)), we estimated male mating success assuming that eggs in different stages were oviposited at different moments either by multiple females or by the same female that returned to the brood several times (as described in [Requena et al. 2012](#)). Because the maximum number of mature eggs observed in *I. pustulosa* ovaries is 48 ([Machado et al. 2004](#)), every time we

observed a higher number of eggs in the same stage of development in a given brood, we divided the total number of eggs in this stage by the maximum female fecundity and used the result as a conservative estimate of the number of clutches the male have acquired. In such circumstances, however, we could not precisely assess the number of eggs per clutch, and thus, we discarded these particular events for the analysis about the number of eggs received by males (see details below).

Analyzing male mating success

As in many ecological studies conducted under natural field conditions ([Wade and Shulter 2004](#); [Martin et al. 2005](#)), our data set comprises a large number of zeros ([Figure 2A](#)); more than 80% of our observations ($N = 1145$) regard unsuccessful males at any specific month. To handle this zero-inflated data set, we implemented a Hurdle model approach whereby zero-count and nonzero data are modeled separately ([Martin et al. 2005](#)). First, we fitted a logistic regression model to the zero-count observations and all the nonzero data together. In our case, it estimates the probability of a male acquiring a first clutch (in the case of noncaring males) or a new clutch (in the case of caring males) during the interval between

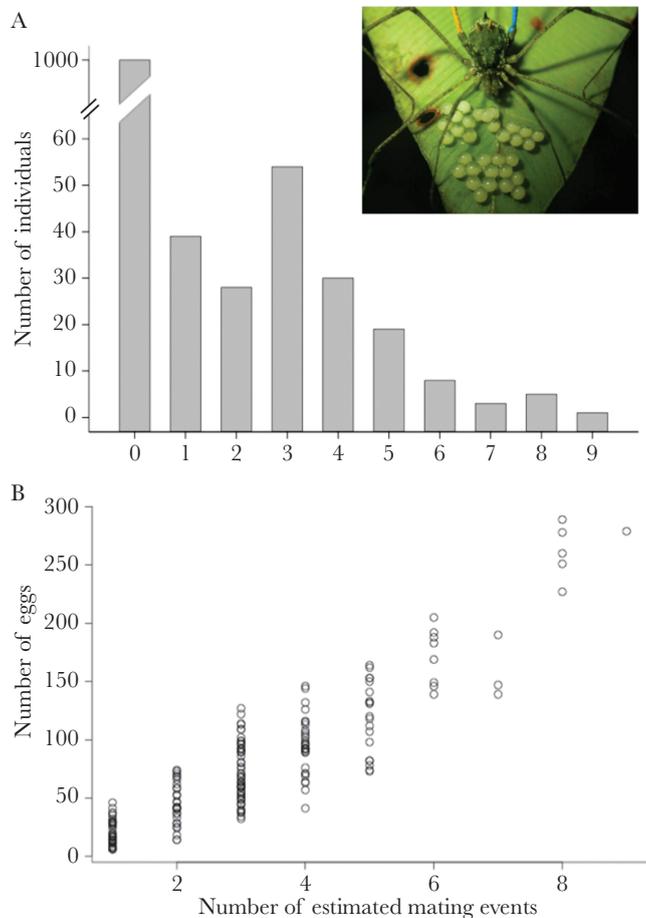


Figure 2 (A) Distribution of estimated egg clutches received by males of the harvestman *Iporangaia pustulosa* between August 2003 and July 2004 in a 200-m-long transect ($N = 494$ males). Noncaring males correspond to the category “0 clutches,” whereas caring males are classified according to the number of clutches in their broods (see text for additional details). (B) Correlation between the estimated number of clutches in a brood and its total number of eggs.

consecutive months. We built alternative generalized linear mixed models (GLMMs) establishing that such probability should not depend on any male attribute (null model) or should depend on male's body size, male's parental status (noncaring vs. caring), or male's previous parental investment (noncaring vs. short-term caring vs. long-term caring). Additionally, we built models considering the additive and the interactive effect between these variables, but always using parental status and previous parental investment in alternative models, never together. If the variables related to male body size and male parental care quality are important to determine an individual's chance of receiving eggs, the best model to fit the observed data should include these variables.

We then fitted a zero-truncated count model particularly to the nonzero data. In our case, we fitted a truncated negative binomial regression model among males that have received at least one clutch between consecutive sampling visits to estimate the number of clutches and the number of eggs per clutch they received. In order to do it, we built alternative GLMMs that considered errors following a linear negative binomial distribution (NBI in Hilbe 2011) truncated in zero. We modeled each response variable as not dependent on any male or plant characteristic or dependent exclusively on host plant quality, male body size, parental status, or previous parental investment. We also built models considering the additive effect between them, but always using parental status and previous parental investment in alternative models, never together. Given that all models including interactions between predictor variables fitted worse to the data than their counterparts that only included additive terms (data not shown), we do not present them in the results for the sake of simplicity. Moreover, we run separate set of analyses considering the host plant quality either as the index based on individuals of each species or the index based on the estimated number of leaves of each species. If the variables related to male body size, host plant quality, and male parental care quality are important to determine how many females oviposit with a male or the number of eggs they lay with him, the best model to fit the observed data should include these variables.

For every candidate model in each separate analysis, we included the month identity as a categorical random variable in order to account for variations in the interval between sampling occasions and also seasonal fluctuations in the population density, adult sex ratio, and reproductive activity. Particularly in the analyses of the number of clutches received and the number of eggs per clutch, we also included an observation-based factor as a random variable in every candidate models in order to minimize the overdispersion usually associated with count data. Moreover, for the analysis of the number of eggs per clutch, we additionally used male identity nested within each month as a random variable given that the same male could have mated more than once in the interval between consecutive sampling occasions. For each analysis, we compared the fit of all alternative GLMMs using a model selection approach (Burnham and Anderson 2002). Depending on the sample size of the data used in each analysis, we used either the Bayesian information criterion or the small sample size bias-corrected version of Akaike information criterion (AIC_c) to rank and calculate the relative weight of all models fitted to the data. We computed the difference in those indexes between the model with the lowest value and all other models in the ranking (Burnham and Anderson 2002). We implemented all models using the package glmmADMB (Fournier et al. 2012), ranked them using the package bbmle version 1.0.16 (Bolker and R Development Core

Team 2014), and obtained the estimates using the package coda (Plummer et al. 2006) in the software R 3.1.0 (R Development Core Team 2014).

Egg adoption experiment

To test for sexual divergence in the adoption of unrelated offspring, we conducted a field experiment, replicated once in the wet and warm season (January and February 2004) and once in the dry and cold season (August 2004). We removed caring males from their broods and compared the behavior of newcomer males and females that visited the experimentally unattended eggs. Conspecific females are one of the main predators of *I. pustulosa* eggs (Requena et al. 2009), and we expected that they should 1) stay with the eggs for short periods, 2) cannibalize eggs, and 3) not protect them against other potential predators. If unprotected eggs solely represent a food resource for newcomer males, they should exhibit the same behavioral pattern as females. On the other hand, if the presence of eggs under a male's attendance increases his chances of mating and receiving new eggs, noncaring males would be willing to adopt unrelated offspring more often than females (Tallamy 2001). In this sense, we would expect that *I. pustulosa* males visiting the experimental unattended broods should 1) stay with the eggs for long periods, 2) not cannibalize eggs, and 3) exhibit parental activities, which in this species consist in remaining prostrated on the brood and attack potential egg predators (Requena et al. 2009).

To test our predictions, we compared males and females regarding 1) their permanence time with the experimentally unattended broods, 2) the proportion of cannibalistic individuals and the amount of eggs consumed, and 3) the proportion of individuals that exhibited protective behaviors, such as repelling potential predators. To compare proportions, we used general linear models with errors following a binomial distribution, and to compare count data (permanence time and amount of eggs consumed by newcomers), we used GLMMs with errors following a Poisson distribution. These GLMMs also included an observation-based factor as a random variable to account for the overdispersion usually associated with count data. We performed a deviance analysis on each model in the software R 3.1.0 (R Development Core Team 2014).

RESULTS

General description of male mating success

The distribution of male mating success was strongly skewed, so that more than 83.7% of the recaptured males were not caring for a clutch. Among caring males, 64% accumulated more than 2 clutches in their broods and 35% accumulated more than 3 clutches (Figure 2A). The median number of clutches accumulated by caring males was 3 (range = 1–9 clutches, $N = 187$ broods). The total number of eggs accumulated in each brood ranged from 6 to 289 (median 68 eggs, $N = 187$ broods), and it was positively correlated with the estimated number of clutches accumulated by each male ($F_{1,185} = 825.1$, $r = 0.903$, $P < 0.001$; Figure 2B).

Probability of acquiring a clutch

The best model to explain the probability of a male acquiring a clutch included only the effect of previous parental investment (Table 1). However, the pattern we found does not follow

the prediction of a monotonic decrease in male success as caring period increases. Males that have not invested in care (i.e., non-caring males) had a small chance of acquiring their first clutch (estimated probability = 0.118, 95% confidence interval [95% CI] = 0.067–0.200; Figure 3A). Once males started caring for some eggs (i.e., short-term caring males), their chance of acquiring additional eggs increased nearly 4 times (estimated probability = 0.458, 95% CI = 0.359–0.561; Figure 3A). Finally, as males became associated with their eggs for more than 1 month (i.e., long-term caring males), their chances of acquiring additional eggs showed a marked decrease, reaching estimates as low as those of noncaring males (estimated probability = 0.069, 95% CI = 0.028–0.158; Figure 3A).

Table 1
Model selection for the probability of *Iporangaia pustulosa* males acquiring new clutches in their broods ($N = 1145$ observations)

Fixed effect predictors	BIC	K	Δ BIC	Weight
Previous paternal investment	947.5	4	0.0	0.921
Body size + previous paternal investment	952.4	5	4.9	0.078
Body size \times previous paternal investment	961.4	7	13.9	<0.001
Parental status	990.9	3	43.5	<0.001
Body size + parental status	995.9	4	48.5	<0.001
Body size \times parental status	998.4	5	51.0	<0.001
Null model	1021.3	2	73.8	<0.001
Body size	1024.0	3	76.5	<0.001

All models include the random effect of the month identity when individuals were sampled. Models are ranked by increasing order of their Bayesian information criterion (BIC). The best model to fit the observed data (whose Δ BIC < 2.0) is indicated in bold. K = number of parameters, Δ BIC = difference between the BIC value of each model and the BIC value of the most parsimonious model, and weight = BIC weight of each model. The symbols + and \times represent additive effect and interaction between variables, respectively.

Number of clutches received

The best model to explain the total number of clutches accumulated by successful males included only the month identity as a random effect (Table 2 and Supplementary Table S2). Although the models that also included the isolated effect of male's parental status or plant quality index (either based on the number of individuals of each species or the estimated number of leaves) presented Δ AIC_c < 2.0, these 2 additional parameters should be considered uninformative. As extensively pointed out elsewhere (Burnham and Anderson 2002; Arnold 2010), this occurs whenever a variable with poor explanatory power is added to a good model (in this case, the model including only the random effect). In fact, the models containing parental status or plant quality index had similar maximized log-likelihood: 1) null model = -300.6, 2) parental status model = -299.9, 3) plant quality index based on individuals model = -300.5, and 4) plant quality index based on estimated number of leaves model = -300.2. Moreover, the 95% CI of the estimated coefficient for the additional parameters includes the value zero (model including parental status = -0.31 to 0.08; model including plant quality based on individuals index = -0.02 to 0.03; model including plant quality based on estimated number of leaves = -0.005 to 0.013). Therefore, our interpretation of the results will be based on the best-ranked model, in which the number of clutches accumulated by successful males is not explained by any male or host plant characteristics that we investigated.

Number of eggs received per clutch

Finally, 2 models were equally plausible to explain the number of eggs laid in each clutch among successful males. These models included either the isolated effect of male parental status or previous parental investment, regardless of the plant quality index used (Table 3 and Supplementary Table S3). For the sake of simplicity, we only present here the values for the index based on individuals

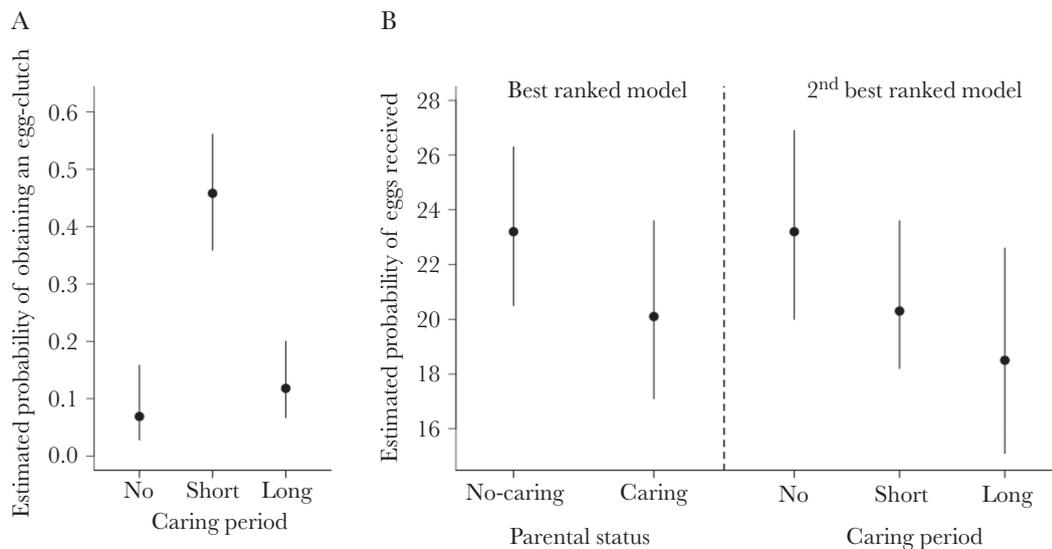


Figure 3

Estimated effect of paternal care quality on male reproductive success in the harvestman *Iporangaia pustulosa*. (A) Males that have had invested in paternal care for only a short period (short-term caring males) are predicted to have the highest chance of receiving a new clutch in comparison with both noncaring males and males that have had been caring for a brood for a long period (long-term caring males). (B) When noncaring males are able to obtain their first clutch, however, they receive the largest amount of eggs in comparison with the quantity received by males that have had previously invested in parental activities, regardless of the time spent in the caring status. Estimates were based on coefficients of the selected model (see text and Tables 1 and 3 for additional details) and their corresponding 95% CIs.

Table 2

Model selection for the number of clutches received by *Iporangaia pustulosa* males in their broods ($N = 187$ observations)

Fixed effect predictors	AIC _c	<i>K</i>	ΔAIC _c	Weight
Null model	609.4	4	0.0	0.268
Parental status	610.0	5	0.6	0.191
Plant quality index	611.3	5	1.9	0.101
Body size	611.4	5	2.0	0.099
Previous paternal investment	612.0	6	2.6	0.073
Plant quality index + parental status	612.0	6	2.6	0.073
Body size + parental status	612.1	6	2.7	0.068
Body size + plant quality index	613.3	6	3.9	0.037
Plant quality index + previous paternal investment	613.9	7	4.5	0.027
Body size + previous paternal investment	614.0	7	4.6	0.026
Body size + plant quality index + paternal status	614.1	7	4.7	0.026
Body size + plant quality index + previous paternal investment	616.0	8	6.6	0.010

All models include the random effect of the month identity when individuals were sampled and an observation-level categorical variable. Plant quality index in this analysis is based on the number of individuals of each host plant species available in the transect. Models are ranked by increasing order of their AIC_c. The best models to fit the observed data (whose ΔAIC_c < 2.0) are indicated in bold. *K* = number of parameters, ΔAIC_c = difference between the AIC_c value of each model and the AIC_c value of the most parsimonious model, and weight = AIC_c weight of each model. The symbol + represents the additive effect between variables.

(Table 3), but the results considering the index based on the estimated number of leaves can be found in Supplementary Table S3. Despite quantitative differences in the estimated number of eggs received by males, both models predict that noncaring males should receive more eggs in their first clutch when compared with the additional eggs received by caring males (Figure 3B). Particularly for the estimates based on the model that includes the previous parental investment, the number of eggs is predicted to decay as the caring period increases (Figure 3B). Regardless of the model, however, the estimates for males of different parental categories greatly overlap and their absolute differences consist of just a few eggs (Figure 3B).

Egg adoption

During the wet and warm season, the experimentally unattended broods received 24 visits of males and 24 visits of females, during which individuals exhibited similar behaviors (Table 4). Individuals of both sexes usually stayed on the broods for short periods (males: median = 17.5 min; females: median = 19.0 min). More than half of all observed males ($n = 13$) and females ($n = 15$) cannibalized at least 1 egg, with no sexual difference in the proportion of cannibalistic events or in the number of eggs consumed (Table 4). Finally, the same proportion of males and females remained prostrated on the eggs (Table 4), but we did not witness any defensive behaviors during our observations.

During the dry and cold season, probably due to the low activity of the individuals, the 7 experimental broods received visits of only 2 males and 1 female. One of the males stayed 3 min with the unattended eggs and did not consume any egg. The other male stayed almost 30 min on the brood and, during this time, cannibalized 1 egg. The female was also observed cannibalizing 1 egg, but

Table 3

Model selection for the number of eggs received by *Iporangaia pustulosa* males in their broods ($N = 402$ observations)

Fixed effect predictors	AIC _c	<i>K</i>	ΔAIC _c	Weight
Parental status	2957.1	6	0.0	0.315
Previous paternal investment	2957.9	7	0.8	0.208
Body size + parental status	2959.1	7	2.0	0.115
Plant quality index + parental status	2959.2	7	2.1	0.112
Body size + previous paternal investment	2959.9	8	2.8	0.076
Plant quality index + previous paternal investment	2960.0	8	2.9	0.075
Body size + plant quality index + parental status	2961.2	8	4.1	0.041
Body size + plant quality index + previous paternal investment	2962.0	9	4.9	0.027
Null model	2962.9	5	5.8	0.017
Body size	2965.0	6	7.9	0.006
Plant quality index	2965.0	6	7.9	0.006
Body size + plant quality index	2967.0	7	9.9	0.002

All models include the random effect of the month identity, the individual male identity nested within each month, and an observation-level categorical variable. Plant quality index in this analysis is based on the number of individuals of each host plant species available in the transect. Models are ranked by increasing order of their AIC_c. The best models to fit the observed data (whose ΔAIC_c < 2.0) are indicated in bold. *K* = number of parameters, ΔAIC_c = difference between the AIC_c value of each model and the AIC_c value of the most parsimonious model, and weight = AIC_c weight of each model. The symbol + represents the additive effect between variables.

her permanence time could not be accurately estimated because she was apparently disturbed by the headlamp during the nocturnal observation.

DISCUSSION

Our results show that male mating success in the harvestman *I. pustulosa* is not affected by male size or oviposition site quality, but instead by a combination of presence of eggs and previous paternal investment. Specifically, males caring for recently laid eggs had higher chances of acquiring additional clutches when compared with the chances of noncaring males to acquire a first clutch. Additionally, the time invested by males in parental activities negatively affected their mating success because after 1 month of egg attendance, the chances of a caring male to acquire additional clutches showed a marked decrease, with estimates quantitatively similar to that of noncaring males. Although the total number of clutches accumulated by successful males was not influenced by any attribute evaluated here, the number of eggs per clutch was slightly higher in the first clutch received by noncaring males. Therefore, the highly skewed distribution of the number of clutches among *I. pustulosa* males (Figure 2A) is likely to be the result of male allocation to paternal care rather than oviposition site characteristics and male body size. In what follows, we elaborate this argument and discuss the implications of our findings for the interaction between paternal care and male mating success in species exhibiting exclusive paternal care.

Female mating preference based on male parental behavior has been suggested as one of the main selective pressures favoring the evolution and maintenance of exclusive male care (Hoelzer 1989;

Table 4
Comparison of the behavioral responses exhibited by
***Iporangaia pustulosa* males ($n = 24$) and females ($n = 24$) toward**
experimentally unattended broods during the wet and warm
season

	Males	Females	Analysis of deviance
Permanence time (min)	1–1440	4–330	Δ deviance = 0.290, $P = 0.590$
Percentage of individuals that cannibalized eggs	54.2	62.5	Δ deviance = 0.343, $P = 0.558$
Number of eggs consumed per cannibalistic event	1–5	1–6	Δ deviance = 0.477, $P = 0.490$
Percentage of individuals that remained prostrated on the eggs	29.1	33.3	Δ deviance = 0.097, $P = 0.755$

Tallamy 2001; Kvarnemo 2006; Klug et al. 2012). Using the readily available information on the presence of eggs under a male's attendance to bias mating decision is equivalent to passive mate choice based on copying the decision of other females (Trumbo 1996). Such mate decision may reduce the costs of searching and assessing mates (Trumbo 1996; Vakirtzis 2011), which increases the time available for foraging and, consequently, egg production in iteroparous species (Tallamy 2001; Goulet and Goulet 2006), which is the case for the great majority of arthropod species exhibiting exclusive paternal care (Requena et al. 2013). Nonindependent female mate choice may also improve offspring hatching success by 1) reducing predation risk of any particular egg due to dilution effect, 2) intensifying male care toward an enlarged brood, or 3) promoting oviposition with a successful male that exhibits high-quality parental behavior (Sargent 1988). Particularly for *I. pustulosa*, females cover their eggs with a thick mucus coat that deters some egg predators and reduces egg consumption rates by conspecifics (Requena et al. 2009). In this species, therefore, mate choice copying may also benefit females because their eggs would enjoy the protection provided by the mucus previously deposited in the same brood by other females. Although there is empirical demonstration of the benefits of female mate choice copying in some fish species with exclusive paternal care (e.g., Kraak and Groothuis 1994; Forsgren et al. 1996; Östlund and Ahnesjö 1998; Lindström et al. 2006; Hale 2008; Matsumoto and Takegaki 2013), the only evidence for arthropods regards the pattern of differential mating success of caring males (Gilbert et al. 2010; Nazareth and Machado 2010; this study). Therefore, additional information about the particular benefits females acquire by choosing mates based on the presence of eggs under their protection still needs further investigation.

Consistency of male care quality is crucial when female mating decisions are based on the expected survival chances of the offspring (Hoelzer 1989; Price et al. 1993; Wagner 2011). In *I. pustulosa*, prolonged food deprivation erodes male body condition during the caring period and may compromise their self-maintenance (Requena et al. 2012). Given that filial cannibalism is extremely rare in this species (Requena et al. 2012), starving caring males are likely to leave the brood unattended more frequently in order to seek food, which may condemn the eggs to death due to predation during temporary desertions (Requena

et al. 2009; see also Chelini and Machado 2012). In this situation, females would benefit from accurately assessing each caring male's body condition, a trait that may determine the quality of future paternal care. In fact, *I. pustulosa* females touch males with chemically sensitive legs during mating interactions (Requena and Machado 2014), and we suggest that females are able to evaluate male condition using cuticular hydrocarbons (CHCs), which are contact pheromones involved in sexually selected processes in arthropods (e.g., Rundle et al. 2005; Thomas and Simmons 2009; Weddle et al. 2013). Considering that short-term *I. pustulosa* caring males are in good body conditions (Requena et al. 2012), they would be able to synthesize the most attractive CHCs (Johansson and Jones 2007), increasing their chance of acquiring a new clutch containing many eggs. Long-term caring males, however, are in poor body condition (Requena et al. 2012), which may lead to a deterioration in their CHC profiles (Johansson and Jones 2007) and a consequent decrease in their chances of acquiring a new clutch and also in the number of eggs per clutch. Therefore, we argue that, in species in which paternal care imposes severe energetic costs to the males and the caring period is prolonged, females should have been selected to base their mating decisions on reliable indicators of the prospects of offspring survival, such as male body condition.

The suggestion that the presence of a brood only affects female mate choice if combined with a caring male's good condition may also explain the results of our experimental manipulation. Noncaring males of *I. pustulosa* in poor body condition (either because they have recently molted to adult or finished parental activities) should search for food to replenish their energetic reserves. Well-fed noncaring males, on the other hand, could afford to be stationary on the vegetation and wait for the approach of a receptive female in order to mate and acquire a clutch (Requena and Machado 2014). Therefore, vagrant poorly fed males should have found the unattended broods more often than stationary well-fed males, which may explain why most males in the experiment considered the eggs mainly as food resource and cannibalized them, behaving in the same way as females. Moreover, the lack of egg adoption reported here suggests that even an increase in attractiveness for noncaring males in good body condition does not overcome the energetic costs of paternal care (Requena et al. 2012), especially when caring for unrelated eggs. Female preference for parental males has been suggested to be the main selective pressure favoring the evolution of egg mimicry, egg thievery, and brood adoption in fishes and arthropods with exclusive paternal care (e.g., Porter et al. 2002; Thomas and Manica 2005; Nazareth and Machado 2010). We argue, however, that this female-driven process should occur only when the presence of eggs provides enough information for females to make their mating decisions. Whenever paternal care imposes severe energetic costs or is depreciable, so that the offspring number negatively affects caring quality (Clutton-Brock 1991), females should take into account reliable information to evaluate the prospects of offspring survival, including male body condition and the amount of eggs already present in the brood.

A nonexclusive explanation for the decrease in male mating success over the course of the caring period in *I. pustulosa* is related to sperm depletion. Males that attract or monopolize a great number of females become sperm depleted if they are not able to replenish their ejaculates between mating events (e.g., Preston et al. 2001; Radhakrishnan et al. 2009; see also Kvarnemo and Simmons 2013). Therefore, high mating frequency of short-term

I. pustulosa caring males (Requena and Machado 2014; this study) and low food intake while caring (Requena et al. 2012) may act together, compromising sperm production. Because fertilization in harvestmen occurs internally and females store sperm from previous mates (Macías-Ordóñez et al. 2010), the risk of sperm competition for sperm-depleted long-term caring males would be higher than the risk for short-term caring males. Thus, long-term caring males could avoid prolonging the severe energetic costs of paternal care and the risk of caring for unrelated offspring by aggressively rejecting newcomer females (Requena and Machado 2014), resulting in low probability of acquiring new clutches. This male-driven process, however, is somehow incompatible with other results reported here. For instance, *I. pustulosa* noncaring males are, on average, in better conditions and have presumably mated less often than short-term caring males, which would not explain the great difference in mating success between males in these 2 categories. Future studies with *I. pustulosa* and other species with exclusive paternal care, therefore, should investigate the relative importance of female- and male-driven processes on male mating success.

In conclusion, we argue that detailed comprehension of the costs and benefits of paternal activities, as well as the direct benefits of female preferences, is fundamental to better understand the interaction between paternal care and female- and male-driven processes of sexual selection (see Requena et al. 2013). Particularly for the harvestman *I. pustulosa*, male mating success is likely to be determined by 2 complementary processes. The first is straightforwardly based on the presence or absence of eggs under a male's protection, with clear female preferences for caring males. However, evaluating male's parental status seems not to be sufficient because the cumulative energetic costs imposed by paternal care are likely to decrease the quality of egg protection over the course of the caring period. Therefore, females may also carefully evaluate the caring male's body condition, which we suggest to be a good indicator of the future survival chances of the offspring. The costs associated with decreased feeding activities during the caring period have been traditionally considered to be stronger for females than males because they reduce the production of additional eggs, negatively affecting females' future reproduction and fecundity (Tallamy and Wood 1986; Tallamy 2001). Our results, however, suggest that energetically costly paternal care may also affect males' reproductive success due to decreased attractiveness during the caring period in a species with overlapping clutches. Therefore, we claim that exploring the natural variation observed in the energetic costs of paternal activities may have profound implications in our ability to make a priori predictions about the direction and the intensity of sexual selection in species with exclusive male care.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>

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