

RESEARCH ARTICLE

Effects of Nest-Site Availability on Male–Male Competition and the Foraging Costs of Egg Attendance in an Arachnid With Exclusive Paternal Care

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ABSTRACT

Natural cavities are monopolizable resources used as nest sites across many species exhibiting exclusive male care. However, our understanding of how the availability of this type of reproductive site influences male–male competition and the foraging costs associated with parental care is limited and based on studies of fish. The harvestman *Magnispina neptunus* offers the opportunity to explore these questions in invertebrates because males defend natural cavities used as oviposition sites and provide exclusive parental care. We hypothesized that low nest availability would increase male–male competition and the foraging costs of egg attendance. To test this hypothesis, we collected observational data in the field and conducted a laboratory experiment with two groups, low and high nest availability. Field data indicate natural cavity scarcity, as only 50% of the males were nest holders. Larger males were more likely to hold nests in the field, but body size did not predict nest ownership in the laboratory. In the field, nests with openings smaller than average were equally occupied by small and large males, while nests with openings larger than average were occupied almost exclusively by large males. The nest opening in the laboratory experiment was adjusted to be equal to the average found in the field, which may have increased nest defensibility, regardless of male size. Thus, prior residency may outweigh body size in determining nest possession. Because nest owners seem to have an advantage over intruders, the costs of abandoning a nest are likely high. This may explain why the frequency of nest takeovers and foraging outside the nests did not differ between experimental groups. In conclusion, although underexplored in empirical studies, external factors, such as the opening size of cavities defended by males of many species with resource-defense mating systems, may play a key role in the defensibility of nest sites.

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1 | Introduction

The spatial distribution and availability of breeding resources critically influence male–male competition in species with resource-based mating systems (Emlen and Oring 1977). When breeding resources are scarce or clustered, a limited number of males can monopolize them through agonistic interactions. Consequently, successful males gain exclusive access to females, securing most copulations and resulting in high variance in male reproductive success (Emlen and Oring 1977; Shuster and Wade 2003). Natural cavities, such as preexisting holes in the soil, tree trunks, fallen logs, rocks, and corals, serve as monopolizable nest sites across various species. For instance, males in certain fish and anuran species defend natural cavities to attract ovipositing females, who leave their eggs under the nest owner's protection (reviewed in Wells 2007 and Bessa, Brandão, and Gonçalves-de-Freitas 2022). In these taxa, the scarcity of natural cavities limits the number of available breeding sites, favoring larger or stronger males capable of monopolizing them (fish: e.g., Lindström 1988; Forsgren, Kvarnemo, and Lindström 1996; frogs: e.g., Heying 2004; Wickramasinghe et al. 2004). Additionally, in situations of natural cavity scarcity, the costs of nest defense may increase, as males likely reduce foraging and allocate more time to maintaining nest possession, especially if they have eggs in the nest (e.g., Nazareth and Machado 2010).

The impact of breeding resource availability on male–male competition has been extensively examined in vertebrates, mostly in fish species displaying exclusive paternal care (e.g.,

Lugli et al. 1992; Lindström and Seppa 1996; Lindström 2001; Singer et al. 2006; Takahashi 2008; Natsumeda, Mori, and Yuma 2012; Wacker and Amundsen 2014). This highlights a taxonomic bias in animal behavior research (Rosenthal et al. 2017) and raises the question: should we expect the patterns reported for fish to also apply to distantly related taxa, such as invertebrates? In the yellow dung fly *Scatophaga stercoraria* (Linnaeus, 1758), for instance, experimental manipulation of the availability of dung pats revealed that in sites with abundant dung pats, smaller males achieved relatively greater success in attracting females compared to sites with fewer dung pats. Similarly, in the lobster *Homarus gammarus* (Linnaeus, 1758), the relationship between male body size and mate acquisition was less pronounced when shelters were abundant compared to when they were scarce (Debusse, Addison, and Reynolds 2003). Conversely, in the harvestman *Serracutisoma proximum* (Mello-Leitão, 1922), the intensity of selection remained unaffected by the availability of oviposition sites (Muniz and Machado 2015). However, it is noteworthy that in none of the species mentioned above do males exhibit exclusive egg attendance, highlighting a knowledge gap.

The harvestman *Magnispina neptunus* Mendes (2011) is an ideal study system for investigating the effect of breeding resource availability on the intensity of male–male competition and the foraging costs associated with egg attendance in invertebrates. Males in this species fight to secure possession of natural cavities in roadside or riverside banks, serving as oviposition sites for females (Nazareth and Machado 2010; Figure 1). These fights may result in nest takeover, but it is

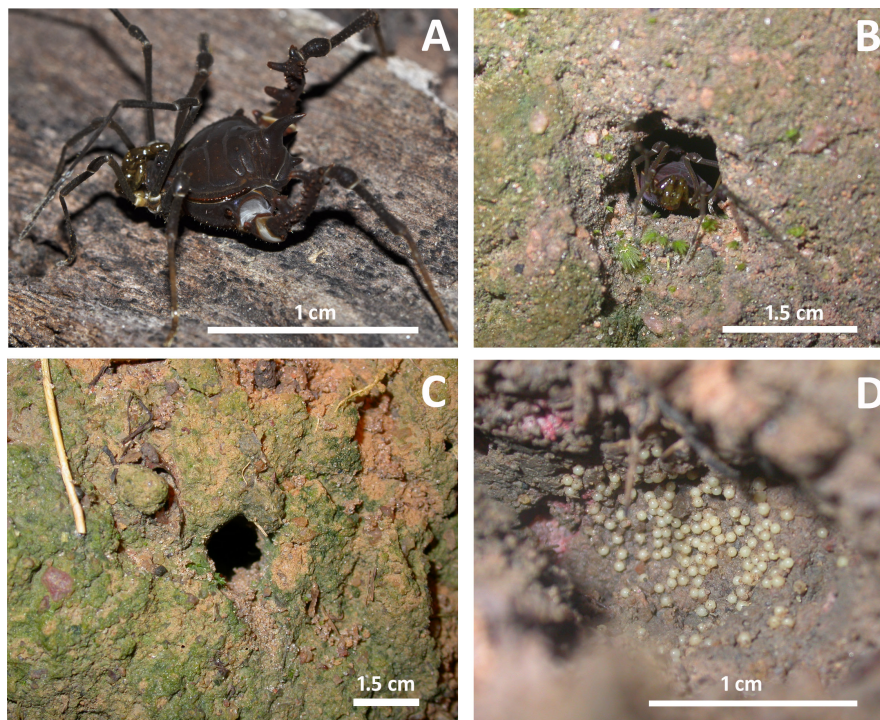


FIGURE 1 | (A) Male of *Magnispina neptunus* (photo: Adriano B. Kury). The conspicuous spines on the fourth pair of legs are used in male–male fights for nest possession. (B) Male at the opening of his nest (photo: Glauco Machado). Note that, when the nest opening is small, the male can entirely block it with his body. (C) Nest opening with nearly 1.5 cm, which was the mean value we observed in our field collection (photo: Glauco Machado). (D) Interior of a nest shows the eggs. To better visualize the eggs, the male was temporarily removed from the nest, and its opening was widened (photo: Glauco Machado).

unclear whether larger males have some advantage. Exclusive egg attendance is provided by males, which actively repel conspecific intruders and potential egg predators from their nests (Nazareth and Machado 2010). Under laboratory conditions, the size of nest-holding males does not affect their likelihood of acquiring eggs (Nazareth and Machado 2010). However, experimental evidence shows that females exhibit a preference for ovipositing inside nests that already contain eggs from other females, regardless of individual male traits (Nazareth and Machado 2010). This finding suggests that paternal care is a sexually selected trait and may explain why males adopt unrelated eggs when parental males are experimentally removed from their nests (Requena, Munguía-Steyer, and Machado 2013).

Given the potential for multiple and asynchronous mating opportunities, the caregiving period in *M. neptunus* may extend beyond 2 months, during which males have limited foraging opportunities (Nazareth and Machado 2010). However, it remains unknown whether this translates into a reduction in male body condition. In the harvestman *Iporangaia pustulosa* Mello-Leitão, 1935, for instance, parental males reduce their foraging activities compared to males without eggs, resulting in a decline in body condition over the caregiving period (Requena et al. 2012). In contrast, in another harvestman species, *Quindina albomarginis* (Chamberlin, 1925), the body condition of parental males remains unchanged over the caregiving period, probably because they have access to abundant food in the vicinity of their nests (Requena and Machado 2014). Contrary to these two species, males of *M. neptunus* engage in filial cannibalism, which may be a response to the prolonged period of reduced food intake, as observed in some fish with paternal care (Manica 2002; Bose 2022).

In this study, we first used field-collected data to answer three basic questions: (a) Does male body size predict the probability of securing a nest and acquiring eggs? (b) Is there a correlation between male size and the opening size of his nest? (c) Is male body condition influenced by nest possession or the presence of eggs in the nest? The field-collected data were used not only to gain a deeper understanding of the reproductive biology of the study species but also to provide insights into the outcomes of a laboratory experiment. This experiment was designed to address a broader question: does limited nest-site availability intensify male–male competition and the foraging costs of exclusive paternal care? We tested the following predictions associated with male–male competition in our laboratory experiment (Table 1): (1) the probability of a male holding a nest should increase with higher nest-site availability and larger body size; and (2) the proportion of occupied nests, (3) the number of male–male fights, (4) the number of nest take-overs, and (5) the probability of a male acquiring eggs should increase with decreasing nest-site availability. Additionally, a scarcity of nest sites should increase the foraging costs of parental care, leading to the following predictions (Table 1): (6) the foraging frequency of nest-owner males should decrease, especially when they have eggs in their nests, because parental males are known to remain inside their nests for longer periods (Nazareth and Machado 2010), and (7) the number of events of filial cannibalism should increase with decreasing nest-site availability.

2 | Materials and Methods

2.1 | Collection and Maintenance of Individuals in Captivity

In March 2011, we conducted a field trip to Arraial d'Ajuda (16°24'51" S; 39°04'17" W), state of Bahia, northeastern Brazil. The location where the individuals were collected is a small fragment of secondary Atlantic Forest on the outskirts of the city and about 1 km from the coast. The monthly temperature at the site is high throughout the year, with monthly averages ranging from 23°C to 30°C. Annual precipitation ranges from 1200 to 1800 mm, with a pronounced seasonality. The rainy season typically runs from April to August, while the dry season extends from September to March.

We searched for adults (both males and females) and nests of *Magnispina neptunus* inside two parallel plots (17 m long and 1 m wide), one at each riverside bank of a 1 m wide stream, between 20:00 h and 23:00 h. We identified nest-owner males and also recorded the presence of eggs in their nests. Additionally, we measured the diameter of each nest opening at its widest point using calipers (to the nearest 0.01 mm). In total, we found 103 females and 141 males, 71 nonnest-holding and 70 nest-holding (26 with eggs in their nests). In addition to the individuals found inside the plots, we collected 77 females and 39 males outside the plots, totaling 180 individuals of each sex.

After collection, we brought all individuals to our laboratory at the University of São Paulo, Brazil. The individuals were transported in styrofoam boxes containing leaf litter and pieces of wetted cotton to maintain the humidity. The day after arrival at the laboratory and before being fed, all males found inside the plots were weighed using a digital scale (to the nearest 0.001 g). Subsequently, we used calipers (to the nearest 0.01 mm) to measure the body width at the widest portion of the dorsal scute. Following the measurements, all individuals received individual marks with enamel paint applied to their dorsum (Figure 2).

Last, we separated the males from the females and housed them in four communal terraria (40×90 cm base, 20 cm height) for 45 days to enhance their motivation for mating. Throughout the study period (including the experiment), we maintained the laboratory with a temperature of 25°C, air humidity at 80%, and a photoperiod of 13:11 h (light: dark). We provided pieces of mealworms (Tenebrionidae) inside a Petri dish in the center of the terrarium three times a week. Thus, owner males had to leave their nests to have access to food as probably occurs in the field.

Field observations, animal transportation, and laboratory experiments followed the ASAB/ABS Guidelines for the treatment of animals in behavioral research.

2.2 | Experimental Design

To replicate the natural cavities used by *M. neptunus* individuals as nest sites, we built artificial nests from clay blocks (6×2 cm base, 3 cm height). Each nest had a central opening

TABLE 1 | Effects of nest-site availability on male–male competition and the foraging costs of paternal care in the harvestman *Magnispina neptunus*.

Variable	Prediction	Rationale
Male–male competition		
1. Probability of a male holding a nest	LOW < HIGH Large males > Small males	When nests are scarce, only a few males are likely to become nest owners, and these males are likely to be the largest ones because they probably have higher resource holding potential
2. Proportion of occupied nests	LOW > HIGH	When nests are scarce, most or all of them should be occupied by a male; the same is not true when nests are abundant
3. Number of male–male fights	LOW > HIGH	When nests are scarce, the number of fights between nest owners and invaders should be higher than when nests are abundant
4. Number of nest takeovers	LOW > HIGH	When nests are scarce and the fights for nest possession are frequent, the number of nest takeovers should be higher than when nests are abundant
5. Probability of a male acquiring eggs	LOW > HIGH	When nests are scarce, there are only a few owner males available for mate choice, and the chances of acquiring eggs should be higher than when nests are abundant
Foraging costs of paternal care		
6. Frequency of foraging outside the nest	LOW < HIGH Parental < Nonparental	When nests are scarce, unattended nests have a high chance of being usurped by other males, and owner males, especially those caring for eggs, should forage outside the nest less frequently than when nests are abundant
7. Number of events of filial cannibalism	LOW > HIGH	When nests are scarce, parental males could reduce the frequency of foraging outside the nest and acquire food by cannibalizing some eggs; the benefits of filial cannibalism are likely to be lower when nests are abundant

Note: Our experimental design included two groups: Low nest-site availability (LOW = 4 nests in each terrarium) and high nest-site availability (HIGH = 8 nests in each terrarium). The symbols < and > indicate “lower than” and “higher than,” respectively.

with a 1.5 cm diameter, consistent with the mean nest opening diameter recorded in the field (Figure 1B,C), and an internal chamber (4 cm wide, 2 cm height) crossing the clay block from one side to the other (Figure 2). These blocks were positioned against the glass wall of a terrarium (54×27 cm base, 23 cm height), enabling us to observe individual behaviors within the artificial nests.

Each experimental terrarium contained soil and small pieces of tree fern trunks for shelter and accommodated 12 males and 12 females. We selected each set of 12 males so that the average dorsal scute width did not differ between the terraria (mean ± SD = 6.68 ± 0.59 mm; ANOVA, $F = 1.25$, $df = 166$, $p = 0.26$). In total, we established 14 terraria (all of equal size) distributed between two experimental groups: seven terraria in low nest availability (referred to as LOW) with four nests per

terrarium ($n = 28$ nests in total), and seven terraria in high nest availability (referred to as HIGH) with eight nests per terrarium ($n = 56$ nests in total; Figure 2). We selected four nests as the low availability scenario because, if all nests were occupied, the occupancy rate would be approximately 33% of males with nests, which is 17 percentage points lower than the 50% observed in the field (see Section 3.1). In contrast, in the high availability scenario with 8 nests, full occupancy would result in an occupancy rate of around 67%, which is 17 percentage points higher than the field observation. The arrangement of the eight nests in the HIGH group followed the layout shown in Figure 2, with four nests on each side. For the LOW group, we placed two nests on each side (positions 1, 4, 5, and 8 in Figure 2).

We conducted our observations between July and November 2011, tracking each terrarium over a period of 29–32 consecutive

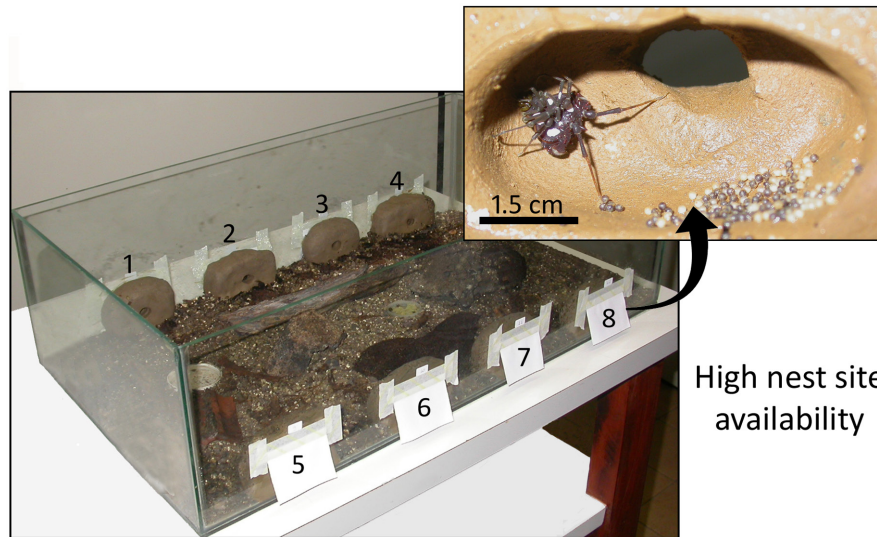


FIGURE 2 | Terrarium belonging to the high availability experimental group (HIGH) containing eight artificial nests made of clay (photo: Glauco Machado). The nests had an opening with a diameter of 1.5 cm facing the interior of the terrarium, through which individuals could enter and exit. The numbers indicate the position of each nest. The rear wall of the block was open and was placed in contact with the side wall of the terrarium. On the external side of the glass, we placed pieces of paper that, when flipped upward, allowed us to record the identity of the males inside the nests, and also monitor their behavior during the experiment. Inside one of the nests, a marked male with white dorsal dots is caring for his eggs.

days. During this time, we conducted six to eight scans with regular 30-min intervals every night, resulting in a total of 176–212 scans per terrarium. Given that *M. neptunus* individuals are strictly nocturnal, our observations were focused on the early hours of darkness (i.e., from 20:30 h to 00:00 h) when both males and females are most active. During each scan, we recorded if the nests were occupied, as well as the identity and behavior of the individuals inside the nests, with special attention to:

(1) *Male–male fights*, which occur when two males engage in aggressive interactions through intense leg tapping with the second pair of legs or entwining of the fourth pair of spiny legs (Nazareth and Machado 2010; Figure 1A). If the same two males were recorded fighting during two or more consecutive scans, we considered these instances as a single fighting interaction in our analysis. In addition to instances where we directly observed male–male fights during a scan, if we noted a male entering an already occupied nest in one scan and did not record his presence inside the same nest in the subsequent scan, we categorized this situation as a fight. This decision aligns with a prior study where we demonstrated that fights consistently occur when an intruder male enters a nest already occupied by another male (Nazareth and Machado 2010).

(2) *Filial cannibalism*, encompassing all instances in which parental males were observed consuming eggs inside their own nests. If the same male was observed consuming his own eggs during two or more consecutive scans, we treated these instances as a single event of filial cannibalism in our analysis. In addition to direct observations of filial cannibalism during the scans, we also inferred the occurrence of this behavior based on photos of each clutch we took every morning. If a parental male remained inside his nest throughout the entire night without any other individual entering, any reduction in the total number of eggs was recorded as an instance of filial cannibalism. This reduction was assessed by comparing the number of eggs in a

nest on day D + 1 with the number of eggs in the same nest on day D.

We considered a male as a nest owner only when he occupied the same nest for a minimum of six consecutive scans, equivalent to at least one full night of observation. In cases in which a nest owner male was displaced from his nest by another male, we considered this event as a nest takeover. However, if a male voluntarily abandoned a nest and this nest was then reoccupied by another male in subsequent scans, we did not consider it as a nest takeover.

2.3 | Statistical Procedures

2.3.1 | Field Data

The first question we asked using the field-collected data was whether male body size affects the probability of securing a nest and acquiring eggs. We predicted that larger males would have a higher resource-holding potential and, therefore, be more likely to secure a nest. To test this prediction, we initially employed a generalized linear mixed model (GLMM) with template model builder (TMB), using dorsal scute width as the predictor variable and nest possession (with a binomial error distribution) as the response variable. Subsequently, focusing solely on nest-holding males, we employed another GLMM-TMB in which the predictor variable was again the dorsal scute width, but the response variable (with a binomial error distribution) was the presence or absence of eggs in the nest. In both cases, we compared the fit between the full and null models using a likelihood ratio test.

In our second question, we explored a possible correlation between male size and the opening size of his nest. During fieldwork, we observed significant variation in the diameter of nest openings (see Section 3.1). Smaller nest openings allow males

to completely block them with their bodies, thus increasing resource defense efficiency and enabling even small males to maintain nest possession (Figure 1B). Conversely, larger nest openings pose a greater challenge to resource defense, suggesting that only larger males should be able to maintain nest possession. Therefore, nests with small openings should be occupied by males of various sizes, whereas nests with large openings should be occupied exclusively by large males. To test this prediction, we employed a null model approach.

Using the original field-collected data, we constructed a scatter plot with nest opening size on the x-axis and dorsal scute width on the y-axis. The scatter plot was divided into four quadrants based on whether they fell above or below the mean nest opening size and above or below the mean dorsal scute width. As per our prediction, the quadrant above the mean nest opening size and below the mean dorsal scute width (hereafter referred to as the “bottom right quadrant”) should contain few points, as only large males are expected to secure a nest when its opening is large. The number of points located within the bottom right quadrant was our statistic of interest. To assess whether the number of points found in the bottom right quadrant was lower than expected by chance, we randomized male sizes while keeping nest opening sizes fixed. In each randomization, we counted the number of points located in the bottom right quadrant. We repeated this randomization process 1000 times, generating a null distribution of the statistic of interest. The p value was calculated as $p = n/1000$, where n is the number of randomizations with a statistic of interest value lower or equal to the observed field value.

Our last question aimed to determine whether male body condition is influenced by nest possession or parental status. To investigate whether the limitation of foraging opportunities decreases the body condition of *M. neptunus* males, we first performed a linear regression between body weight and dorsal scute width. The residuals of this linear regression serve as a proxy for body condition, where positive values indicate well-fed individuals, whereas negative values indicate poorly-fed individuals (Jakob, Marshall, and Uetz 1996). In contrast to previous studies with harvestmen, we were unable to use body density as a proxy for male condition because the abdominal tergites of Heteropachylinae males are fused (Mendes 2011), resulting in individuals experiencing minimal changes in volume after a substantial meal. To analyze the data, we conducted an analysis of variance in which the response variable was the residuals of the linear regression, and the categorical variable was male status, categorized into three levels: (a) males without nests, (b) males holding nests without eggs, and (c) males holding nests with eggs.

2.3.2 | Laboratory Experiment

We tested our predictions using GLMM-TMBs and treated the terraria as a random variable to account for the possible variations among terraria, including differences in the total number of scans. When the response variable had a substantial number of zeros, we used zero-inflated (ZI) models (predictions 3, 4, and 7), also treating the terraria as a random variable. This kind of model assumes that the response variable is a function of two processes: (a) a binomial process, corresponding to the probability of occurrence of the event (fight, takeover, and filial

cannibalism) and (b) a count process, representing the number of events that occur. The structure and type of statistical models we used to test each prediction are summarized in Table 2. For all predictions, we used likelihood ratio tests to compare the fit of the full with fit of the null model.

We used the packages *glmmTMB* (Brooks et al. 2017) and *lme4* (Zeileis and Hothorn 2002) for building and comparing the models, *DHARMa* (Hartig 2022) for exploring the models fit, and *ggplot2* (Wickham 2016) and *ggeffects* (Lüdtke 2018) for visualizing the results. All analyses were performed in R version 4.3.3 (R Core Team 2024).

3 | Results

3.1 | Field Observations

The nest opening diameter ranged from 0.75 cm to 3.42 cm, with a mean (\pm SD) of 1.52 ± 0.55 cm ($n = 68$). Among all nest-owner males found in the field, only two (ca. 3% of the total) had a dorsal scute width larger than the smallest nest opening diameter. In all cases, the nest-owner males had a dorsal scute width smaller than the nest opening diameter. Larger males had a higher probability of holding a nest (deviance: $\chi^2 = 8.29$, $df = 1$, $p = 0.004$, Figure 3A). However, among the nest-holding males, body size did not predict the probability of having eggs in the nest (deviance: $\chi^2 = 1.40$, $df = 1$, $p = 0.24$, Figure 3B).

We found that small males were less likely to occupy nests with large openings (randomization test: $p = 0.003$; Figure 4). Additionally, only 8% of males ($n = 6$) with body sizes below the population average were found in nests with above-average opening widths.

The index of body condition did not differ between males without nests (mean \pm SD = -0.0011 ± 0.014 ; $n = 71$), males holding nests without eggs (0.0003 ± 0.008 ; $n = 43$), and males holding nests with eggs (0.0026 ± 0.007 ; $n = 26$) (ANOVA: $F = 1.99$, $df = 138$, $p = 0.16$).

3.2 | Laboratory Experiment

3.2.1 | Prediction 1: Probability of a Male Holding a Nest

The mean (\pm SD) dorsal scute width of males that hold a nest was 6.79 ± 0.53 mm ($n = 41$) in the LOW group and 6.68 ± 0.60 mm ($n = 55$) in the HIGH group. The probability of a male holding a nest was not influenced by the dorsal scute width or the experimental group (deviance: $\chi^2 = 4.56$, $df = 3$, $p = 0.21$, Figure 5A).

3.2.2 | Prediction 2: Proportion of Occupied Nests

In the LOW group, 26 of the 28 nests (93% of the total) were occupied at least once by a male, whereas in the HIGH group, 41 of the 56 nests (73% of the total) were occupied at least once by a male. The proportion of occupied nests was higher when

TABLE 2 | Structure and type of the statistical models used to test predictions regarding the effects of nest-site availability on male–male competition and the foraging costs of paternal care in the harvestman *Magnispina neptunus*.

Model structure	Type of statistical model
Male–male competition for nests	
1. Probability of finding a male as a nest owner at least once ~ Experimental group * Dorsal scute width	GLMM-TMB with a binomial error distribution
2. Proportion of nests occupied at least once by an owner male ~ Experimental group	GLMM-TMB with a binomial error distribution
3a. Number of male–male fights per occupied nest ~ Experimental group	ZI with a Poisson error distribution for the count component
3b. Proportion of nests with at least one male–male fight ~ Experimental group	GLMM-TMB with a binomial error distribution
3c. Outcome of the fight for the focal individual (nest owner) ~ Experimental group * Difference in dorsal scute width between the individuals engaged in fight (nest owner—intruder)	GLMM-TMB with a binomial error distribution and dyad identity as random effect
4a. Number of takeovers ~ Experimental group	ZI with a negative binomial error distribution for the count component
4b. Proportion of occupied nests in which we recorded at least one takeover ~ Experimental group	GLMM-TMB with a beta-binomial error distribution
5. Proportion of owner males that received eggs ~ Experimental group	GLMM-TMB with a binomial error distribution
Foraging costs of paternal care	
6. Proportion of scans in which an owner male was recorded outside his nest (in relation to the total number of scans as a nest owner) ~ Experimental group * Parental status (parental × nonparental)	GLMM-TMB with a binomial error distribution and male identity as a random effect
7a. Number of eggs consumed by males that received eggs ~ Experimental group	ZI with a Poisson error distribution for the count component
7b. Proportion of occupied nests in which we recorded at least one event of filial cannibalism ~ Experimental group	GLMM-TMB with a binomial error distribution

Note: The numbers before the models correspond to the predictions presented in Table 1. The experimental groups include LOW nest-site availability (4 nests per terrarium) and HIGH nest-site availability (8 nests per terrarium). The asterisk denotes statistical interaction. Abbreviations: GLMM-TMB, generalized linear mixed model with template model builder; ZI, zero-inflated model.

nest-site availability was low (deviance: $\chi^2 = 3.88$, $df = 1$, $p = 0.05$, Table 3).

3.2.3 | Prediction 3: Number and Outcome of Male–Male Fights

The number of male–male fights was low in both experimental groups. In the LOW group, we recorded 18 male–male fights, and the number of occupied nests where we recorded at least one fight was 10 (36% of the total). In the HIGH group, we recorded 13 male–male fights, and the number of occupied nests where we recorded at least one fight was also 10 (18% of the total). The mean number of male–male fights (deviance: $\chi^2 = 5.59$, $df = 2$, $p = 0.06$, Table 3) and the proportion of occupied nests where we recorded at least one male–male fight (deviance: $\chi^2 = 1.48$, $df = 1$, $p = 0.22$, Table 3) were not influenced by nest availability. Finally, the outcome of the fights was not influenced by the difference in the dorsal scute width between the owner and the intruder male (deviance: $\chi^2 = 1.60$, $df = 3$, $p = 0.65$, Figure 5B).

3.2.4 | Prediction 4: Number of Nest Takeovers

In the LOW group, we recorded 13 takeovers, and the number of occupied nests where we recorded at least one takeover was 9 (32% of the total). In the HIGH group, we recorded 11 takeovers, and the number of occupied nests where we recorded at least one takeover was 8 (14% of the total). The frequency of takeovers (deviance: $\chi^2 = 3.64$, $df = 2$, $p = 0.16$, Table 3) and the proportion of occupied nests where we recorded at least one takeover (deviance: $\chi^2 = 1.88$, $df = 1$, $p = 0.17$, Table 3) were not influenced by nest-site availability.

3.2.5 | Prediction 5: Probability of a Male Acquiring Eggs

In the LOW group, we recorded 14 males that acquired eggs and in the HIGH group we recorded 15 males that acquired eggs. The probability of a male acquiring eggs was not influenced by nest-site availability (deviance: $\chi^2 = 0.47$, $df = 1$, $p = 0.49$, Table 3).

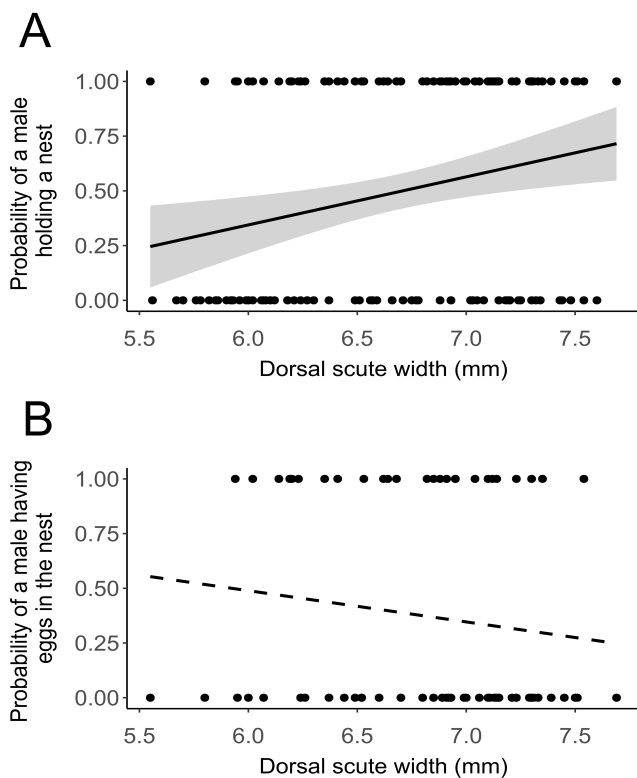


FIGURE 3 | (A) Effect of male body size (dorsal scute width) on the probability of males of the harvestman *Magnispina neptunus* holding a nest ($n=70$ nest-holding males and 71 nonnest-holding males). Slope \pm standard error: 0.91 ± 0.32 . The shaded area represents the 95% confidence interval. (B) Effect of male body size (dorsal scute width) on the probability of males having eggs in their nests ($n=26$ parental males and 44 nonparental males). Slope \pm standard error: -0.60 ± 0.52 . The dashed line indicates a nonsignificant pattern.

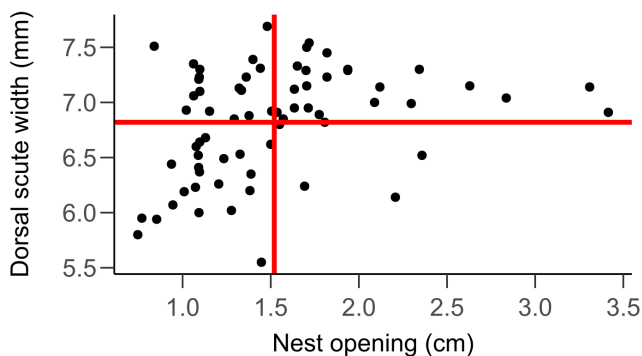


FIGURE 4 | Scatter plot showing the correlation between nest opening and body size (dorsal scute width) of males of the harvestman *Magnispina neptunus* ($n=68$). The red vertical line indicates the mean nest opening size (1.52 cm), whereas the red horizontal line indicates the mean body size (6.82 mm).

3.2.6 | Prediction 6: Frequency of Foraging

Males in both experimental groups spent most of the time inside their nests (Figure 6). The full model, which includes the effects of nest-site availability and parental status, showed a better fit than the null model in explaining the proportion of scans in

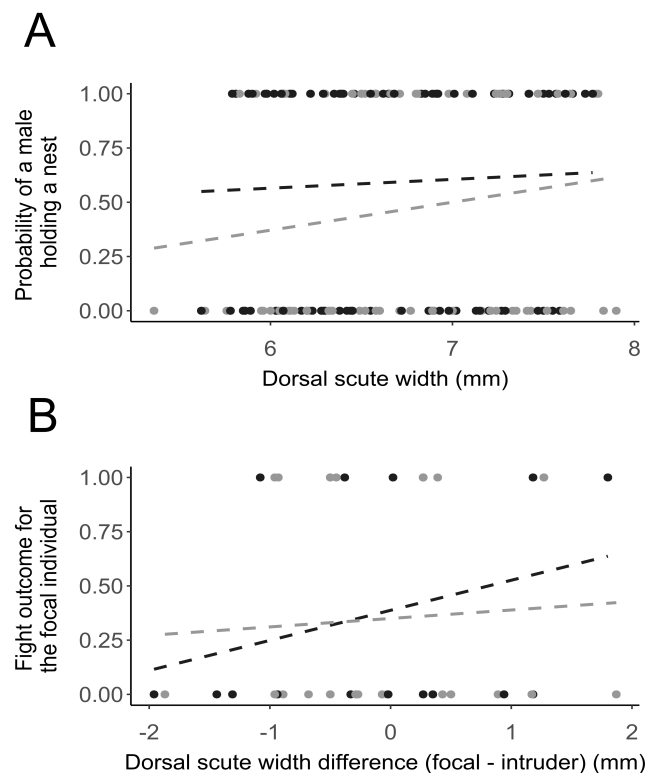


FIGURE 5 | (A) Probability of a male of the harvestman *Magnispina neptunus* holding a nest based on body size (dorsal scute width) and nest site availability: Slope \pm standard error of the LOW group (gray dots and line): 0.64 ± 0.37 ; slope \pm standard error of the HIGH group (black dots and line): 0.18 ± 0.37 . (B) Fight outcome (0: Defeat, 1: Victory) for nest owner males based on the dorsal scute width difference between the nest owner and intruder, and nest site availability: Slope \pm standard error of the LOW group (gray dots and line): 0.17 ± 0.48 ; slope \pm standard error of the HIGH group (black dots and line): 0.63 ± 0.56 . In both graphics, the dashed lines indicate nonsignificant patterns.

which owner males were recorded outside their nests (deviance: $\chi^2 = 75.2$, $df = 3$, $p < 0.001$, Figure 6). However, while the effect of parental status was significant ($p < 0.001$), with nonparental males foraging more than parental males, the effect of the nest-site availability was not ($p = 0.33$).

3.2.7 | Prediction 7: Number of Events of Filial Cannibalism

The mean (\pm SD) number of eggs cannibalized by the nest owners was 11.3 ± 27.5 in the LOW group and 16.1 ± 22.4 in the HIGH group. The mean number of eggs cannibalized (deviance: $\chi^2 = 0.5$, $df = 1$, $p = 0.48$, Table 3) and the proportion of occupied nests where we recorded at least one event of filial cannibalism (deviance: $\chi^2 = 0.05$, $df = 1$, $p = 0.82$, Table 3) were not influenced by nest-site availability.

4 | Discussion

In this study, we integrated observational field data with a laboratory experiment to understand how the availability of nest

TABLE 3 | Estimates of the models and 95% confidence intervals (in parentheses) for the effects of nest-site availability on male–male competition and the costs associated with paternal care in the harvestman *Magnispina neptunus*.

Variable	LOW	HIGH
Male–male competition for nests		
2. Proportion of occupied nests	0.95 (0.75, 0.99)	0.76 (0.56, 0.88)
3a. Number of fights (mean)	2.09 (1.37, 3.18)	1.13 (0.59, 2.15)
3b. Proportion of occupied nests where fights were recorded	0.38 (0.22, 0.58)	0.24 (0.14, 0.40)
4a. Number of nest takeovers (mean)	0.69 (0.36, 1.32)	0.32 (0.07, 1.54)
4b. Proportion of occupied nests where takeovers were recorded	0.35 (0.19, 0.54)	0.20 (0.10, 0.34)
5. Probability of acquiring eggs	0.34 (0.20, 0.51)	0.27 (0.16, 0.42)
Costs associated with paternal care		
7a. Number of events of filial cannibalism	18.24 (6.86, 48.50)	27.74 (14.07, 59.69)
7b. Proportion of occupied nests where filial cannibalism was recorded	0.19 (0.08, 0.39)	0.17 (0.08, 0.32)

Note: The numbers before the variables correspond to the predictions presented in Table 1. The estimates for Prediction 1 are presented in Figure 5, whereas the estimates for Prediction 6 are presented in Figure 6.

Abbreviations: HIGH, high nest-site availability; LOW, low nest-site availability.

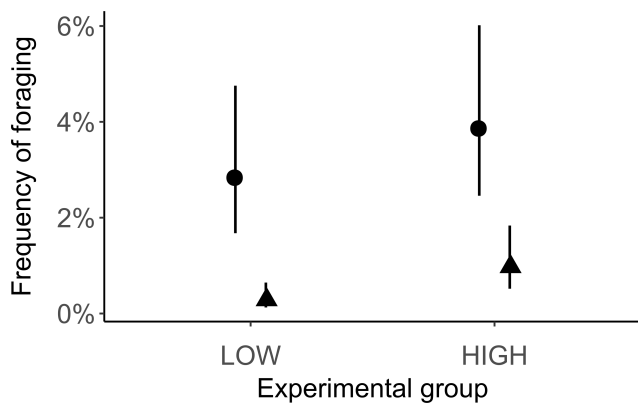


FIGURE 6 | Frequency of foraging of nest-owner males of the harvestman *Magnispina neptunus* according to the experimental group (LOW or HIGH nest site availability) and parental status (nonparental males: Circles, parental males: Triangles). Error bars represent the 95% confidence interval. Although the analysis was performed using proportions, the data are presented as percentages of scans in which males were recorded outside their nests.

sites influences the intensity of male–male competition and the foraging costs of paternal care in the harvestman *Magnispina neptunus*. The field data suggest that natural cavities are scarce, as less than 50% of the males in the population were nest holders. Assuming that the probability of detecting and capturing males without a nest is lower than that of nest holders (e.g., Requena et al. 2012; Requena and Machado 2014), it is possible that the percentage of males lacking access to natural cavities is even higher in nature. Consequently, intrasexual competition for access and possession of oviposition sites is likely intense, and theory predicts that only males with high resource-holding potential (RHP) would be able to secure a nest (Parker 1974; Vieira and Peixoto 2013). In harvestmen, the size of male weaponry,

including the spines in the fourth pair of legs used in male–male fights (Figure 1A), is influenced by body size (e.g., Willemart et al. 2009; Palaoro et al. 2022), and both traits are linked to RHP (reviewed in Kelly 2008), which may explain why larger males exhibited an increased probability of holding a nest in the field.

The relationship between RHP (i.e., body size) and the probability of holding a nest observed in the field was not replicated in either of the two experimental groups in the laboratory experiment. A possible explanation for this result lies in the defensibility of the resource, which is influenced by nest opening size. In contrast to the field, where nest opening diameters ranged from 0.75 cm to 3.42 cm, all nests used in the experiment had an opening diameter of 1.5 cm (i.e., the average observed in the field). We suggest that a smaller opening size enhances defensibility, decreasing the significance of body size in aggressive interactions for nest ownership. Conversely, when the nest opening size is larger, body size may exert a greater influence on the outcome of aggressive interactions, with larger individuals enjoying advantages over smaller counterparts. Our field results support this hypothesis, as nests with openings smaller than average were equally occupied by small and large males, while nests with openings larger than average were occupied almost exclusively by large males (Figure 4). These findings suggest that RHP can also be affected by extrinsic traits, such as nest opening size, which influence resource defensibility. The only similar example in the literature that we are aware of involves the sand goby *Pomatoschistus microps* (Krøyer, 1838), in which males build their own nests. In a laboratory experiment, it was shown that males decrease the nest opening size in the presence of sneaker males, thereby increasing nest defensibility against sneak invasions (Svensson and Kvarnemo 2003). Thus, nest opening size may represent a critical extrinsic trait affecting RHP in species that defend burrows or cavities, a topic that has received little attention in empirical studies (reviewed in Briffa and Hardy 2013).

The resource defensibility hypothesis, based on the nest opening size, may also explain why the frequency of fights and turnovers recorded in the experiment was so low and unaffected by nest availability. According to this hypothesis, prior residency (more than differences in size) likely serves as the primary determinant of the outcome of agonistic interactions between males, akin to several insect species that defend territories or nests, such as butterflies and burrowing bees (e.g., Kemp 2000; Alcock, Simmons, and Beveridge 2006). One underlying mechanism behind the residency effect in *M. neptunus* may be the advantage of being inside the nest and being able to block its opening using the fourth pair of legs equipped with strong spines (Figure 1A). Indeed, in a previous laboratory experiment conducted with the study species, nest-holding males were highly effective in blocking the opening of their nests, thereby preventing conspecifics from entering (Nazareth and Machado 2010). Females of the orchard mason bee *Osmia lignaria* Say, 1837 also defend their nests by being entirely inside them and, regardless of their size, they are capable of repelling most intruders (Tepedino and Torchio 1994). Thus, once an individual secures a nest, the chances of being dislodged are low, regardless of the size of the rivals.

Assuming that females of *M. neptunus* perceive male size as an indicator of genetic quality or caregiving ability, larger males should have a higher probability of acquiring eggs (Hoelzer 1989). However, this was not observed in either the field or the laboratory, regardless of the experimental group. Indeed, a meta-analysis examining the effect of RHP (e.g., body size or weapon size) on male reproductive success across various taxa revealed a weak correlation between these variables (Kelly 2008). It appears that females of *M. neptunus* select mates based on traits unrelated to body size. Under field conditions, nest features, such as texture, humidity, or integrity, could affect egg survival rates, thereby influencing females' decisions to oviposit (e.g., Olsson et al. 2019; Rojas et al. 2021; Svensson and Kvarnemo 2023). Additionally, both in the field and laboratory, females could evaluate males based on courtship intensity (e.g., Pampoulie, Lindström, and St. Mary 2004; Pettitt, Bourne, and Bee 2020) or body condition (e.g., Alissa, Machado, and Requena 2024; Östlund-Nilsson 2001). These traits may provide information on caregiving quality (Hoelzer 1989) or simply male quality (Kelly and Alonzo 2009). Regardless of the factors affecting the chances of a *M. neptunus* male receiving a first clutch of eggs, once he is caring for them, his attractiveness increases, and females seem to base their mating decisions primarily on the presence of eggs in the nest, suggesting that paternal care in the species is a sexually selected behavior (Nazareth and Machado 2010).

Because nest-owner males seem to have a significant advantage over intruder males in agonistic interactions for nest possession (Nazareth and Machado 2010; this study), the costs of abandoning a nest are likely high. Therefore, it is not surprising that the frequency with which males abandoned their nests to forage was very low in both experimental groups. However, as reported in a previous study with *M. neptunus* (Nazareth and Machado 2010), nonparental males exhibited a foraging frequency considerably higher than parental males. Although precise quantitative comparisons cannot be made due to different protocols used in the two studies, the consistent difference in the frequency of

foraging between parental and nonparental males likely has a common explanation. Given that eggs increase male attractiveness (Nazareth and Machado 2010), nests with eggs represent a more valuable resource, and males may invest more in their maintenance. Additionally, unattended eggs are readily attacked and consumed by conspecifics (Nazareth and Machado 2010), as also observed in many species of arthropods (Santos et al. 2017) and amphibians (Machado and Macedo-Rego 2023). Thus, the lower frequency of foraging of parental males compared to nonparental males can also be interpreted as an investment in offspring protection.

Faced with almost complete suppression of foraging, filial cannibalism may be a strategy to minimize the energetic costs associated with paternal care without losing possession of the nest and its contents (Manica 2002; Bose 2022). Indeed, males from the two experimental groups consumed eggs from their clutches at similar frequency and quantity. Males of the assassin bug *Rhinocoris tristis* (Stål, 1855) cease foraging during parental care and feed exclusively on eggs from their own clutches (Thomas and Manica 2003). Although there is no nest, rival males constantly attempt to usurp the clutches, as eggs enhance their attractiveness (Gilbert, Thomas, and Manica 2010). Similar to *M. neptunus*, the costs of abandoning eggs are likely high in *R. tristis*, which may explain filial cannibalism in both species. Additionally, the occurrence of filial cannibalism in *M. neptunus* may explain why the body condition of the parental males did not differ from that of nonparental nest-owner males under field conditions. Interestingly, the body condition of nest-owner males (parental or nonparental) also did not differ from the body condition of males without a nest, which are free to forage. We suggest that filial cannibalism by parental males and sporadic prey consumption by nonparental males, combined with the low metabolic rate of harvestmen as a whole (Santos 2007), may account for the lack of difference in body condition between these males and those without a nest.

In the famous Battle of Thermopylae, a few hundred Spartan warriors were able to hold back the advance of the mighty Persian army, composed of over 300,000 soldiers, for 7 days. Leonidas, the king of Sparta, was able to significantly reduce the asymmetry of forces between the armies because the battle took place in a narrow pass. Similarly, we propose that a narrow nest opening allows even a small male of the harvestman *M. neptunus* to maintain possession of a nest, which is a crucial resource for reproduction. Consequently, many of the canonical predictions regarding the effect of resource availability on male–male competition (and also on the foraging costs of parental care) were not supported in our laboratory experiment. We conclude, therefore, that although underexplored in the literature on agonistic interactions, external factors, such as the opening size of cavities defended by males of many species with resource-defense mating systems, may play a key role in the defensibility of reproductive sites.

Author Contributions

Lais A. Grossel: data curation, formal analysis, writing – review and editing, software, visualization, writing – original draft, methodology, validation. **Rachel M. Werneck:** investigation, writing – original draft, methodology, conceptualization. **Glaucio Machado:** conceptualization,

investigation, funding acquisition, writing – original draft, supervision, resources, project administration, writing – review and editing, methodology, validation, visualization.

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Ethics Statement

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

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data sets used in this study are available in the Zenodo repository ([10.5281/zenodo.11179646](https://doi.org/10.5281/zenodo.11179646)).

References

- Alcock, J., L. W. Simmons, and M. Beveridge. 2006. “Does Variation in Female Body Size Affect Nesting Success in Dawson’s Burrowing Bee, *Amegilla dawsoni* (Apidae: Anthophorini)?” *Ecological Entomology* 31: 352–357.
- Alissa, L. M., G. Machado, and G. S. Requena. 2024. “Good Body Condition Increases Male Attractiveness but Not Caring Quality in a Neotropical Arachnid With Male-Only Care.” *Behavioral Ecology and Sociobiology* 78: 24.
- Bessa, E., M. L. Brandão, and E. Gonçalves-de-Freitas. 2022. “Integrative Approach on the Diversity of Nesting Behaviour in Fishes.” *Fish and Fisheries* 23: 564–583.
- Bose, A. P. H. 2022. “Parent–Offspring Cannibalism Throughout the Animal Kingdom: A Review of Adaptive Hypotheses.” *Biological Reviews* 97: 1868–1885.
- Briffa, M., and I. C. W. Hardy. 2013. *Animal contests*. Cambridge: Cambridge University Press.
- Brooks, M. E., K. Kristensen, K. J. Van Benthem, et al. 2017. “glmmTMB Balances Speed and Flexibility Among Packages for Zero-Inflated Generalized Linear Mixed Modeling.” *R Journal* 9: 378–400.
- Debusse, V. J., J. T. Addison, and J. D. Reynolds. 2003. “Effects of Breeding Site Density on Competition and Sexual Selection in the European Lobster.” *Behavioral Ecology* 14: 396–402.
- Emlen, S. T., and L. W. Oring. 1977. “Ecology, Sexual Selection, and the Evolution of Mating Systems.” *Science* 197: 215–223.
- Forsgren, E., C. Kvarnemo, and K. Lindström. 1996. “Mode of Sexual Selection Determined by Resource Abundance in Two Sand Goby Populations.” *Evolution* 50: 646–654.
- Gilbert, J. D. J., L. K. Thomas, and A. Manica. 2010. “Quantifying the Benefits and Costs of Parental Care in Assassin Bugs.” *Ecological Entomology* 35: 639–651.
- Hartig, F. 2022. “DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed Regression Models).” R package version 0.4.6.
- Heying, H. 2004. “Reproductive Limitation by Oviposition Site in a Treehole Breeding Madagascar Poison Frog (*Mantella laevis*).” *Miscellaneous Publications of the Museum of Zoology* 193: 23–30.
- Hoelzer, G. A. 1989. “Male-Male Competition and Female Choice in the Cortez Damselfish, *Stegastes Rectifraenum*.” *Animal Behaviour* 40: 339–349.
- Jakob, E. M., S. D. Marshall, and G. W. Uetz. 1996. “Estimating Fitness: A Comparison of Body Condition Indices.” *Oikos* 77: 61–67.
- Kelly, C. D. 2008. “The Interrelationships Between Resource-Holding Potential, Resource-Value and Reproductive Success in Territorial Males: How Much Variation Can We Explain?” *Behavioral Ecology and Sociobiology* 62: 855–871.
- Kelly, N. B., and S. H. Alonzo. 2009. “Will Male Advertisement Be a Reliable Indicator of Paternal Care, If Offspring Survival Depends on Male Care.” *Proceedings of the Royal Society of London. Series B* 276: 3175–3183.
- Kemp, D. J. 2000. “Contest Behavior in Territorial Male Butterflies: Does Size Matter?” *Behavioral Ecology* 11: 591–596.
- Lindström, K. 1988. “Male-Male Competition for Nest Sites in the Sand Goby, *Pomatoschistus minutus*.” *Oikos* 53: 67–73.
- Lindström, K. 2001. “Effects of Resource Distribution on Sexual Selection and the Cost of Reproduction in Sandgobies.” *American Naturalist* 158: 64–74.
- Lindström, K., and T. Seppa. 1996. “The Environmental Potential for Polygyny and Sexual Selection in the Sand Goby, *Pomatoschistus minutus*.” *Proceedings of the Royal Society of London B* 263: 1319–1323.
- Lüdtke, D. 2018. “ggeffects: Tidy Data Frames of Marginal Effects From Regression Models.” *Journal of Open Source Software* 3: 772.
- Lugli, M., L. Bobbio, P. Torricelli, and G. Gandolfi. 1992. “Breeding Ecology and Male Spawning Success in Two Hill-Stream Populations of the Freshwater Goby, *Padogobius martensi*.” *Environmental Biology of Fishes* 35: 37–48.
- Machado, G., and R. C. Macedo-Rego. 2023. “Benefits and Costs of Female and Male Care in Amphibians: A Meta-Analytical Approach.” *Proceedings of the Royal Society of London. Series B* 290: 20231759.
- Manica, A. 2002. “Filial Cannibalism in Teleost Fish.” *Biological Reviews* 77: 261–277.
- Mendes, A. C. 2011. “Phylogeny and Taxonomic Revision of Heteropachylinae (Opiliones: Laniatores: Gonyleptidae).” *Zoological Journal of the Linnean Society* 163: 437–483.
- Muniz, D. G., and G. Machado. 2015. “Experimental Limitation of Oviposition Sites Affects the Mating System of an Arachnid With Resource Defence Polygyny.” *Animal Behaviour* 109: 23–31.
- Natsumeda, T., S. Mori, and M. Yuma. 2012. “Size-Mediated Dominance and Aggressive Behavior of Male Japanese Fluvial Sculpin *Cottus pollux* (Pisces: Cottidae) Reduce Nest-Site Abundance and Mating Success of Conspecific Rivals.” *Journal of Ethology* 30: 239–245.
- Nazareth, T. M., and G. Machado. 2010. “Mating System and Exclusive Postzygotic Paternal Care in a Neotropical Harvestman (Arachnida: Opiliones).” *Animal Behaviour* 79: 547–554.
- Olsson, K. H., E. Forsgren, S. Merilaita, C. Kvarnemo, and C. St Mary. 2019. “Effect of Sand Texture on Nest Quality and Mating Success in a Fish With Parental Care.” *Behavioral Ecology and Sociobiology* 73: 96.
- Östlund-Nilsson, S. 2001. “Fifteen-Spined Stickleback (*Spinachia spinachia*) Females Prefer Males With More Secretory Threads in Their Nests: An Honest-Condition Display by Males.” *Behavioral Ecology and Sociobiology* 50: 263–269.
- Palaoro, A. V., S. García-Hernández, B. A. Buzatto, and G. Machado. 2022. “Function Predicts the Allometry of Contest-Related Traits, but Not Sexual or Male Dimorphism in the Amazonian Tusked Harvestman.” *Evolutionary Ecology* 36: 605–630.
- Pampoulie, C., K. Lindström, and C. M. St. Mary. 2004. “Have Your Cake and Eat It Too: Male Sand Gobies Show More Parental Care in the Presence of Female Partners.” *Behavioral Ecology* 15: 199–204.

- Parker, G. A. 1974. "Assessment Strategy and the Evolution of Fighting Behavior." *Journal of Theoretical Biology* 47: 223–243.
- Pettitt, B. A., G. R. Bourne, and M. A. Bee. 2020. "Females Prefer the Calls of Better Fathers in a Neotropical Frog With Biparental Care." *Behavioral Ecology* 31: 152–163.
- R Core Team. 2024. *R: A Language and Environment for Statistical Computing*. Austria: R Foundation for Statistical Computing.
- Requena, G. S., B. A. Buzatto, E. G. Martins, and G. Machado. 2012. "Paternal Care Decreases Foraging Activity and Body Condition, but Does Not Impose Survival Costs to Caring Males in a Neotropical Arachnid." *PLoS One* 7: e46701.
- Requena, G. S., and G. Machado. 2014. "Lack of Costs Associated With Nest-Related Behaviors in an Arachnid With Exclusive Paternal Care." *Oikos* 124, no. 3: 372–380.
- Requena, G. S., R. Munguía-Steyer, and G. Machado. 2013. "Paternal Care and Sexual Selection in Arthropods." In *Sexual Selection: Perspectives and Models From the Neotropics*, 201–233. Amsterdam: Academic Press.
- Rojas, A., D. G. Muniz, D. Solano-Brenes, and G. Machado. 2021. "Nest-Site Selection in a Neotropical Arachnid With Exclusive Male Care: Proximate Cues and Adaptive Meaning." *Ethology* 127: 334–341.
- Rosenthal, M. F., M. Gertler, A. D. Hamilton, S. Prasad, and M. C. B. Andrade. 2017. "Taxonomic Bias in Animal Behaviour Publications." *Animal Behaviour* 127: 83–89.
- Santos, E. S. A., P. P. Bueno, J. D. J. Gilbert, and G. Machado. 2017. "Macroecology of Parental Care in Arthropods: Higher Mortality Risk Leads to Higher Benefits of Offspring Protection in Tropical Climates." *Biological Reviews* 92: 1688–1701.
- Santos, F. H. 2007. "Ecophysiology." In *Harvestmen: The Biology of Opiliones*, edited by R. Pinto-da-Rocha, G. Machado, and G. Giribet, 473–488. Cambridge: Harvard University Press.
- Shuster, S. M., and M. J. Wade. 2003. *Mating Systems and Strategies*. Princeton: Princeton University Press.
- Singer, A., C. Kvarnemo, K. Lindström, and O. Svensson. 2006. "Genetic Mating Patterns Studied in Pools With Manipulated Nest Site Availability in Two Populations of *Pomatoschistus minutus*." *Journal of Evolutionary Biology* 19: 1641–1650.
- Svensson, O., and C. Kvarnemo. 2003. "Sexually Selected Nest-Building - *Pomatoschistus minutus* Males Build Smaller Nest-Openings in the Presence of Sneaker Males." *Journal of Evolutionary Biology* 16: 896–902.
- Svensson, O., and C. Kvarnemo. 2023. "How Sexual and Natural Selection Interact and Shape the Evolution of Nests and Nesting Behaviour in Fishes." *Philosophical Transactions of the Royal Society B* 378: 20220139.
- Takahashi, D. 2008. "Life-History Variation in Relation to Nest Site Abundance in Males of the Freshwater Goby *Tridentiger brevispinis*." *Ecology of Freshwater Fish* 17: 71–77.
- Tepedino, V. J., and P. F. Torchio. 1994. "Founding the Usurping Equally Efficient Paths to Nesting Success in *Osmia lignaria propinqua* (Hymenoptera, Megachilidae)." *Annals of the Entomological Society of America* 87: 946–953.
- Thomas, L. K., and A. Manica. 2003. "Filial Cannibalism in an Assassin Bug." *Animal Behaviour* 66: 205–210.
- Vieira, M. C., and P. E. C. Peixoto. 2013. "Winners and Losers: A Meta-Analysis of Functional Determinants of Fighting Ability in Arthropod Contests." *Functional Ecology* 27: 305–313.
- Wacker, S., and T. Amundsen. 2014. "Mate Competition and Resource Competition Are Inter-Related in Sexual Selection." *Journal of Evolutionary Biology* 27: 466–477.
- Wells, D. K. 2007. *The Ecology and Behavior of Amphibians*. Chicago: University of Chicago Press.
- Wickham, H. 2016. *ggplot2: Elegant Graphics for Data Analysis*. New York: Springer-Verlag.
- Wickramasinghe, D. D., K. L. Oseen, S. W. Kotagama, and R. J. Wassersug. 2004. "The Terrestrial Breeding Biology of the Ranid Rock Frog *Nannophrys ceylonensis*." *Behaviour* 141: 899–913.
- Willemart, R. H., F. Osses, M. C. Chelini, R. Macías-Ordóñez, and G. Machado. 2009. "Sexually Dimorphic Legs in a Neotropical Harvestman (Arachnida, Opiliones): Ornament or Weapon?" *Behavioural Processes* 80: 51–59.
- Zeileis, A., and T. Hothorn. 2002. "Diagnostic Checking in Regression Relationships." *R News* 2, no. 3: 7–10.