



Female mate choice in an arachnid with exclusive paternal care: males in good condition have higher mating success, but only if they can advertise it

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Abstract

Females of many species that exhibit exclusive paternal care prefer parental over non-parental males. According to the essential male care model, once males fulfill the minimum care requirements for offspring survival, they should allocate their surplus energy to advertise their good body condition and increase their attractiveness. To test this prediction, we conducted a field experiment using the harvestman *Iporangaia pustulosa*, in which males provide exclusive parental care. Employing a full factorial design, we manipulated the body condition of parental males (well-fed and poorly fed) and the status of their sexually dimorphic glands (blocked and unblocked), which likely release sexual pheromones. Then, we recorded males' probability of receiving new eggs and estimated their mean fitness. Parental males in good condition with unblocked glands had a higher probability of receiving new eggs compared to those in poor condition with blocked glands. Males in the other two experimental groups exhibited intermediate values. Parental males with unblocked glands had a mean fitness 1.38 times higher when in good condition. Additionally, parental males in good condition had a mean fitness 3.48 times higher when the glands were unblocked. These results suggest that the production of sexual pheromones in harvestmen is condition-dependent and emphasize the significance of sexual advertisement as an indicator of male quality. Overall, our findings support the predictive power of the essential male care model and shed light on the interplay between body condition, sexual advertisement, and mating success in species exhibiting exclusive paternal care.

Significance

Why do females of species with male-only care prefer parental males? The *good parent hypothesis* predicts that if males vary in caregiving quality, females gain direct benefits by selecting the best caregivers. The *essential male care model* posits that if all males fulfill minimum care requirements, females gain indirect benefits by selecting mates that allocate surplus energy to advertise their good condition. A previous study with the harvestman *Iporangaia pustulosa* found that while females prefer males in good condition, their caregiving quality does not differ from that of males in poor condition, which refutes the good parent hypothesis. Here we demonstrate that female preference aligns with the essential male care model, as male fitness was influenced by both body condition and capacity to emit sexual advertisements. This study is the first examination of the essential male care model in invertebrates.

Keywords Body condition · Essential male care model · Harvestman · Mate choice · Sexual selection · Sexual pheromone

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Introduction

Parental care, by definition, improves offspring survival, but it may also impose several costs on the parents. These costs include increased energy expenditure during parental care, reduced foraging opportunities, higher exposure to predators, and decreased reproductive rates (reviewed in

Alonso-Alvarez and Velando 2012). For females, exclusive maternal care may compromise lifetime fecundity, as caring females tend to produce fewer offspring compared to those who are experimentally prevented from caring for their eggs (e.g., insects: Tallamy and Denno 1982; Zink 2003; arachnids: Fink 1986; Buzatto et al. 2007; fish: Smith and Wootton 1995; amphibians: Yurewicz and Wilbur 2004; Dugas et al. 2015). In contrast, exclusive paternal care does not necessarily impose reproductive costs on males. In certain species, males are prevented from acquiring additional mates while caring for the offspring (e.g., seahorses: Jones et al. 1998; mouthbrooding fish: Hess 1993; stomach brooding frogs: Wells 2007) or can only obtain a limited number of mates (e.g., water bugs: Smith 1997; Ohba et al. 2010; pipefish: Jones et al. 1999; back brooding frogs: Wells 2007). However, in other species, males can mate with several females while caring for offspring. When males can receive and care for eggs from different females, paternal care can be a sexually selected behavior. In such cases, females prefer males engaged in parental care over non-parental ones, thus paternal care may improve male reproductive success (e.g., arthropods: Gilbert et al. 2010; Nazareth and Machado 2010; Requena and Machado 2015; Ohba et al. 2016, 2018; fish: Goldberg et al. 2020; frogs: Valencia-Aguilar et al. 2020).

There are two main explanations for why females exhibit mating preferences for parental males: the *good parent hypothesis* (Hoelzer 1989) and the *essential male care model* (Kelly and Alonzo 2009; named after Pettitt et al. 2020). Both explanations consider that certain male traits, such as body size, body condition, color patterns, pheromones, or the frequency of specific behaviors, serve as signals of male quality to females (Hoelzer 1989). According to the good parent hypothesis, morphological and/or behavioral traits communicate to females the quality of a male as caregiver (Hoelzer 1989). Since the expression and maintenance of these traits are assumed to be costly, they function as honest signals of parental quality because only males in good body condition are able to pay the costs (Zahavi 1975). Therefore, if parental care significantly influences offspring survival, females gain direct benefits by selecting males who excel as caregivers (Hoelzer 1989). Numerous tests of the good parent hypothesis have been conducted, but empirical evidence remains inconclusive. While some studies have supported the hypothesis (e.g., birds: Hill 1991; Nishida and Takagi 2018; fish: Forsgren et al. 1996; Lindström et al. 2006; Pagani-Núñez and Senar 2014, 2016), others have not (e.g., birds: Smiseth et al. 2001; Mitchell et al. 2007; Lucass et al. 2016; fish: Rios-Cardenas and Webster 2005).

According to the essential male care model, named so because it assumes that male presence is crucial for offspring survival in species with exclusive paternal care (see

Pettitt et al. 2020), the quality of a parental male is determined by the allocation of energy into two primary components: care for the offspring and the advertisement of its quality (e.g., body condition) in the form of sexual signals directed at females. When relatively low levels of care are required for offspring survival, the model predicts that all males will have sufficient energy to provide parental care. However, only those in good body condition will be able to allocate the surplus energy to advertising their quality, and consequently will attract more females (Kelly and Alonzo 2009). In addition to females securing partners that provide care for the offspring (direct benefits), males that have more energy to invest in sexual advertisement are also signaling their genetic quality, which can provide indirect benefits for females (Kelly and Alonzo 2009). To the best of our knowledge, there are only two empirical studies that have tested the predictions of the essential male care model. One of these studies, conducted with the golden rocket frog *Anomaloglossus beebei*, found no support for the model's predictions (Pettitt et al. 2020). In contrast, the other study, conducted with the peacock blenny *Salaria pavo*, provided supporting evidence for the model's predictions (Pizzolli et al. 2012).

Although rare in the animal kingdom, exclusive paternal care is relatively frequent in fish (Goldberg et al. 2020), anurans (Furness and Capellini 2019), and arthropods (Requena et al. 2014). Notably, within arthropods, cases of independent evolution of exclusive paternal care are disproportionately concentrated in arachnids of the order Opiliones, commonly known as harvestmen. This order constitutes less than 0.6% of arthropod species diversity, yet it accounts for at least 60% of cases of independent evolution of paternal care (Requena et al. 2014). For two non-closely related harvestman species that exhibit exclusive paternal care, *Magnispina neptunus* (Nazareth and Machado 2010) and *Iporangaia pustulosa* (Requena and Machado 2015), females exhibit mating preference for paternal males. For one of these two species, *I. pustulosa*, long-term egg attendance (sensu Smiseth et al. 2012) results in energetic costs for males. Since foraging activities are significantly reduced during the caregiving period, the body condition of parental males declines over time (Requena et al. 2012). This leads to parental males having lower energy reserves after one month, which could decrease their caregiving quality and, consequently, their attractiveness to the females (Requena and Machado 2015).

In a recent field experiment, the body condition of parental males of *I. pustulosa* was manipulated to create two groups, well-fed and poorly fed males (i.e., in good and poor condition, respectively). Subsequently, the probability of receiving new eggs was recorded for nearly one month in both experimental groups. Males in good condition exhibited a

higher chance of receiving new eggs than their counterparts in poor condition. However, when comparing offspring survival, there was no difference between the two experimental groups in terms of the number of eggs consumed by predators (Alissa et al. 2024). Thus, although females exhibit a mating preference for parental males in good condition, the caregiving quality of these males does not differ from that of those in poor condition. As both males in good and poor condition proved equally efficient in protecting offspring against predators, the results refute the good parent hypothesis. In fact, the essential male care model appears to offer a better explanation for the observed patterns in the field experiment. Given that all males can provide care for their offspring, females would gain additional benefits by mating with high-quality males. The intensity or quality of the sexual advertisement displayed by males may serve as the signal used by females to differentiate between males in good and poor condition. We suspect that sexual advertisement is related to chemical compounds released by males through sexually dimorphic glands on the tarsus of the first pair of legs and on the metatarsus of the fourth pair of legs (Fig. 1). These glands are used in intraspecific communication (Murayama and Willemart 2015), and their exocrine products may function as sexual pheromones.

Due to a substantial background of observational and experimental research (see ‘Study species’ below), the harvestman *I. pustulosa* serves as an ideal study system for testing the predictions of the essential male care model. Therefore, we conducted a field experiment to assess the influence of body condition and sexual advertisement on the mating success of paternal males. According to the model, when males fulfil the minimum care requirements

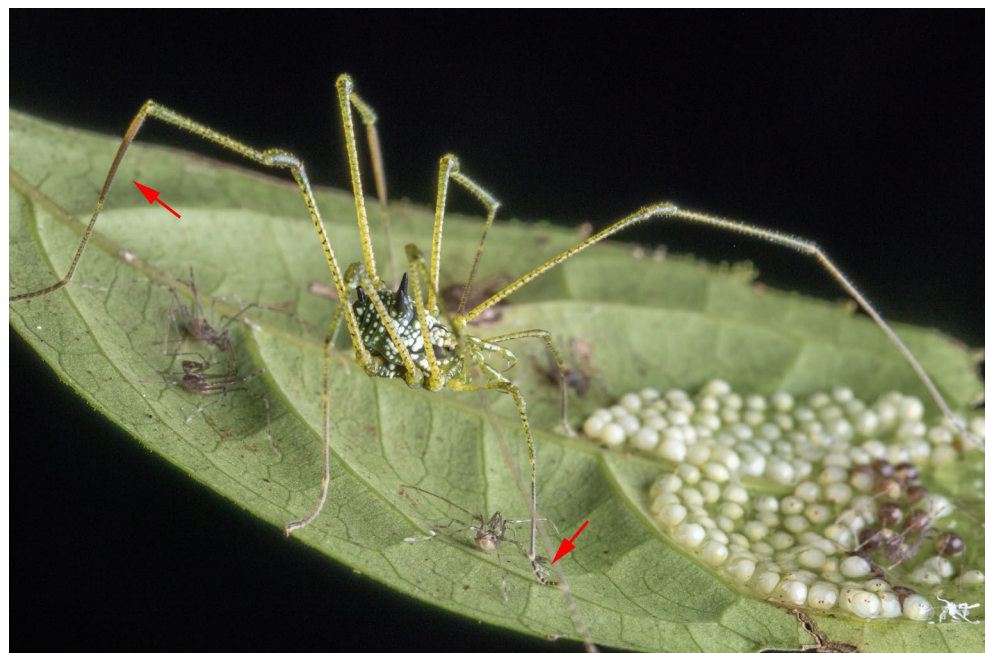
for offspring survival, they are expected to allocate their surplus energy towards advertising their condition to attract females. Therefore, increased advertisement by males in better body condition is expected to serve as a reliable indicator of their quality as mates (Kelly and Alonzo 2009). As a result, parental males in good condition and who are capable of advertising their quality to females through sexual pheromones are expected to achieve higher reproductive success compared to parental males in poor condition and who are unable to advertise their quality to females through sexual pheromones.

Materials and methods

Study species

The harvestman *Iporangaia pustulosa* is found in the marginal vegetation of streams in the Atlantic Forest from south-eastern Brazil. Females deposit their eggs on the underside of leaves, and males care for the eggs throughout the entire embryonic development period. Since multiple females may contribute eggs at different times, a single brood can consist of both recently laid eggs and newly hatched nymphs (Machado et al. 2004; Fig. 1). The embryonic development of the eggs spans approximately 25–35 days, and due to multiple oviposition events within a single brood, the total caregiving period may extend to as long as 3 months. During this time, parental males may occasionally leave their broods to forage or seek shelter, although they typically stay in close proximity to their eggs, which restricts their opportunities for feeding. Consequently, their body condition

Fig. 1 Male of the harvestman *Iporangaia pustulosa* caring for his brood. The red setae indicate the sexually dimorphic glands on the first pair of legs (small and located on the tarsal segments) and on the fourth pair (large and brown, located on the metatarsus). The brood contains already hatched nymphs along with eggs in three development stages: brown eggs near hatching, white eggs with two small black spots corresponding to embryo eyes, and completely white eggs recently laid. Photo: John Uribe Rosas



tends to decrease during the caregiving period (Requena et al. 2012).

Paternal care is crucial for the survival of offspring, as broods from which males are experimentally removed face heightened egg predation when compared to clutches where males are allowed to care for their eggs (Requena et al. 2009). Furthermore, the eggs of *I. pustulosa* are encased in a hygroscopic mucous coat that offers physical protection against certain egg predators, particularly small arthropods. Hence, even in the temporary absence of males, the eggs are not entirely defenseless against natural enemies (Requena et al. 2009). Data collected under natural field conditions indicate that females exhibit pronounced mating preference for parental males, but only when the broods are recent (i.e., less than 1 month old). As the brood ages (i.e., more than 1 month), the attractiveness of parental males decreases significantly and becomes equivalent to that of non-parental males (Requena and Machado 2015). A previous experiment suggests that females can assess male body condition when making their mating decisions (Alissa et al. 2024).

Although it is not clear how *I. pustulosa* females assess male body condition, the most plausible hypothesis is that they receive chemical signals. Harvestmen lack visual acuity, and the primary means of conspecific communication are tactile and chemical signals. Chemical signals, in particular, are detected by chemoreceptors located on the first and especially second pair of legs, also known as antenniform legs, because they are used as sensory rather than ambulatory appendages (Shultz and Pinto-da-Rocha 2007; Willemart et al. 2009). In *I. pustulosa*, the chemical signals are likely emitted through two conspicuous and sexually dimorphic glands in males. The first gland, also found in closely related species, is small and located on the tarsal segments of the first pair of legs (Kury and Pinto-da-Rocha 1997; Fig. 1). The second gland, unique to *I. pustulosa*, is large and situated on the metatarsus of the fourth pair of legs (Fig. 1). Males rub these glands on leaves and the chemicals they deposit on the substrate likely convey information about their location (Murayama and Willemart 2015). Moreover, as both glands are sexually dimorphic and exclusive to males, we suspect they are also used to deposit chemicals as a form of sexual advertisement to females.

Study area

We conducted the study at Intervalles State Park (24°14'S; 48°04'W), a large fragment of Atlantic Forest located in the state of São Paulo, southeastern Brazil. The average annual rainfall in the area is 2,000 to 3,000 mm/year and mean monthly temperature ranges from 12 to 20 °C. There is a well-defined climatic seasonality, with a wet and warm

period from October to March and a dry and cold period from April to September. We conducted the field experiments between January and May 2022, during one of the two peaks of reproductive activity of *I. pustulosa* at the study site (Requena et al. 2012). Samplings were conducted in the marginal vegetation of a stream along a 350-meter-long transect.

Field experiment

We conducted a full-factorial field experiment in which we manipulated both the body condition and the capacity of parental males to release chemicals from their sexually dimorphic glands. We then quantified their probability of receiving new eggs and the number of eggs received. First, we located parental males with their broods in the vegetation. Each brood was photographed to count the number of eggs and was enclosed in a plastic bag to protect the eggs from predators while we manipulated the body condition of the parental male. In the laboratory, each parental male was weighed on an electronic scale (to the nearest 0.001 g) and photographed from dorsal and lateral views to estimate the body condition before manipulation (see 'Estimation of body condition' below).

Due to the low basal metabolism of harvestmen, especially during resting conditions (Santos 2007), we exposed all parental males to forced walking exercises to accelerate the decrease of body condition. The males underwent 12 h of forced exercise in cycles comprising 30 min of continuous walking followed by 30 min of rest (as in Alissa et al. 2024). Then, they were divided into two experimental groups: the well-fed group (hereafter referred to as 'good condition') and the poorly fed group (hereafter referred to as 'poor condition'). In the good condition group, males were provided with a diet consisting of a mixture of sardine, soy oil, and whey protein, along with unrestricted access to water for 24 h. In contrast, males in the poor condition group received no food but had access to water *ad libitum* during the same 24-hour period.

After manipulating the body condition, the males were further divided into two additional groups: blocked sexually dimorphic glands (hereafter referred to as 'blocked glands') and unblocked sexually dimorphic glands (hereafter referred to as 'unblocked glands'). In the blocked glands group, we obliterated both the glands on the tarsus of the first pair of legs and on the metatarsus of the fourth pair of legs by applying enamel ink. Additionally, on the tarsus of the first pair of legs we applied a fast-drying glue (Super Bonder®) to secure the ink since preliminary manipulations revealed that the ink could be removed by the males using their chelicerae. In the unblocked glands group, we used enamel ink

and the same fast-drying glue on other leg segments that did not contain sexually dimorphic glands (i.e., the tarsus of the third pair of legs) and only enamel ink was applied to the femur of the fourth pair of legs. The color combination of enamel ink used on the fourth pair of legs (i.e., metatarsus and femur, depending on the experimental group) was also used for individual identification in the field. After manipulation, all males were re-weighed and photographed to estimate their body condition once again.

Parental males were subsequently returned to their respective broods, at which time the plastic bag enclosing the brood was removed. We revisited all experimental broods 15 and 30 days after manipulation and recorded the presence of parental males. Additionally, we photographed the broods to determine whether new eggs had been added to them and, if so, the number of eggs added (following protocol by Alissa et al. 2024). It is important to note that we do not have records of parental males cannibalizing their own eggs (Requena and Machado 2015), and the efficiency of paternal care against both conspecific and heterospecific predators is very high (Requena et al. 2009). Therefore, our egg counts likely closely reflect the total number of eggs received by the experimental males.

Throughout the course of the 5 months of fieldwork, we manipulated a total of 112 parental males. Among these, 29 were in good condition and with unblocked glands, 27 were in good condition and with blocked glands, 27 were in poor condition and with unblocked glands, and 29 were in poor condition and with blocked glands.

Estimation of body condition

To assess whether our manipulation effectively resulted in differences in body condition between the two experimental groups (i.e., good and poor condition), we compared their body condition before and after manipulation. As a proxy for body condition, we used body density, which has been used in two earlier studies with *I. pustulosa* and has proven to provide reliable information on body condition (Requena et al. 2012; Alissa et al. 2024). Since lipid molecules occupy a larger volume compared to proteins or water, the higher the fat content, the lower the individual body density and consequently the better its body condition (Moya-Laraño et al. 2008).

To determine the body density of all males included in our experiment, we first obtained their body mass (BM). Using the photographs taken from dorsal and lateral views of the males, we measured the following traits with the *ImageJ* software (Schneider et al. 2012): total body length (TBL), measured from the anterior margin of the dorsal scute to the end of the free tergites, body width (BW) at the widest

portion of the dorsal scute, and body height (BH) (Fig. S1 in Supplementary Material). With these three measurements, we calculated body volume (BV) using the formula of an ellipsoid:

$$BV = \frac{4}{3} * \pi * \left(\frac{TBL}{2} \right) * \left(\frac{BW}{2} \right) * \left(\frac{BH}{2} \right)$$

. We then determined body density (g/mm^3) by dividing BM by BV (following Requena et al. 2012 and Alissa et al. 2024).

We used a paired t-test to compare the body density of parental males before and after manipulation within each experimental group, and found significant differences (good condition: $t=5.62$, $df=96$, $p<0.001$; poor condition: $t=-2.05$, $df=103$, $p=0.04$; Figure S2 in Supplementary Material). As expected, the body density of males in the good condition group decreased (i.e., their lipid reserves increased) while the body density of males in the poor condition group increased (i.e., their lipid reserves decreased). Next, we used an independent samples t-test to compare the body density between parental males of the two experimental groups after manipulation, and found significant differences between them ($t=6.52$, $df=176.21$, $p<0.001$; Fig. S3 in Supplementary Material). As expected, males in the good condition group exhibited lower body density than males in the poor condition group, which means that the former had a greater amount of lipid reserves than the latter. Consequently, our manipulation successfully created the desired differences between the experimental groups.

Data analyses

We predicted that males in good body condition and with unblocked glands would (1) have a higher probability of receiving new eggs and (2) receive a greater number of eggs than males in poor body condition and with blocked glands. For males in good body condition and with blocked glands and males in poor condition and with unblocked glands, we predicted intermediate values. To test prediction (1), we classified the parental males as ‘successful’ if they received new eggs during the 15 and/or 30 days following experimental manipulation and as ‘unsuccessful’ if they did not receive new eggs during the same period. The response variable was the proportion of successful and unsuccessful males. To test prediction (2), we considered the total number of eggs received during the 15 and/or 30 days following manipulation as the response variable.

To test our predictions, we used a zero-inflated negative binomial model (ZINB), which assumes that the response variable is a function of two processes. In our case, these processes are: (a) a binomial process, corresponding to receiving or not receiving eggs during the 15 and/or 30 days following manipulation, and (b) a count process, representing the number of eggs received by the successful

males. Process (a) has a binomial distribution of errors with a logit link function and is similar to generalized linear models (GLM) dealing with binomial data. Process (b) has a negative binomial distribution of errors with a log-link function and is similar to GLMs dealing with count data. Because ZINB returns two outputs separately and each one is based on one of these two processes, the same model was employed to test both predictions and used the same predictor variables: body condition (with two levels: good and poor) and gland status (with two levels: blocked and unblocked).

We fitted a full model with the predictor variables in an additive and interactive way. However, because the *p*-value of the interaction was non-significant neither in the process (a) nor in the process (b), we used a likelihood ratio test to compare the fit of the model with the interaction and without the interaction in both processes (deviance: $X^2=2.07$, $df=2$, $p=0.35$). Then, we removed the interaction term and fitted a model with the predictor variables only in an additive way. Similarly, because the *p*-value for body condition was marginally non-significant in process (a), we performed a likelihood ratio test to compare the model's fit with and without the term "condition" in process (a) (deviance: $X^2=3.83$, $df=1$, $p=0.05$). Based on the test results, we retained the term "condition" when modeling process (a). Although neither glands nor body condition were significant in process (b), we included them only to calculate the estimates. Thus, the final model used for analysis is specified as follows: Process (a)~glands+body condition and Process (b)~glands+body condition.

After fitting the model, we calculated the exponentiated coefficients to determine the effect size of the predictor variables in terms of odds ratios and computed the predicted values for the experimental groups. Because the process (a), which represents the probability of receiving eggs, returns the coefficients of the odds ratio for the *non-occurrence* of the event (Beaujean and Morgan 2016), we inverted the sign of the coefficients to obtain the odds ratio of *occurrence*. Additionally, for the same process, we considered that the collection date ($n=7$ visits to the field between January and May) could introduce potential temporal effects among

visits. We then fitted a generalized linear mixed model (GLMM) incorporating the date as a random effect. However, since we observed that the variation explained by the collection date was very low (variance=0.05, $SD=0.21$), we removed the random effect from the analysis. For process (b), we aggregated the number of eggs received by males over 15 and/or 30 days post-manipulation as the response variable, because the sample size was insufficient to model the two periods separately.

To calculate the mean fitness of males in each experimental group we multiplied the predicted probability of receiving new eggs by the predicted count of eggs received. Unfortunately, we do not have data on the number of eggs fertilized by the experimental males, which would be important for a more precise evaluation of their fitness. Therefore, in our fitness calculations, we assume that all eggs tended by a male were fertilized by him.

We used the following packages for our analysis: *lme4* (Bates et al. 2015) and *pscl* (Zeileis et al. 2008) for building the models, *arm* (Gelman and Su 2024) for obtaining the coefficients as probabilities, *lmtest* (Zeileis and Hothorn 2002) for comparing the fit of the models, *VGAM* (Yee 2023) and *DHARMa* (Hartig 2022) for exploring the fit of the models, and *ggplot2* (Wickham 2016) and *ggeffects* (Lüdtke 2018) for visualizing the results. All analyses were performed using R software version 4.3.3 (R Core Team 2024).

Results

Prediction (1): probability of receiving new eggs

After manipulation, 39.3% (22 out of 56) of the males with unblocked glands from both body condition treatments received new eggs, whereas only 12.5% (7 out of 56) of the males with blocked glands from both body condition treatments received new eggs. The percentage of males in each experimental group that received new eggs was as follows: 44.8% (13 out of 29) in good condition and with unblocked glands; 22.2% (6 out of 27) in good condition and with blocked glands; 33.3% (9 out of 27) in poor condition and with unblocked glands; and 3.5% (1 out of 29) in poor condition and with blocked glands. Considering the coefficients of the model in the binomial process (Table 1), the chance of males receiving new eggs was 2.5 times higher when they were in good condition and 4.7 times higher when they had unblocked glands (Fig. 2a). The probability of receiving new eggs was markedly different between males in good condition and with unblocked glands and those in poor condition and with blocked glands; males in the other two experimental groups exhibited intermediate values (Fig. 2a).

Table 1 Model to evaluate the probability of parental males of the harvestman *Iporangaia pustulosa* receiving new eggs (binomial process) and the estimated number of eggs received (count process) after experimental manipulation of their body condition and sexually dimorphic glands. SE is the standard error

Model process	Parameter	Estimate	SE	<i>p</i> -value
(a) Binomial	Intercept	2.43	0.51	<0.001
	Glands	-1.54	0.50	0.002
	Condition	-0.92	0.48	0.055
(b) Count	Intercept	3.38	0.52	<0.001
	Glands	0.21	0.45	0.634
	Condition	-0.23	0.40	0.569

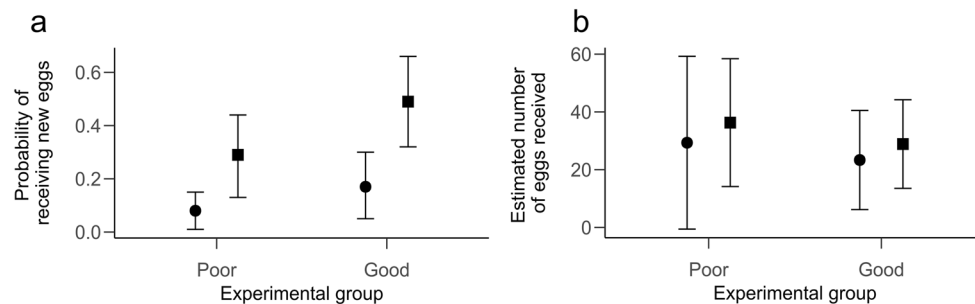


Fig. 2 (a) Probability of parental males of the harvestman *Iporangaia pustulosa* receiving new eggs and (b) estimated number of new eggs received by them after experimental manipulation of their body condition and sexually dimorphic glands. Circles represent the average val-

ues for males with blocked glands, and squares represent the average values for males with unblocked glands. In (a) and (b), vertical bars represent the 95% confidence interval

Prediction (2): number of new eggs received

The average (\pm SD) number of new eggs received by males with unblocked glands from both body condition treatments was 32.9 ± 30.1 (range: 2–115 eggs, $n=22$ males), whereas the average number for males with blocked glands from both body condition treatments was 24.7 ± 31.5 (range: 4–94 eggs, $n=7$ males). The average number of new eggs received by males in each experimental group was as follows: 29.1 ± 32.2 (range: 3–115 eggs, $n=13$ males) in good condition and with unblocked glands; 25.3 ± 34.4 (range: 4–94 eggs, $n=6$ males) in good condition and with blocked glands; and 38.3 ± 27.7 (range: 2–87, $n=9$ males) in poor condition and with unblocked glands. Only one male received new eggs (21 in total) in the poor condition and with blocked glands group. Considering the coefficients of the model in the count process (Table 1), the effect of gland status was positive, as unblocked glands increased the number of eggs received by a factor of 1.24. The effect of body condition was slightly negative, as good condition decreased the number of eggs by a factor of 0.79 (Fig. 2b). Nevertheless, both coefficients were non-significant. Overall, the estimated number of eggs received was similar across all experimental groups, with great overlap in the confidence intervals (Fig. 2b).

Male fitness

Males in good condition and with unblocked glands had a mean fitness 1.38 times higher (14.7 eggs) than males in poor condition with unblocked glands (10.6 eggs). Males in good and poor condition, but with blocked glands, had lower mean fitness (4.2 and 2.4 eggs, respectively). When in good condition, males with unblocked glands received, on average, 3.48 eggs more than those with blocked glands. In the same way, when in poor condition, males with unblocked glands received, on average, 4.46 eggs more than those with blocked glands.

Discussion

The primary objective of our study was to evaluate the effect of body condition and sexual advertisement on the mating success of parental males using the Neotropical harvestman *Iporangaia pustulosa* as our study system. We tested a key prediction of the essential male care model, which posits that males, upon fulfilling the minimum care requirements for offspring survival, should allocate their surplus energy towards advertising their good body condition to attract females (Kelly and Alonzo 2009). In a full-factorial experiment conducted in the field, we manipulated the body condition of the parental males and their capacity to emit products from sexually dimorphic glands. Our results corroborate the model's prediction: parental males in good body condition and with unblocked glands, exhibited a significantly higher probability of acquiring new eggs compared to parental males in poor body condition and with blocked glands. Also as expected, the probability of acquiring new clutches for parental males of the other two experimental groups (good condition with blocked glands and poor condition with unblocked glands) showed intermediate values. The same qualitative pattern was also observed when we estimated the mean fitness of the parental males in the four experimental groups. In all analyses, the effect size of the gland status consistently outweighed that of the body condition.

When males were allowed to emit the products of their sexually dimorphic glands, those in good body condition had a higher probability of acquiring matings than those in poor body condition. The effect for body condition found here, although marginally significant, aligns with the conclusions of a previous study, which clearly demonstrated that females prefer males in better body condition, despite not being better caregivers than males in poor body condition (Alissa et al. 2024). According to the essential male care model (Kelly and Alonzo 2009), the higher mating success of males in good body condition is attributed to their increased investment in sexual advertisement. Mounting

evidence suggests that females of various species respond to variations in the emission rate and chemical composition of sexual pheromones released by males. These variations are often associated with male quality, playing a key role in mate choice (Johansson and Jones 2007). While the specific features of the chemicals released by the sexually dimorphic glands in *I. pustulosa* remain unclear, our study provides the first unequivocal evidence of sexual pheromones in harvestmen, a major arachnid group in which species heavily rely on chemicals for intraspecific communication (e.g., Machado et al. 2002; Willemart and Chelini 2007; Willemart and Hebets 2012). Moreover, our results suggest that the production of these sexual pheromones is condition-dependent, as reported for the production of defensive secretions in another harvestman species (Nazareth et al. 2016). Condition-dependent traits, whether morphological, behavioral, or chemical, often serve as indicators of mate quality across taxa (Bussière et al. 2007), and our study emphasizes their significance in the mate choice process in a species exhibiting exclusive paternal care.

Even when males were unable to emit sexual pheromones, those in good body condition exhibited a higher probability of acquiring matings compared to those in poor body condition. This finding clearly indicates that females are capable of evaluating males based on cues not related to sexual pheromones. Backup cues, which consist of multiple redundant sources of information regarding mate quality, play a crucial role in the mate choice process because only high-quality males can afford the costs associated with the expression of various costly traits (Candolin 2003). The front legs of *I. pustulosa* possess sensory organs responsible for the perception of chemical stimuli (Willemart and Chelini 2007), and we posit that females can use cuticular hydrocarbons (CHCs) to evaluate males' body condition during the intense leg tapping that precedes copulation (Requena and Machado 2014). CHCs in insects exhibit variability in composition and abundance, influencing females' mate decisions (e.g., Howard et al. 2003; Thomas and Simmons 2009; Lane et al. 2016). Moreover, CHCs are condition-dependent, and experiments with insects demonstrate that the chemical profiles change with diet quality, making males more or less attractive depending on how well-fed they are (e.g., Delcourt and Rundle 2011; Gosden and Chenoweth 2011; Weddle et al. 2012; Ingleby et al. 2014). Thus, in the absence of pheromones emitted by the sexually dimorphic glands, CHCs may serve as a backup cue for *I. pustulosa* females to assess males' body condition, a trait often associated with genetic quality (Bussière et al. 2007).

Males in poor body condition but capable of emitting sexual pheromones were more successful in acquiring matings than males in good body condition but unable to emit pheromones. This finding underscores the multifaceted nature of

chemical signals, which not only provide information about the characteristics of potential mates during mate choice, such as size (e.g., Beeler et al. 2002), age (e.g., López et al. 2003), or social status (e.g., Kortet and Hedrick 2005), but also about their spatial location (e.g., Lonsdale et al. 1998; Byrne and Keogh 2007). Given that harvestmen rely primarily on contact chemoreception or close-range olfaction for intersexual communication (Willemart and Chelini 2007; Willemart et al. 2009), and that *I. pustulosa* males rub their sexually dimorphic glands on the substrate (Murayama and Willemart 2015), we suggest that they are chemically advertising their presence to attract females. Thus, when males in good body condition are unable to use their glands for advertisement, they attract a lower number of females compared to males in poor body condition that are capable of marking the surroundings of their broods. Considering that males remain mostly stationary during the caregiving period, and females are solely responsible for mate search in the species (Requena and Machado 2014), the emission of sexual pheromones may have a more important role than body condition in the males' mating success. In fact, this suggestion is further supported by our findings, indicating that the effect sizes of the gland status on the probability of acquiring new eggs were consistently higher than that of the body condition.

Although our results do not indicate an effect of both gland status and body condition in the average number of eggs received by males, this analysis only considers males who were successful in acquiring new eggs. When comparing the mean fitness of all experimental males, taking into account the probability of acquiring new eggs, the pattern is clear: both the experimental decline in body condition and the blocking of the sexually dimorphic glands lead to a marked decrease in the fitness of the parental males. According to the essential care model, when offspring survival has a minimum care requirements, an increase in sexual advertisement becomes an indicator of higher male quality (Kelly and Alonzo 2009). If parental care is an important factor for female choice, as is the case in *I. pustulosa* (Requena and Machado 2015), the selection pressure lies on the minimum level of advertisement for female acceptance. Even a small increase in advertisement may translate into a marked increase in male quality, and, consequently, in mating success. A long-term field study has shown that nearly 84% of the *I. pustulosa* males do not acquire eggs during the breeding season (Requena and Machado 2015). Moreover, using the data on the number of matings presented on Fig. 2A in Requena and Machado (2015), we calculated the I_s (a metric of intra-sexual variation in mating success) and found a value of 2.645. For comparative purposes, the average I_s value obtained in a meta-analysis with more than 80 animal species was only 0.151 (Janicke et al. 2016). Based on our

estimation of mean fitness in different experimental groups, we argue that this variation can be explained by differences in the surplus energy males in good body condition have to invest in sexual advertisement.

To the best of our knowledge, this study represents the first examination of the essential male care model in invertebrates. The other two studies that tested predictions of the model were conducted with vertebrates: the peacock blenny *Salarias pavo* (Pizzolon et al. 2012) and the golden rocket frog *Anomaloglossus beebei* (Pettitt et al. 2020). While the first study found support for the predictions of the model, the second one did not. The essential male care model posits stringent premises, requiring both exclusivity and indispensability of male care for offspring survival (Kelly and Alonzo 2009). Only *S. pavo* conforms to these two premises, as males are solely responsible for egg attendance, and broods from which males are experimentally removed experience high mortality (Barata et al. 2008). In contrast, parental care in *A. beebei* is performed by both males and females, and a significant number of eggs survive to hatching when males are experimentally removed, likely due to the heightened effort by females (Pettitt et al. 2020). Given that *A. beebei* males qualitatively vary as caregivers, females may enhance their fitness by selecting males that invest significant effort in offspring care. In fact, females prefer males emitting longer calls, a trait positively correlated with the caregiving quality of the males (Pettitt et al. 2020). In *S. pavo* and *I. pustulosa*, all males seem capable of providing the minimum care requirements for egg survival, thus there is little interindividual variance in their caregiving quality (Barata et al. 2008; Alissa et al. 2024). In cases like this, the essential male care model predicts that females would receive the most benefits in both care and mate quality by choosing males that allocate more resources to advertisement. This expectation is supported by experimental evidence (*S. pavo*: Barata et al. 2008 and Pizzolon et al. 2012; *I. pustulosa*: this study), suggesting that the model has great predictive power for species that fulfill its premises.

In conclusion, our findings contribute to our understanding of mate choice mechanisms in species with exclusive paternal care, a subject that has historically been more intensively explored in fish (e.g., Jamieson 1995; Östlund and Ahnesjö 1998; Östlund-Nilsson 2001; Pampoulie et al. 2004; Lindström et al. 2006; Hale and St Mary 2007; Lehtonen et al. 2007). Similar to what has been reported for this vertebrate group, we demonstrate that harvestman females may evaluate males based on multiple backup cues, including both chemical signals and body condition (Candolin 2003). Furthermore, our study suggests that the production of sexual pheromones in harvestmen is condition-dependent and emphasizes the significance of chemical sexual advertisements as indicators of male quality, not

only in *I. pustulosa*, but also other species showing exclusive paternal care (e.g., Östlund-Nilsson 2001; Barata et al. 2008). Overall, our findings support the predictive power of the essential male care model and shed light on the interplay between body condition, sexual advertisement, and mating success in species exhibiting exclusive paternal care. Further research with our study species is warranted to explore the costs of sexual pheromone production and the effect of males' body condition on the quantity and quality of this pheromone.

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Data availability The datasets used in this study are available in the Zenodo repository (<https://doi.org/10.5281/zenodo.13620000>).

Declarations

Ethical approval The procedures used in this study comply with Brazilian legislation regarding the collection and handling of invertebrates.

Competing interests The authors declare no competing interests.

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