



Original Article

Gone with the rain: negative effects of rainfall on male reproductive success in a nest-building arachnid

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In nest-building species, offspring survival and reproductive success of parental individuals are strongly influenced by nest quality. Thus, quantifying the influence of abiotic conditions on nest integrity is important to predict the effects of weather variability on the fitness of parental individuals. Here, we investigated how rainfall affects nest integrity and how nest integrity influences males' attractiveness and nest tenure. Our study species was the harvestman *Quindina limbata*, in which males build mud nests on fallen logs and protect the eggs against predators and fungi. Our data set comprises 12 months of regular inspections of 149 nests in a Costa Rican rainforest. We found that almost 50% of the nests were destroyed by rainfall. The drag force caused by rainfall running on the fallen log surface negatively affected nest integrity. Fungi cover on nests was influenced by an interaction between rainfall and nest position on the fallen log. Irrespective of their body size, males in nests with high integrity received more eggs than males in nests with low integrity. Fungi cover did not influence the number of eggs received by the males. Finally, nest integrity and fungi cover did not affect nest tenure, but males that did not receive eggs for a long time tended to abandon their nests. Considering that intense rainfall occurs all year long in tropical forests, males should build their nests in protected sites that preserve nest structure. Protected sites may keep nest structure better preserved, improve offspring survival, attract more females, and increase males' reproductive success.

Key words: abiotic conditions, fungi, harvestman, male attractiveness, nest abandonment, nest integrity, paternal care, reproductive success.

INTRODUCTION

In species in which individuals build nests for their offspring, the location and quality of the nests are key determinants of offspring survival and ultimately of the reproductive success of parental individuals. Inadequate nesting sites may expose both the parents and the offspring to a wide range of unfavorable factors, including attacks of natural enemies and harsh abiotic conditions (reviewed in Refsnider and Janzen 2010). Abiotic conditions, in particular, can negatively affect nesting success in different ways. For instance, among aquatic organisms, such as fish, cold temperatures in the nest site may decrease egg development rate and larval growth speed (e.g., Osenberg et al. 1988), extending the caring period and

increasing the probability of nest abandonment by the parents (e.g., Wrenn 1984). Among terrestrial species, such as birds, heavy, prolonged rainfall and cold temperatures may increase the probability of 1) nestling mortality due to exposure (e.g., Boersma and Rebstock 2014), 2) nestling starvation due to reduced adult foraging efficiency (e.g., Dawson and Bortolotti 2000; Öberg et al. 2014), 3) nest destruction caused by rainfall (e.g., Thompson and Furness 1991), and 4) nest abandonment by parental individuals (e.g., Griebel et al. 2007). Thus, quantifying the influence of abiotic conditions on offspring survival and reproductive success of parental individuals is important to predict the effects that weather variability may have on animal populations (Parmesan et al. 2000).

When males alone are responsible for nest building and parental care, females are expected to make mating decisions based not only on morphological male traits, which may indicate the overall

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quality of a male as mating partner, but also on traits that indicate his parental abilities and the quality of his nest. By evaluating male parental abilities and nest quality, females may benefit indirectly through the inheritance of either good genes that increase offspring fitness (Tallamy 2001) or genes that will increase the attractiveness of the male offspring (Candolin 2003). In addition, females may also benefit directly because offspring survival is expected to increase when they mate with males that show high-quality parental care and have well-built nests or nests in favorable locations. Indeed, females select males based on their parental ability and also on particular traits of their nests, including location, size, shape, and ornamentation, in many species of fish (e.g., Lindström 1992; Forsgren 1997; Candolin and Reynolds 2001; Östlund-Nilsson and Holmlund 2003), frogs (e.g., Felton et al. 2006), and birds (e.g., Hoi et al. 1994; Quader 2006; Kleindorfer 2007). Therefore, any factor decreasing nest quality may have profound consequences for males' reproductive success because it may negatively affect both their mating success and offspring survival.

Even though exclusive paternal care has evolved at least 16 times independently among arthropods (Requena et al. 2013), nest building by males is known to occur only in a small clade of harvestmen belonging to the genus *Quindina* (Arachnida: Opiliones). Males of *Quindina albomarginis* (= *Zygodactylus albomarginis*) and *Quindina limbata* (= *Poassa limbata*), for instance, build cup-like nests made of wood debris on the surface of fallen logs (Mora 1990; Figure 1a). These nests are composed of a circular floor where females lay their eggs, surrounded by a wall 5–15-mm high that serves as a barrier against possible predators, such as millipedes (Platydesmidae) (Figure 1b). Resident males remain in their nests for several weeks or months, constantly repairing the wall and floor of their nests from damages (Rodríguez and Guerrero 1976; Mora 1990). Field experiments with *Q. albomarginis* and *Q. limbata* showed that male presence inside the nest is crucial for offspring survival because unattended eggs may be infested by fungi or consumed by predators (Mora 1990; Quesada-Hidalgo et al. 2019). Moreover, females of both *Quindina* species seem to copulate exclusively with nest-owning males and carefully inspect nest structure before copulating and laying eggs (Mora 1990; Toscano-Gadea and Rojas 2014). Therefore, nest possession and nest quality are likely to be important determinants of male reproductive success in these 2 arthropod species with exclusive male care.

All *Quindina* species occur in neotropical rainforests (Pinto-da-Rocha and Bragagnolo 2017), where nests are exposed to intense rainfall (Figure 1d). Males continuously repair their nests from small damages but may respond to extensive nest destruction by either rebuilding or abandoning their nests (Mora 1990; Figure 1e). Here, we investigate the effects of rainfall on nest integrity and males' reproductive success using *Q. limbata* as our study species. In particular, we investigated how rainfall affects nest integrity and how nest integrity, in turn, influences males' attractiveness and nest tenure. We expected that rainfall would have a direct negative effect on nest integrity, washing away both nest wall and floor. We also expected an indirect effect of rainfall on nest integrity because high humidity favors the growth of fungi on fallen logs (Schmidt 2006) and consequently on the nests (Figure 1c). Given that nest integrity is likely to be important for egg survival, we expected that males occupying well-preserved nests would be more attractive to females and, therefore, they would receive more eggs. Finally, the costs of nest maintenance and the benefits of female attraction should affect males' nest tenure. Accordingly, we expected the probability of nest abandonment to be higher in sites where nests are constantly damaged by



Figure 1

Nests of the harvestman *Quindina limbata* built on the surface of fallen logs in a Costa Rican rainforest. (a) Fallen trunk suspended from the ground where we monitored several nests. The location of each nest is marked with a small color flag. (b) Intact nest with 1 male (marked with a white color on the dorsum and on the last right leg) and 1 female (unmarked). The nest wall is approximately 5-mm high and its texture is finely granulated. The nest floor is thick, completely circular, and has a spongy texture containing pores where females insert their eggs. Outside the nest there are several flat-backed millipedes that are prevented from entering the nest by the intact walls. (c) Nest heavily covered with fungi. Although males can actively remove and consume hyphae, sometimes they cannot prevent fungi growth inside the nest. This seems to be the case of the nest in the photo. (d) Nest heavily damaged by rainfall. Both the wall and the floor are destroyed in some parts and considerably damaged in other parts. The general texture of the nest wall is roughly granulated, and the floor is smooth, without the typical spongy texture (i.e., with no pores where females can insert their eggs). (e) Male repairing a damaged nest, adding debris mixed with saliva to the wall. In all photos, scale bars = 1 cm.

rainfall and receive fewer eggs by females. In these sites, the costs of nest maintenance should be higher than the benefits in terms of egg gaining, thus males' nest tenure should be low.

METHODS

Study species

Males of *Q. limbata* build their nests on the surface of large fallen logs that are partially suspended from the ground (Figure 1a). They collect small particles of wood debris on the fallen log surface and use them to build both the wall and the floor of their nests. The wood debris is possibly mixed with saliva, and males use both their chelicerae and pedipalps to manipulate the material and place it in the proper places of the nest (Figure 1e). The entire process of nest building may last from 2 to 4 weeks and if nest structure is

somehow damaged, the resident male promptly starts to repair it. Depending on the intensity of the damage, the repairing process may last several days. Another important activity of nest maintenance is cleaning fungi because intense fungi infestation may kill the eggs (Mora 1990). *Quindina* males are known to feed on macroscopic fungi, so nest cleaning may not only improve egg survival but may also provide food for the resident males (Requena and Machado 2015).

Some males of *Q. limbata* do not build nests, instead they either occupy abandoned nests or attack and dislodge resident males from their nests. Nest takeovers are relatively rare in the study population (Rojas et al. 2017), and agonistic interactions involving resident males are mainly related to egg protection against predators, such as ants, crickets, beetles, millipedes, and flatworms, which may climb the wall and enter the nest (Quesada-Hidalgo et al. 2019). Nests are also visited by conspecific females, which inspect the floor and the wall with their front legs before initiating courtship interactions with the resident males. When a female enters the nest, the resident male moves toward the internal wall of the nest and remains close to the wall while the female inspects the nest (Toscano-Gadea and Rojas 2014). If the female stays inside the nest after the inspection, she may copulate with the resident male and lay from 1 to 4 eggs, which are inserted in the nest floor. Eggs hatch in 20–25 days and nymphs may stay inside the nest during the first 2 or 3 instars. Contrary to the close-related species *Q. albomarginis*, which shows marked reproductive seasonality and breeds only from July to December (Mora 1990), males of *Q. limbata* build nests all year long and there is no interruption in egg production by females.

Study site and nest monitoring

We studied a population of *Q. limbata* found at Veraguá Rainforest ($9^{\circ}55'35.7''N$, $83^{\circ}11'27.9''W$; altitude 400 m a.s.l.), in the district of

Las Brisas, province of Limón, Costa Rica. The area is a primary rainforest that receives an annual precipitation of nearly 3000 mm and has a mean annual temperature of $23^{\circ}C$ (Holdridge 1967). The local climate has no well-defined seasons, the mean monthly temperature is always above $19^{\circ}C$, and the mean monthly precipitation is always above 150 mm (data from a meteorological station located 21 km from our study site). Between May 2012 and May 2013, we followed all nests found on the surface of 4 fallen logs, which were 17, 19, 21, and 22 m long. These 4 fallen logs were partially suspended from the ground so that males could build their nests on the lower half of the logs (Figures 1a and 2).

During the entire study period, we performed 41 fieldtrips with intervals ranging from 6 to 28 days (median = 8 days). In each fieldtrip, which lasted 1 or 2 days, we visited all 4 fallen logs and photographed all nests and their corresponding resident males. Moreover, we individually measured the dorsal scute (carapace) width of all resident males and marked them with enamel ink applied to their dorsal scute and femora of their hind legs (following Requena and Machado 2015; see marked male in Figure 1b). Finally, we individually labeled all nests with small color flags (Figure 1a) and measured the angle of each nest on the fallen log surface using a protractor and a level. According to our criterion, angles were measured relative to an imaginary vertical line (orthogonal to the ground) crossing the center of the fallen log (see examples in Figure 2).

Rainfall and drag

We obtained daily rainfall values from a meteorological station located 21 km from the study site, in the district of Matina, Limón. We calculated accumulated rainfall between fieldtrips by adding the daily precipitation between 2 consecutive fieldtrips. When raindrops hit a fallen log, the direct impact can be strong enough to

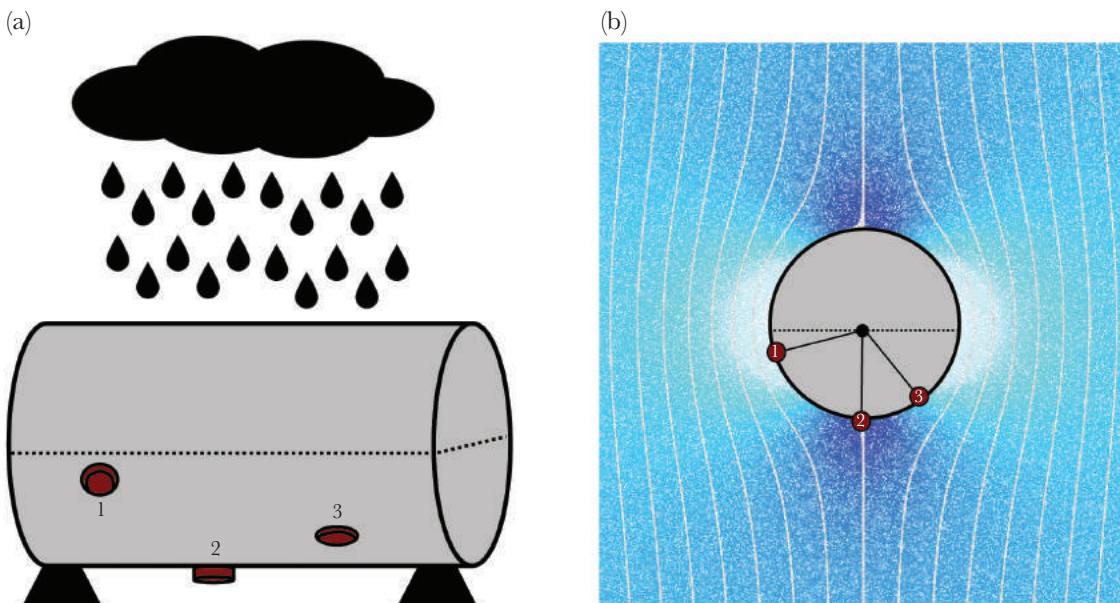


Figure 2

Scheme of the drag force caused by rainfall running on the surface of a fallen log suspended from ground (objects are not in scale). (a) Lateral view of a fallen log (gray cylinder) showing 3 cup-like mud nests (brown circles) of the harvestman *Quindina limbata* at the lower half of the fallen log. In this position, nests are protected from the direct impact of the rain. (b) Transversal view of the fallen log showing the angle of each nest (the numbers of the nests are the same as in (a): (1) nearly 75° , (2) 0° , and (3) nearly 30° . The blue area around the fallen log represents the velocity of the water running on the surface of a cylinder: lighter shades of blue indicate high velocity and darker shades of blue indicate low velocity. Because the drag force is proportional to the velocity, lighter shades of blue indicate areas with high values of drag force. According to fluid dynamics, nest 1 is subject to a higher drag force than nests 2 and 3, and thus has a higher chance of being washed away during intense rainfall.

completely destroy any nest exposed on the upper half of the fallen log (Figure 2). In turn, nests located on the lower half of the fallen log are protected from the direct impact of raindrops. However, water flowing down the surface of the fallen log exerts a drag force that can damage the nests and even wash them away. According to fluid dynamics theory, this force is proportional to the amount of flowing water and to the angle of the nest on the surface of the fallen log (Mallick and Kumar 2014; Figure 2). Assuming that fallen logs are approximately cylindrical (Figure 1a), we used the following formula to estimate the drag force $D_{i,t}$ of flowing water acting on nest i at time t (modified from Mallick and Kumar 2014; see also Supplementary Material): $D_{i,t} = (r_t \cdot \sin(\theta_i))^2$, where r_t is the accumulated rainfall between one fieldtrip (time $t-1$) and the subsequent fieldtrip (time t), which is a proxy of the total amount of water flowing on the fallen log surface, and θ_i is the angle of the nest on the fallen log surface (Figure 2). We used the values of $D_{i,t}$ as the predictor variable in the analysis of physical damage caused by rainfall on both nest wall and floor (see below). We stress that the rainfall accumulated between 2 consecutive fieldtrips is strongly correlated with the mean daily rainfall between 2 consecutive fieldtrips (Pearson correlation, $r = 0.820$); thus, the values of $D_{i,t}$ generated by these 2 proxies of water flow on the fallen log surface are very similar (data not shown).

Nest integrity

When there is no physical damage caused by rainfall, the nest wall usually is 5–15-mm high and its general texture is finely granulated (Figure 1b, see also Supplementary Figure S1). Moreover, the nest floor is a continuous, circular layer of wood debris with a spongy texture in the pores of which females insert their eggs (Figure 1b). On physical damage caused by rainfall, the height of the nest wall is reduced and its general texture becomes smoother or, in some cases, roughly granulated (Figure 1d, see also Supplementary Figure S1). Also, whole sectors of the wall may be eroded so that in damaged nests the floor may not be totally surrounded by walls. Finally, the nest floor may be partially or completely eroded by rainfall, losing its circular shape (Figure 1d). Rainfall may also erode the nest floor, changing it from a spongy substrate (i.e., with well-defined pores in which females can insert their eggs) to a smooth substrate (completely deprived of pores; Figure 1d). The erosion of the wall and the floor can be easily observed in the photographs taken from the nests in each fieldtrip (Supplementary Figure S1). Thus we used the photographs to estimate the proportion of intact wall and intact floor in each nest in every fieldtrip. To estimate wall integrity, we divided the wall of each nest in 10 sectors and visually inspected how many sectors were intact (Supplementary Figure S1a,b). We used the proportion of intact wall sectors as a proxy of wall integrity. In the case of the nest floor, we divided the floor area in a grid of 24 squares and considered the proportion of intact squares (i.e., those with a clear spongy texture) as a proxy of floor integrity (Supplementary Figure S1c,d).

We also used photographs to estimate the percentage of nest covered with macroscopic fungi, which can be easily recognized due to the presence of white hyphae growing on the floor and/or the walls of the nest (Figure 1c). The macroscopic fungi may create a mat on the nest floor that prevents females from inserting their eggs in the pores of the spongy substrate built by the resident male. Moreover, at least some macroscopic fungi are known to be an important source of egg mortality in the closely related species *Q. albomarginis* (Mora 1990). We scored the percentage of fungi cover in each nest

at each fieldtrip as a 4-level ordinal variable, using the following categories: (0) no fungi cover, (1) low fungi cover (i.e., 1–25% of the nest covered), (2) intermediate fungi cover (i.e., 26–50% of the nest covered), and (3) high fungi cover (i.e., ≥51% of the nest covered).

Reproductive success and nest tenure

Recently laid eggs of *Q. limbata* are white and can be seen partially buried in the pores of the nest floor. Given that harvestman eggs get darker during embryonic development and that it takes 5–7 days for the white eggs of *Q. limbata* to become pale brown, we could use the photographs to identify and count recently laid white eggs inside each nest in each field trip. Although some eggs can be entirely buried in the spongy substrate of the nest floor, and thus cannot be seen in the photographs, there is a high positive correlation between the number of visible eggs and the total number of eggs in a nest (Supplementary Figure S2). Thus, the number of visible eggs is a reliable proxy of the total number of eggs received by resident males.

In all analyses described below, we only included males that we observed building their own nests. *Quindina* males sometimes fight each other for the possession of nests, and some resident males can be displaced from their nests by invader males (Mora 1990; Rojas et al. 2017). Thus, by selecting only males that we observed building their own nests we did not include in our data set males that usurped a nest and did not pay the costs of nest construction, which may influence both nest tenure and the investment in nest maintenance. We considered that a nest was abandoned when: 1) its resident male was no longer recorded inside the nest during the study period and 2) the nest remained during at least one fieldtrip consecutive fieldtrips before being occupied by a new resident male.

Statistical analyses

In all analyses described below, we used information from previous observations of a given nest to predict what would happen to this same nest in the following observations so that our sampling units were always a given nest at a given time (i.e., fieldtrip). Because we have repeated observations of the same nests and their respective resident males on 4 fallen logs, in all analyses described below, we included both male identity and fallen log identity as random effects. We tested our predictions using generalized linear mixed models (GLMMs), adopting different distributions to best fit our data (Gelman and Hill 2006). Prior to model fitting, we standardized the continuous predictor variables to produce comparable effect sizes (Scheiplzeth 2010). We implemented all models using the *stan* probabilistic programming language (Carpenter et al. 2017) and fitted the models in a Bayesian approach using Markov Chain Monte Carlo (MCMC) optimization (Gelman et al. 2014). The Bayesian analyses were performed in the software R version 3.4.1 (R Core Team 2017) using the package *rstan* (Stan Development Team 2018). In all model fits, we ran 3 MCMC chains with 5000 iterations plus 5000 warm-up iterations and adopted the default *rstan* noninformative priors. We checked the convergence of the MCMC chains by visually inspecting the chains of all models and by inspecting the R values. The \bar{R} values for all effect sizes were ≤ 1.01 and multivariate \bar{R} values for all models were ≤ 1.08 , indicating that the MCMC chains converged adequately (Gelman and Rubin 1992).

Nest integrity analyses

To test the prediction that exposure to intense rainfall would decrease the overall nest integrity, we fit 2 models in which the

predictor variable was the drag force ($D_{i,j}$) and the response variables were the proportion of intact wall (model 1) and the proportion of intact floor (model 2) observed at each fieldtrip after the nest was first located on a fallen log. We did not include male body size as a predictor in this analysis because dorsal scute width is not correlated with body mass in *Q. limbata* (Supplementary Figure S3). Thus, body size alone or the residuals of the regression between dorsal scute width and body mass cannot be regarded as good proxies of male body condition, which is a potential explanatory variable of nest integrity or quality in species with exclusive paternal care (e.g., Olsson et al. 2009).

In both models 1 and 2, we adopted a beta distribution for the response variable, which is the most adequate for proportion data (Bolker 2008). Moreover, we allowed both the expected mean (μ) and the precision (φ) parameters of the beta distribution to vary as a function of the response variable and adopted an inverse logit link function for μ and an exponential link function to φ (following Ferrari and Cribari-Neto 2004). Prior to model fitting, we transformed the proportions using the formula: $y' = y \cdot (N - 1)/N$, where y' is the transformed value, y is the observed proportion, and N is the total sample size. This transformation simply ensures that y' will not assume the values of exactly 0 or 1, which can cause problems during model fitting (following Ferrari and Cribari-Neto 2004).

Fungi cover analysis

To test the prediction that fungi cover on nests would increase after periods of intense rainfall, we used an ordered multinomial logit model, which is similar to a logistic regression model, but with multilevel categorical data as response variable (Gelman and Hill 2006). The fitted model contains one slope for each predictor variable and a number of intercepts equal to the number of categories in the response variable minus 1. We used the level of fungi cover (from 0 to 3) as the categorical response variable, and as predictor variables we used the accumulated rain between 2 consecutive fieldtrips, the position (i.e., angle) of the nest on the fallen log, and the interaction between these 2 variables. We included the position of the nest and its interaction with accumulated rainfall because nests located at the lower half of the fallen log (see nest 2 in Figure 2) are more protected from wind and sunlight. These nests should stay humid for longer periods after rainfall and thus are likely to be more susceptible to fungi attack. Moreover, if we assume that a fallen log absorbs water from rainfall, nests at the lower half of the fallen log should be more humid due to water percolation through the wood (Schmidt 2006). Instead of using the angle of the nest directly in the analysis, we calculated an index of position of each nest as $p = (90 - A)/90$, where p is the position index and A is the angle of the nest in degrees (Figure 2). Following this formula, nests at the lower half of the fallen log have $p = 1$, whereas nests close to the lateral sides of the fallen log have $p \sim 0$. Thus, our expectation was to find a positive effect of p on fungi cover. We did not include male size as a predictor variable in the fungi cover analysis because, as stated above, dorsal scute width is not a good proxy of body condition in *Q. limbata* (Supplementary Figure S3) and because we do not anticipate any causal relationship between male size and his ability to keep the nest clean from fungi.

Reproductive success analysis

To test the predictions that 1) nest integrity would increase the number of eggs received by the resident males and 2) fungi cover would decrease this number, we used a model in which the response

variable has a gamma distribution, which is a positive continuous distribution adequate for data with high variance (Bolker 2008). Moreover, we adopted an exponential link function for the expected mean (μ) of the distribution and fit a single value for the shape parameter. The response variable of our model was the number of newly laid eggs in the nest plus 10^{-6} . We added a small value to all egg counts to prevent the presence of zeros in the data set, which can be a problem during model fitting with gamma distribution (Bolker 2008). To evaluate the sensitivity of the results to the addition of this small value, we repeated the analysis using two other values (10^{-3} and 10^{-9}). The results were qualitatively the same (Supplementary Figure S4), so only the results considering the value of 10^{-6} are presented in the main text. The predictor variables were: nest integrity, the categorical level of fungi cover (from 0 to 3), and male dorsal scute width, which is a standard measure of body size in harvestmen (Buzatto et al. 2014). In this analysis, we estimated nest integrity as the mean between nest floor and nest wall integrity because these 2 variables are positively correlated (Pearson correlation, $r = 0.440$). We included body size in the model to investigate the potential effect of this variable on males' reproductive success because body size is under directional sexual selection by females in many animal species (examples in Andersson 1994). Both mean nest integrity and level of fungi cover used in the analysis were those observed at the fieldtrip prior to egg counting. The values of these 2 predictor variables are not correlated (Pearson correlation, $r = -0.017$), indicating no problem of multicollinearity in our model.

Nest tenure analysis

To test the predictions that males would be more likely to remain in nests 1) that have maintained high integrity and low fungi cover throughout the time and 2) where males have received eggs regularly, we used a binomial logistic model. The data used in this analysis includes only nests that were naturally abandoned by the resident males and does not include any case in which a resident male was likely displaced from his nest by a conspecific male (i.e., nest takeover). Therefore, we did not use male size as a predictor variable because nest abandonment is probably not the result of aggressive physical interactions between males, in which male size could play an important role in the outcome of the contests (Andersson 1994). Moreover, the inclusion of male size in the analysis of nest tenure would be redundant because this variable has already been used as a predictor in the reproductive success (i.e., egg gain) analysis, which in turn is a predictor of nest tenure.

In this statistical analysis, the sampling units were all observations of each nest, except the one in which it was first found, until it was abandoned by the resident male. The binary response variable of tenure received a value of 1 if the male was still present in the nest in fieldtrip F and 0 if he abandoned the nest at fieldtrip F . The predictor variables were the number of fieldtrips since the male last received eggs in his nest at fieldtrip $F-1$, as well as the mean nest integrity and mean level of fungi cover from the moment the nest was built until fieldtrip $F-1$. As in the previous analysis, nest integrity at each fieldtrip was calculated as the mean between wall and floor integrity. In this analysis, however, we considered fungi cover as a continuous variable because we used the mean value of fungi cover calculated as $\sum_{i=1}^{F-1} L_i / F-1$, where L is the level of fungi cover (from 0 to 3). According to this formula, a mean value of fungi cover close to 0 indicates that the nest was rarely attacked by fungi, whereas a mean value of fungi cover close to 3 indicates that the nest was heavily attacked by fungi during the entire study period.

The values of mean nest integrity and mean fungi cover were only weakly correlated (Pearson correlation, $r = -0.088$), indicating no problem of multicollinearity in our model.

RESULTS

General description of the data

We found 181 nests during our study, from which 132 nests were monitored from the construction until the moment they were destroyed or permanently abandoned by their respective resident males. A total of 78 nests were completely destroyed during the study period: 65 (83%) by rainfall, 9 (11%) by fungal attack, and 4 (6%) by damage caused by fallen branches. In all these cases, the resident males abandoned their nests after complete destruction. Additionally, 54 nests that were not completely destroyed were abandoned by their respective resident males. From the 78 males that abandoned their nests after complete destruction, 16 were later found on the same fallen log, with ($N = 9$) or without a new nest ($N = 7$). The remaining 62 males were never observed again on the same fallen log.

Effect of rainfall on nest integrity

The drag force caused by rainfall running on the fallen log surface affected nest integrity by decreasing the wall perimeter and the floor area (Figure 3). High drag values caused more damage to nest wall than to nest floor (Table 1). The variance in nest wall and nest floor integrity increased with the drag force. In general, when the drag force was low, mean nest integrity was high and the variance of nest integrity was low (Table 1; Figure 3). In turn, when the drag force was high, mean nest integrity was low and the variance of nest integrity increased, indicating that for the same drag value some nests were heavily damaged, whereas others remained almost intact (Figure 3). Finally, both fallen log and male identities had a relatively large effect on the variation in the integrity of both nest wall and floor (Table 1).

Effect of rainfall and nest position on fungi cover

A total of 893 observations of 149 nests were included in this analysis. Nearly 62% ($N = 93$) of the monitored nests were recorded as being attacked by fungi at least once during the sampling period, whereas 38% ($N = 56$) of them were never recorded containing fungi. In most observations ($N = 530$), nests were free of fungi and, among the observations in which we recorded fungi on the nests, the most frequent level of fungi cover was 1 (low), with 327 records, followed by 2 (intermediate), with 25 records, and 3 (high), with 11 records. The level of fungi cover was explained by both the accumulated rainfall between fieldtrips and the interaction between rainfall and position (i.e., angle) on the fallen log surface (Table 2). On the lateral surface of the fallen log, mean fungi cover increased with rainfall, whereas on the underside surface of the fallen log, mean fungi cover decreased with increasing rainfall (Figure 4). Overall, however, mean expected fungi level was always low (Figure 4). Both fallen log and male identities had a strong effect on the variation in fungi cover (Table 3).

Effect of nest integrity and fungi cover on reproductive success

The number of new eggs received by resident males between 2 consecutive fieldtrips ranged from 0 to 51 (Figure 5). The number of eggs received was neither influenced by body size of the resident males or nest fungi cover, however nests with high integrity received more eggs than nests with low integrity (Figure 5, Table 3),

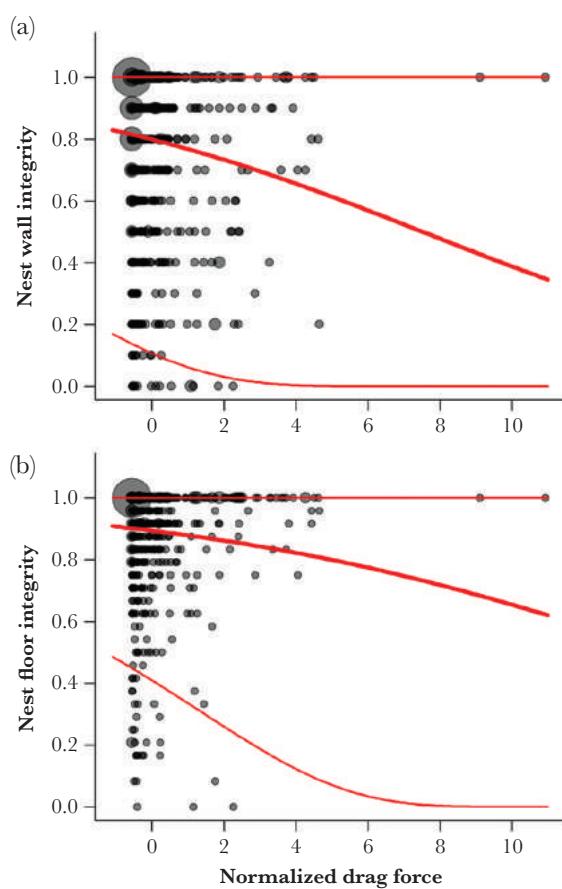


Figure 3

Effect of the drag force on the integrity of (a) nest wall and (b) nest floor. In both graphics, 0 indicates that the wall or the floor of a nest are completely destroyed by rainfall running on the surface of the fallen log and 1 indicates that they are intact. The thick red line represents the mean value predicted by the fitted model, and the thin red lines represent the 95% prediction interval, which delimits a region where 95% of the data points should be according to the fitted model. In both graphics, bubble area is proportional to the number of superimposed data points.

also the variance in the number of eggs received was also higher for nests with higher integrity (Figure 5A). Both fallen log and male identities had a strong effect on the variation in fungi cover (Table 3).

Effect of nest integrity, fungi cover, and reproductive success on nest tenure

The mean ($\pm SD$) nest tenure was 49 ± 55 days (min–max = 1–267 days; $N = 132$ resident males). Nest integrity and fungi cover did not affect nest tenure, but the recent reproductive success of the resident males did (Figure 6). We found that the probability of males abandoning their nests increased with time they did not receive eggs. Once more, both fallen log and male identities had a strong effect on the variation in nest tenure (Table 4).

DISCUSSION

Here, we followed a large number of nests of the harvestman *Q. limbata* to evaluate how rainfall could influence nest integrity and consequently males' reproductive success and nest tenure. Rainfall caused severe damages that lead to total nest destruction and abandonment by males in almost 50% of the nests we monitored since

Table 1

Summary of the statistical models used to explain nest floor and nest wall integrity (response variables). The predictor variable was the drag force, which was estimated based on the accumulated rainfall between fieldtrips and the angle of the nest on the fallen log surface. We employed a beta distribution and allowed both the mean (μ) and the precision (φ) to vary in function of the response variable. We included nest identity and fallen log identity as random variables. The results are presented as mean estimate \pm standard error and 95% credible interval (CI). We also present the standard deviation (SD) of the random effects, which represents how much of the variance in the data is explained by variation between fallen logs and between resident males

Parameters	Nest floor		Nest wall	
	Estimate	95% CI	Estimate	95% CI
Mean (μ)				
Intercept	2.159 \pm 0.433	1.455 to 3.196	1.378 \pm 0.389	0.981 to 1.761
Drag force (slope)	-0.121 \pm 0.064	-0.247 to 0.005	-0.183 \pm 0.059	-0.298 to -0.069
Precision (φ)				
Intercept	0.930 \pm 0.067	0.798 to 1.063	0.286 \pm 0.058	0.171 to 0.4
Drag force (slope)	-0.163 \pm 0.064	-0.286 to -0.034	-0.139 \pm 0.048	-0.232 to -0.045
Random effects (SD)				
Male identity	0.426 \pm 0.072	0.288 to 0.572	0.424 \pm 0.082	0.268 to 0.59
Fallen log identity	0.586 \pm 0.713	0.131 to 2.301	0.290 \pm 0.606	0.024 to 1.182

Table 2

Summary of the model used to explain fungi cover on the nests. The response variable was a categorical measure of fungi cover per nest in each fieldtrip with 4 levels (0, 1, 2, and 3). The predictor variables were the accumulated rainfall between fieldtrips, an index of nest position (i.e., angle) on the fallen log, according to which higher values indicate nests closer to the underside of the fallen log (see Figure 2), and the interaction between these 2 variables. We used an ordered multinomial logit model in which the intercepts represent thresholds between categories of the response variable. Fungi cover effects were calculated using fungi cover 0 as baseline. We included nest identity and fallen log identity as random variables. The results are presented as mean estimate \pm standard error and 95% CI. We also present the SD of the random effects, which represents how much of the variance in the data is explained by variation between fallen logs and between resident males

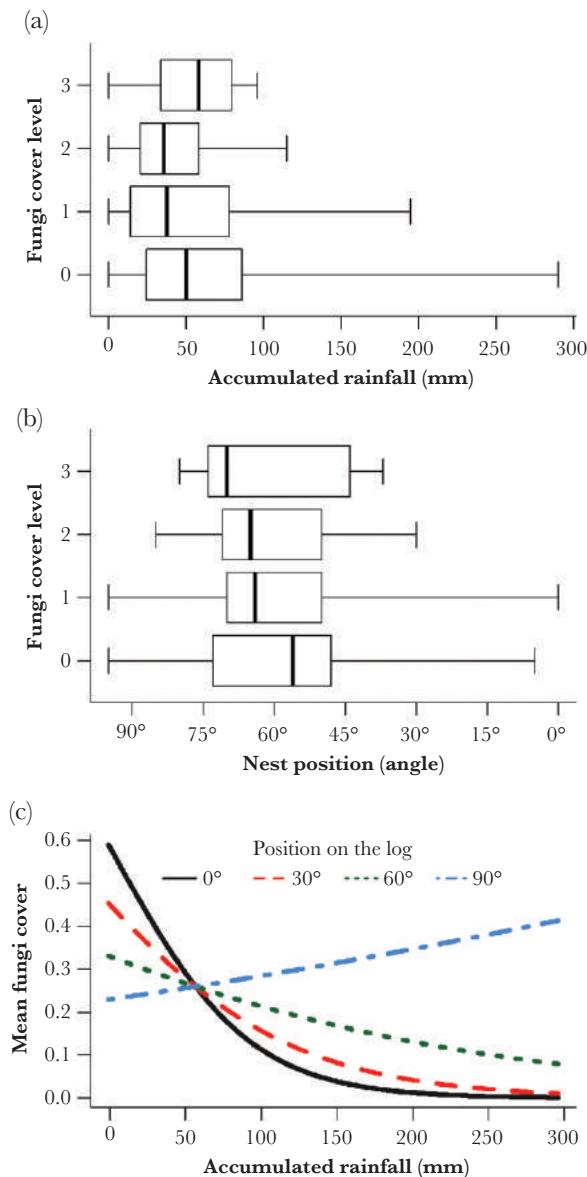
Parameters	Estimate	95% CI
Slopes		
Rainfall	-0.295 \pm 0.087	-0.467 to -0.126
Nest position	-0.151 \pm 0.188	-0.525 to 0.217
Nest position \times rainfall	-0.235 \pm 0.092	-0.417 to -0.054
Intercepts (thresholds)		
(1) Low fungi cover (1–25%)	1.090 \pm 1.622	-1.639 to 4.773
(2) Intermediate fungi cover (26–50%)	4.981 \pm 1.640	2.264 to 8.657
(3) High fungi cover (\geq 51%)	6.387 \pm 1.668	3.607 to 10.091
Random effects (SD)		
Male identity	1.855 \pm 0.228	1.456 to 2.337
Fallen log identity	2.227 \pm 2.765	0.478 to 8.659

the moment they were built. Moreover, damage to nest wall and floor was higher when nests were exposed to a higher drag force caused by water running on fallen log surface. Fungal growth inside the nests was positively related to the rainfall, but only in the lateral portion on the fallen log, where the drag force is stronger. As we expected, nest integrity had a positive effect on males' reproductive success as males with well-preserved nests received more eggs. However, male body size and the level of fungal cover on the nest had no effect on males' reproductive success. Finally, nest tenure was influenced only by reproductive success: males that received eggs recently had a lower chance of abandoning their nests than

males that had not received eggs in a long time. In what follows, we integrate these findings and discuss their implications to our understanding on how abiotic conditions may affect the reproductive success of males in a species in which they are the sole responsible for nest building and maintenance.

Although *Q. limbata* males consistently build their nests on the lower half of fallen logs, where they are protected from direct rainfall (Figures 1a and 2), the probability of nest destruction by the water running on the fallen log surface was high. However, nest destruction was not indiscriminate so that some nests were severely damaged after intense rainfall, whereas other remained almost intact despite being subject to the same drag force (Figure 3). Previous studies with vertebrates have shown that abiotic conditions do not affect all nests in the same way because the nest site selected by the parents may make the nest more or less exposed to unfavorable conditions, including strong wind (e.g., Bellrose et al. 1964), direct sunlight (e.g., Consolmagno et al. 2016), flooding (Thompson and Furness 1991), or cold temperatures (e.g., Mallory et al. 2009). In *Q. limbata*, part of the variation in nest integrity after intense rainfall may be explained by the fact that the fallen logs are not perfectly cylindrical and their surfaces have irregularities, which certainly interfere with the water flow and velocity, attenuating the drag force experienced by some nests. Moreover, the density of foliage on the canopy above the fallen logs is not homogeneous, and some fallen logs or even some parts of the same fallen log are more likely to be exposed to the rain. In fact, fallen log identity explained a great part of the variation in the data of nest integrity (Table 1). This finding indicates that nest site selection by males should take into account not only the angle on the fallen log surface, but also the fallen log per se because some fallen logs are probably more affected by rainfall than others.

Variation between males in their capacity to repair their nests may also explain part of the variance we found in the effect of rainfall on nest integrity. Although there is no study on the energetic costs of nest building and maintenance in *Q. limbata*, these activities are known to be energetically demanding in fish (Hinch and Nicholas 1991) and birds (Mainwaring and Hartley 2013). We know, however, that *Q. limbata* males may take as much as 1 month to build a nest, which represents a great part of their adult lifetime, estimated to be no more than 12 months (A. Rojas, unpublished

**Figure 4**

Effect of (a) accumulated rainfall and (b) nest position (i.e., angle) on the intensity of fungi cover according to the following classes: (0) no cover, (1) low cover (1–25% of the nest covered), (2) intermediate cover (26–50% of the nest covered), and (3) high cover ($\geq 51\%$ of the nest covered). The central line represents the median, the box represents the central quartiles (25–75%), and whiskers represent the minimum and maximum observed data. (c) Mean value of fungi cover (in a scale from 0 to 3) predicted by the model according to the accumulated rainfall between fieldtrips. Although nest position (i.e., angle) is a continuous variable ranging from 0° to 90° , for the sake of simplicity, we show here values for only 4 positions: 0° , 30° , 60° , and 90° . Given that the expected values of mean fungi cover are never higher than 1, they can be interpreted as the probability of finding fungi on a nest according to the accumulated rainfall and the position of the nest on the fallen log.

data). Even though we do not have a good proxy of male body condition in the study species (Supplementary Figure S2), we argue that only males with enough energy reserves should be able to pay the costs of repairing the frequent nest damages caused by rainfall. If energy reserves of resident males decrease, the integrity of their

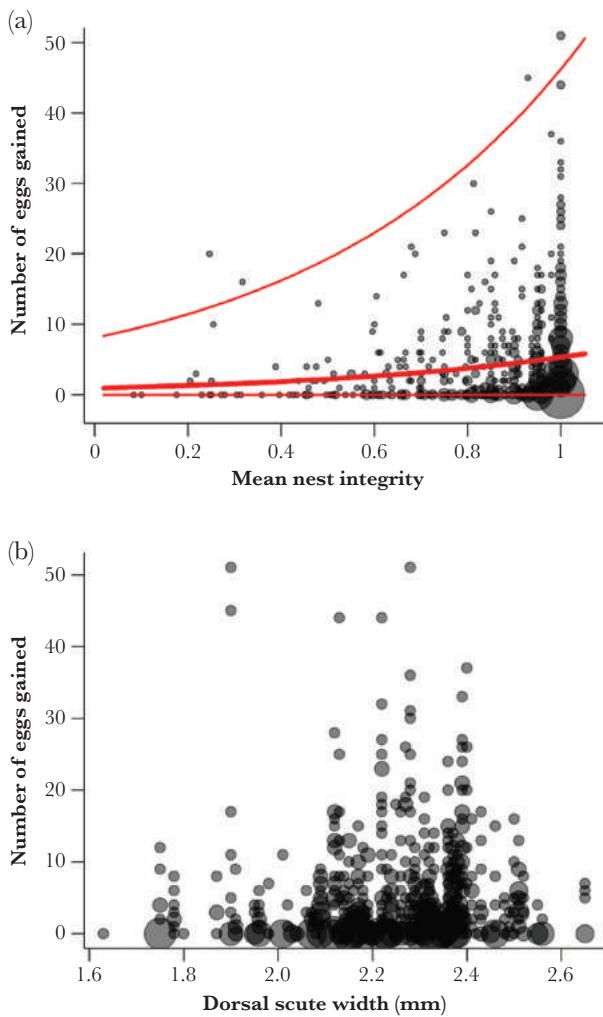
Table 3

Summary of the statistical model used to explain males' reproductive success. The response variable was the number of new eggs observed in each nest per male in each fieldtrip. The predictor variables were male dorsal scute width (body size), nest integrity, and fungi cover, which is a categorical variable with 4 levels (0, 1, 2, and 3). We adopted a gamma distribution and fit a single shape parameter. Fungi cover effects were calculated using fungi cover 0 as baseline. We added male identity and fallen log identity as random effects in the model. The results are presented as mean estimate \pm standard error and 95% CI. We also present the SD of the random effects, which represents how much of the variance in the data is explained by variation between fallen logs and between resident males

Parameters	Estimate	95% CI
Main model parameters		
Intercept	1.276 ± 0.268	0.790 to 1.796
Shape parameter	0.142 ± 0.006	0.132 to 0.154
Mean nest integrity (slope)	0.298 ± 0.103	0.087 to 0.491
Dorsal scute width (slope)	0.162 ± 0.120	-0.079 to 0.395
Fungi cover effects		
(1) Low (1–25%)	0.376 ± 0.232	-0.087 to 0.824
(2) Intermediate (26–50%)	0.973 ± 0.715	-0.256 to 2.526
(3) High ($\geq 51\%$)	1.427 ± 1.433	-0.718 to 4.822
Random effects (SD)		
Fallen log identity	0.309 ± 0.456	0.015 to 1.293
Male identity	0.302 ± 0.175	0.019 to 0.657

nests should also decrease because they would be unable to keep up with the constant damages caused by rainfall. Nests exposed to low drag force produced by water running on the fallen log surface would demand low maintenance effort, and males in both poor and good body condition should be able to keep their nests intact, generating low variance in nest integrity (as shown in Figure 3). On the other hand, nests exposed to high drag force would demand high maintenance effort, and only males in good body condition should be able to keep their nests intact. If we assume that males' ability to repair their nests is influenced by body condition, the variance in nest integrity should increase in response to higher values of drag force (as shown in Figure 3). As in the case of fallen log identity, male identity also explained a great part of the variation in data of nest integrity (Table 1). This finding suggests that in places where nests are subject to intense drag force, nest integrity may be an indicator of male body condition that can be used by females to select the best mating partners, as already suggested for some nest-building fish with exclusive paternal care (e.g., Barber et al. 2001; Olsson et al. 2009).

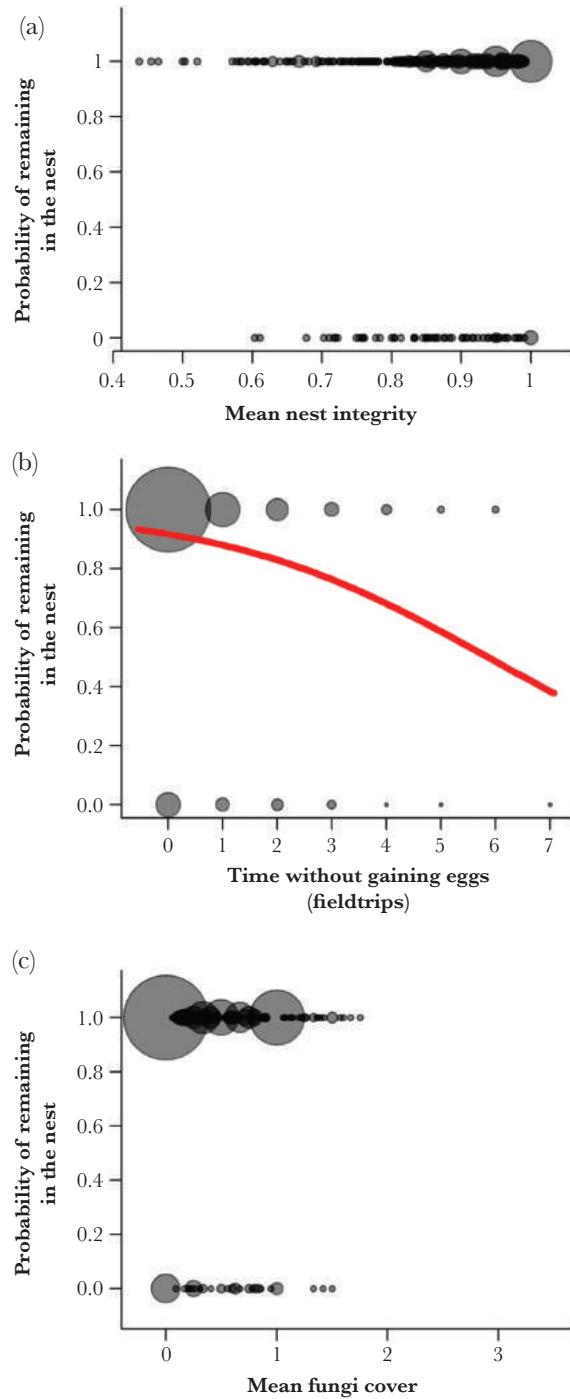
Fungal attack was an important source of nest destruction, and males abandoned their nests after extensive infestation in nearly 7% of the nests we monitored since the moment they were built. Although we predicted that rainfall would favor fungal growth due to an increase in humidity (Schmidt 2006), we found a more complex scenario. On the lateral surface of the fallen logs, where the drag force caused by running water is stronger, there was indeed an increase in the mean fungi cover with increasing rainfall. On the underside surface of the fallen logs, however, rainfall caused a decrease in the mean fungi cover (Figure 4c). This pattern of fungal attack may happen because the growth of several wood-decay fungi is optimal when wood moisture content is below 90%, and it is fully inhibited as the cellular spaces of wood become saturated with water (reviewed in Griffin 1977). The high velocity of the water

**Figure 5**

Effect of (a) nest integrity and (b) male body size (measured as dorsal scute width) on the number of recently laid eggs found inside a nest. In x axis of (a), 0 indicates that the a nest is completely destroyed and 1 indicates that a nest is intact. In (a), the thick red line represents the mean value predicted by the fitted model, and the thin red lines represent the 95% prediction interval, which delimits a region where 95% of the data points should be according to the fitted model. In both graphics, bubble area is proportional to the number of superimposed data points.

on the lateral surface of the fallen logs probably decreases percolation, maintaining wood moisture content below 90%, and creating favorable conditions for fungi growth. On the lower part of the fallen log, in turn, where water velocity is close to zero, percolation is expected to be high, and wood probably gets frequently saturated with water, inhibiting fungal growth. Regardless of rainfall and nest position on the fallen log, the risk of fungal attack varied between sites because fallen log identity explained a great part of the variation in data of fungal attack (Table 2). Taken together, these findings reinforce the importance of nest site selection both in terms of the angle where the nest is built and also in terms of which fallen log is used by the males for building their nests.

Considering that our study site is a tropical rainforest with no clear seasonal variation in precipitation, moisture is consistently high throughout the year, which may explain why a great proportion of the nests was attacked by fungi at least once. This pattern

**Figure 6**

Effect of (a) reproductive success (measured as the time without receiving eggs), (b) nest integrity, and (c) fungi cover on nest tenure. In (a), the thick red line represents the mean expected by the adjusted model (see Table 4). In all graphics, bubble area is proportional to the number of superimposed data points.

differs from what happens with clutches of the cave harvestman *Acutisoma longipes* that are also heavily attacked by fungi. In this species, fungal attack on clutches is highly seasonal because the river that crosses the cave suffers great reduction in water volume during the dry season. Only 17% of the clutches are attacked by fungi during the dry season, whereas 50% are attacked during the wet

Table 4

Summary of the statistical model used to explain nest tenure of resident males. The binary response variable was male presence or absence inside his nest at fieldtrip F. The predictor variables (i.e., mean nest integrity and mean fungi cover) were estimated from nest building to fieldtrip F-1. We added male identity and fallen log identity as random effects in the model. The results are presented as mean estimate \pm standard error and 95% CI. We also present the SD of the random effects, which represents how much of the variance in the data is explained by variation between fallen logs and between resident males.

Parameters	Estimate	95% CI
Main model parameters		
Intercept	2.209 \pm 0.886	0.783 to 3.819
Mean nest integrity (slope)	0.184 \pm 0.142	-0.1 to 0.451
Mean fungi cover (slope)	0.030 \pm 0.160	-0.288 to 0.351
Time without egg gain (slope)	-0.416 \pm 0.118	-0.65 to -0.188
Random effects (SD)		
Fallen log identity	1.149 \pm 1.577	0.146 to 4.441
Male identity	0.435 \pm 0.278	0.032 to 1.063

season (Machado and Oliveira 1998). Moreover, although parents (females) of *A. longipes* are unable to prevent extensive fungal infestation (Machado and Oliveira 1998), parents (males) of *Quindina* can feed on the hyphae and control fungal attack to a certain degree (Mora 1990). Intense nest cleaning behavior may explain why the values of mean fungi cover were consistently low during the entire study period. However, male identity explained a great part of the variation in the data of fungal attack (Table 2), suggesting that parental quality probably varies among resident males. Whereas some males are able to remove fungi and keep their nests clean, other males seem to be unable to prevent extensive fungi infestation. In the future, it would be interesting to investigate whether nest cleaning is related to male body condition in *Q. limbata* (see below).

There is evidence that nest quality is correlated with female attraction in fish species with exclusive paternal care (e.g., Lindström 1992; Candolin and Reynolds 2001; Östlund-Nilsson and Holmlund 2003; Olsson et al. 2009). To the best of our knowledge, this study is the first to show that nest traits also influence female attraction in arthropods. Males of *Q. limbata* owning high-integrity nests had higher reproductive success than males owning low-integrity nests, which suggests that females choose their mates according to nest quality. Given that male size did not influence mating success and that precopulatory male–female interactions are very brief in *Quindina* (Mora 1990; Toscano-Gadea and Rojas 2014), nest quality may be one of the main drivers of female mating decisions. In fact, behavioral data of both *Q. limbata* and *Q. albomarginis* show that females carefully inspect nest structure before any physical contact with the resident male and that after this inspection, some females may leave the nest without mating (Mora 1990; Quesada-Hidalgo et al. 2019). As we mentioned above, nest integrity may be a honest signal of male body condition, specially in sites where nests are subject to high drag force. Additionally, damaged nests may expose the offspring to high mortality due to predation, as reported for some fish (e.g., Whoriskey and FitzGerald 1985) and birds (Elkins 2010). In the case of *Q. limbata*, high nest walls may prevent the entrance of some egg predators, such as millipedes (Figure 1b). Moreover, given that females insert their eggs in pores of the spongy nest floor, a damaged floor may make the eggs more exposed and vulnerable

to predators. Thus, females that select males based on nest integrity may acquire both indirect benefits related to male body condition and direct benefits related to increased offspring survival. We stress, however, that both the mean and the variance in egg gain increased with nest integrity (Figure 5). This result clearly indicates that high nest integrity is a necessary but not sufficient condition for a male to acquire eggs. In fact, the reproductive success of resident males may also be influenced by other factors that were not evaluated in our study, such as male body condition and the number of receptive females and competing males in the fallen log.

Contrary to our prediction, females of *Q. limbata* did not base their mating decisions on the fungi cover inside the nests. In several groups with exclusive paternal care, including arthropods (e.g., Mora 1990), fish (Okuda et al. 2002), and frogs (e.g., Simon 1983), fungi are a major source of egg mortality. To our knowledge, though, there is no evidence that females in these groups consistently avoid nests infested by fungi. This general pattern is puzzling because severe fungal infestation may lead to nest destruction and eggs infested by fungi may die. Two nonexclusive explanations could explain females' behavior in *Q. limbata*. Previous studies with the closely related *Q. albomarginis* showed that male body condition does not decrease during the caring period, probably because males feed on small arthropods found close to their nests and also on the fungi growing inside their nests (Requena and Machado 2015). If fungi are an important food source for resident males, females should not necessarily avoid nests with more fungi because in these nests males would be able to keep good body condition during the caring period and perhaps would provide better care to the eggs. Another possibility is that not all fungi growing inside the nests are pathogenic. If females are capable of recognizing pathogenic from nonpathogenic fungi, mating and oviposition decisions should be based on a much more subtle criterion than fungi cover per se.

Nest tenure by resident males was influenced exclusively by their reproductive success so that males that did not receive eggs for a long time tended to abandon their nests. The nests built by *Q. limbata* males, as well by males of some vertebrate species, can be regarded as an extended phenotype with a double function: female attraction and egg protection (Schaedelin and Taborsky 2009). As in the case of other extended phenotypes that are immobile structures, such as the pits built by antlion larvae (e.g., Scharf and Ovadia 2006), the decision to keep investing or abandoning a nest should depend on the current benefits of remaining in the nest and the costs involved in finding a new site and building a new nest. As we expected, nests in which males were unsuccessful in attracting females and/or receiving eggs for a long time were more likely to be abandoned than nests in which males regularly received eggs (Figure 6). Moreover, some of the males that abandoned their nests built a new nest in other parts of the same fallen logs, which suggests that they were indeed relocating their nests, as occurs with some bird species after nest failure (e.g., Beckmann et al. 2015). Although we did not find a direct effect of nest integrity on nest tenure, it is important to note that nest integrity was the most important predictor of male reproductive success (Table 3). Thus, we argue that nest integrity has an indirect effect on nest tenure because well-preserved nests attract more females and receive more eggs, decreasing the chances of nest abandonment by the resident males.

Studies on the effects of abiotic factors on the breeding biology of ectotherms are traditionally focused on aquatic species, such as waterbugs (Belostomatidae) and fish, in which water temperature, oxygen concentration, and salinity are known to affect male

attractiveness, offspring survival, and the costs of parental care (e.g., St Mary et al. 2001, 2004; Lissåker et al. 2003; Green and McCormick 2005; Hale and St Mary 2007; Munguía-Steyer et al. 2008; but see Delia et al. 2013). Here we explored how rainfall, an important abiotic factor in tropical forests, may affect nest integrity and males' reproductive success in a terrestrial arthropod with exclusive paternal care. Our findings indicate that intense rainfall has a major negative effect on males' reproductive success, mostly caused by nest destruction. Considering that storms occur all year long in many tropical forests and that they are unpredictable in time, the best the males can do to decrease the chances of nest destruction is to select protected places to build their nests and to perform nest maintenance continuously. This way, males can ensure that their nests remain well preserved, improving offspring survival, attracting more females, and ultimately increasing their reproductive success.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Rojas et al. (2019).

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