

## RESEARCH ARTICLE

# Nest-site selection in a neotropical arachnid with exclusive male care: Proximate cues and adaptive meaning

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## Abstract

Nest-site selection is a crucial decision made by parents because inadequate sites may expose the offspring and the parent to harsh abiotic and biotic conditions. Although nest-site selection has been reported for some species of arthropods, the *proximate cues* used by parents to select the nest site and the *adaptive meaning* of nest-site selection are still poorly understood. We investigated nest-site selection in the harvestman *Quindina limbata*, in which males build mud nests on the surface of fallen logs and perform parental care. This species inhabits tropical forests where rainfall destroys nearly 50% of the nests, representing an important selective force shaping nest-site selection. We followed 139 nests and recorded the position (angle) where these nests were located on the fallen log surface. Males showed a complex pattern of nest-site selection that responded to three proximate cues: the direct impact of raindrops on the upper half of the fallen log, the drag force caused by flowing water on the laterals of the fallen log, and water saturation on the lowest part of the fallen log. These selective pressures created a bimodal pattern of nest distribution on the lower half of the fallen logs. The peaks of this distribution occurred in places where nests are protected from the direct impact of raindrops, the drag force caused by flowing water is not high, and the risk of nest flooding is low. The possible adaptive meaning of nest-site selection is to minimize the risk of nest destruction, which imposes energetic costs to males that need to build another nest. Nest-site selection may also minimize reproductive costs because males with damaged nests show decreased attractiveness to females. Finally, nest-site selection may increase offspring fitness minimizing the risk of egg mortality associated with nest destruction and anoxia when nests are flooded.

## KEYWORDS

egg mortality, nest destruction, offspring fitness, parental care, rainfall, reproductive success

## 1 | INTRODUCTION

Egg survival and development can be highly influenced by biotic and abiotic conditions, so that oviposition site selection is an important decision for parental fitness (Refsnider & Janzen, 2010). A suitable

oviposition site should provide good thermal and hydric conditions for the offspring (e.g., Huey, 1991; Pike et al., 2012), decrease its exposure to predators and parasites (e.g., Huang & Pike, 2012; Rosenheim, 1988), and increase the chances of the early-hatched young finding food (e.g., Turner & McCarty, 1997). In species with prolonged parental care, the oviposition site should also provide appropriate conditions for the parents, because an inadequate place

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may expose them to stressful and/or risky conditions (e.g., Griebel & Savidge, 2007; Montgomerie & Weatherhead, 1988; Morse, 1985). Finally, if parents build nests to brood eggs and early-hatched young, the oviposition site should be located in places protected from harsh abiotic conditions, such as heavy wind and rainfall, which may destroy the nest, kill the offspring, and even harm the parent (e.g., Boersma & Rebstock, 2014; Thompson & Furness, 1991).

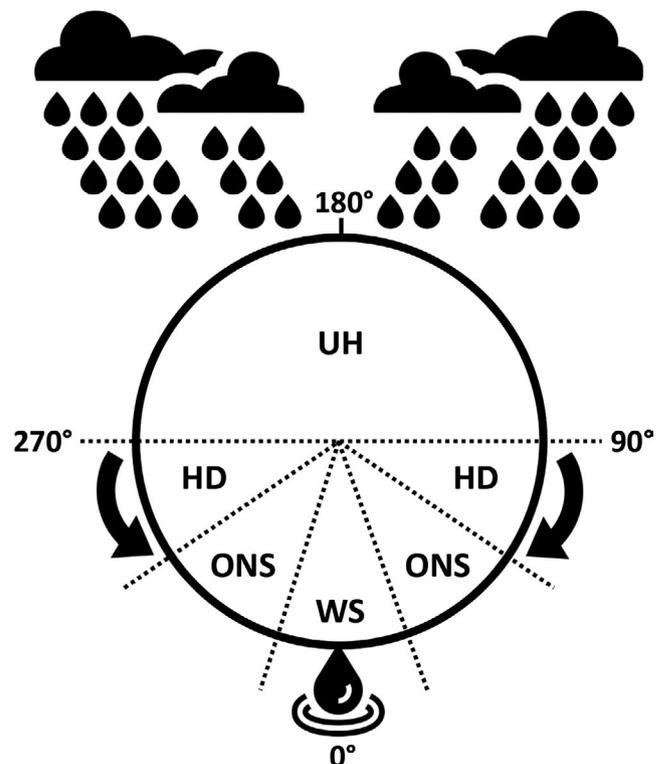
The effects of harsh abiotic conditions on offspring survival and nest-site selection have been intensively studied in vertebrates (examples in Refsnider & Janzen, 2010). In fish, for instance, egg development rate and larval growth speed are reduced in nest sites located in cold water, which extends the caring period and increases the probability of nest abandonment by the parents (e.g., Osenberg et al., 1988; Wrenn, 1984). Among birds, nests exposed to heavy rainfall are more prone to destruction (e.g., Thompson & Furness, 1991), whereas cold temperatures increase nestling mortality (e.g., Boersma & Rebstock, 2014) or starvation (e.g., Dawson & Bortolotti, 2000; Öberg et al., 2014). Thus, parents should select nest sites where the risk of nest destruction is minimized, and the probability of offspring survival is maximized. In fact, there is extensive empirical evidence for fish (reviewed in Wootton & Smith, 2015), frogs (reviewed in Silva & Giaretta, 2008), and birds (reviewed in Collias & Collias, 2014) showing that parents select nest sites and that this behavior increases their reproductive success.

Many arachnid species build nests to brood eggs and recently hatched young (harvestmen: Rojas et al., 2019; pseudoscorpions: Weygoldt, 1969; scorpions: Warburg, 2012; solifuges: Punzo, 1998; spiders: Yip & Rayor, 2014). Although nest-site selection has been reported for some of these species, the *proximate cues* used by parental individuals to select where to build their nests and the *adaptive meaning* of nest-site selection are still poorly understood (e.g., Hanna & Cobb, 2006; Hironaka & Abé, 2012; Morse, 1985). However, there are a few studies of spiders that explored in more detail how and why parental individuals select nest sites. For instance, females of the jumping spider *Psecas chapoda* (Salticidae) build their silk nests only on the bromeliad *Bromelia balansae*, and ovigerous females select bromeliads without debris. The debris (mainly leaves falling from the canopy) blocks the axils of the rosettes that are used as shelter against predators and also as foraging site by both nymphs and adults (Romero & Vasconcellos-Neto, 2005). In the flat-rock spiders *Hemicloea major* (Gnaphosidae), females build their silk nests on the substrate beneath sun-exposed rocks. By building their nests on the coolest locations beneath the hottest rocks, eggs experience moderate temperatures during daytime (Pike et al., 2012).

Here, we investigate nest-site selection in the harvestman *Quindina limbata* (Nomoclastidae), in which males build cup-shaped mud nests on fallen logs that are partially suspended from the ground. The architecture of the nests is complex as they possess a protective wall and a circular, porous floor in which females insert their eggs (Figure 1). This study expands our comprehension on nest-site selection in arachnids in three ways: (a) It is the first time that nest-site selection is studied in a non-spider species; (b) nests are built by males rather than females, as in all species studied so far;



**FIGURE 1** Fallen log suspended from the ground in a Costa Rican rainforest. The inset shows a well-preserved nest with a resident *Quindina limbata* male (arrow) inside it (scale bar = 1 cm). It is possible to see that the nest floor has a porous texture containing pores where females insert their eggs. Moreover, the wall is finely granulated indicating that it has not been washed by the rain. The white patches inside and outside the nest are fungi [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



**FIGURE 2** Scheme of a fallen log in transversal view showing four zones: (1) upper half (UH), where nests are subjected to direct impact of raindrops; (2) high drag (HD) zone, where nests located on the lower half of the fallen log are subjected to high values of drag force that can damage both the wall and floor of the nests, and even wash them away; (3) water-saturated (WS) zone, where wood gets frequently saturated with water, soaking the nest floor and probably increasing egg mortality by anoxia; and (4) optimum nesting site (ONS) zone is where nests are protected from the direct impact of raindrops, the drag force is not the highest, and the wood is not saturated with water. We hypothesized that the nests would be concentrated on the ONS zone

and (c) when compared with the silk nests built by many spiders and pseudoscorpions, or the burrows dug by scorpions and solifuges, *Q. limbata* nests are much more elaborate and take longer to be constructed (see “Study species” below). In a previous study, we showed that heavy rainfall may destroy as much as 50% of the *Q. limbata* nests, leading to offspring mortality, reduction in male attractiveness, and nest abandonment by resident males (Rojas et al., 2019). Considering the negative impact of rainfall on the nests (i.e., the *proximate cue*) and the importance of the nests for offspring survival and male mating success (i.e., the *adaptive meaning*), males should carefully select places to build their nests. But what is the best place to build a nest on a fallen log in a tropical rainforest?

Tropical rainforests are subject to intense rainfall, and when drops of heavy rain hit a fallen log, the direct impact can be strong enough to destroy nests exposed on the upper half of the log (Figure 2). Thus, males should avoid building nests on this part of the fallen log. Nests located on the lower half of a fallen log are protected from raindrops, but water flowing down the log surface exerts a drag force that can damage the nests and even wash them away. According to fluid dynamics theory, if we consider the fallen log to be approximately cylindrical, for the same volume of water flowing down the log surface, the drag force is the highest on the laterals of the fallen log (Mallick & Kumar, 2014; Figure 2). Thus, males should avoid building nests on places where the drag force is high, and the risk of nest damage is known to be high (Rojas et al., 2019). On the lowest part of a fallen log, water velocity is close to zero, but percolation is high, and wood gets saturated with water (Schmidt, 2006; Figure 2). These conditions inhibit fungal growth on the wood (Griffin, 1977) and on the nests (Rojas et al., 2019), but the soaking of the nest floor probably increases egg mortality by anoxia. Thus, males should also avoid building nests on the lowest part of the fallen logs. Based on the rationale presented above, there are two zones on the fallen log that offer suitable conditions for nest building (Figure 2). If males select nest sites based on the risks of nest destruction by rainfall and of egg mortality by anoxia, we expect to find most of the nests inside these two zones, which we call “optimum nesting sites.” Moreover, if a nest is built on an unsuitable site and is then destroyed by rainfall, we expect that the resident male should build his next nest closer to the optimum nesting sites.

## 2 | METHODS

### 2.1 | Study species

The nests of *Q. limbata* are composed of a circular floor with a porous texture containing pores where females insert their eggs (Figure 1). The floor is entirely surrounded by a 5–15 mm high wall that serves as a barrier against some wandering predators (Rojas et al., 2019). Males build their nests using small particles of mud and wood debris that are collected on the fallen log surface and are possibly mixed with saliva. Nest building takes from 2 to 4 weeks, and when the nest is not extensively damaged, the resident male promptly starts

repairing it. Mean nest tenure is nearly 50 days, and during this period, males may receive as much as 100 eggs from several females (Rojas et al., 2019). The number of eggs received by a male is positively related to the integrity of his nest, so that males with well-preserved nests have higher reproductive success (Rojas et al., 2019). Eggs laid by females are actively protected by the males, which are able to repel predators, such as ants, conspecifics, and earthworms (Quesada-Hidalgo et al., 2019). If a nest-owner male dies or deserts, his nest may be promptly occupied by another male that may even care for the unprotected eggs (Quesada-Hidalgo et al., 2019).

### 2.2 | Study site

We conducted this study at Veragua Rainforest (9°55′35.7″N, 83°11′27.9″W; altitude 400 m a.s.l.), a natural reserve located in the province of Limón, Caribbean slope of Costa Rica. The vegetation in the reserve is a primary tropical rainforest, and the climate is wet and warm throughout the entire year, with no well-defined seasons (Holdridge, 1967). The annual precipitation is between 3,000 and 4,000 mm, and the mean monthly precipitation is always above 140 mm. The mean annual temperature is 23°C, and the mean monthly temperature is always above 19°C (data from a meteorological station located 21 km from the study site).

### 2.3 | Data collection

From May 2012 to May 2013, we performed 41 field trips to the study site, with intervals between field trips ranging from 6 to 28 days (median = 8 days). During this period, we followed all nests found on the surface of four large fallen logs, which were between 17 and 22 m long and were all partially suspended from the ground (Figure 1). In each field trip, which lasted one or two days, we inspected all four fallen logs searching for nests. We individually labeled all nests with a numbered color flag at the moment we found them and recorded the position (angle) of each nest on the fallen log surface using a protractor and a level. We measured the angles relative to an imaginary vertical line orthogonal to the ground and crossing the center of the fallen log (see scheme in Figure 2). Finally, we individually marked each resident male with enamel ink applied to his dorsal scute (carapace) and femora of the hind legs (following Requena & Machado, 2015).

We considered that a nest was extensively destroyed when all the following conditions were met: (a) More than 50% of the nest wall was damaged, (b) the general texture of the wall was roughly granulated, and (c) the floor was smooth, without the typical porous texture (see Figure 1d in Rojas et al., 2019). After nest extensive destruction, resident males usually abandon their nests and are no longer recorded on the fallen log (Rojas et al., 2019). However, some males may build a second nest on the same fallen log and, whenever it happened, we recorded the position of the new nest in the same way described above. We included in this dataset only nests

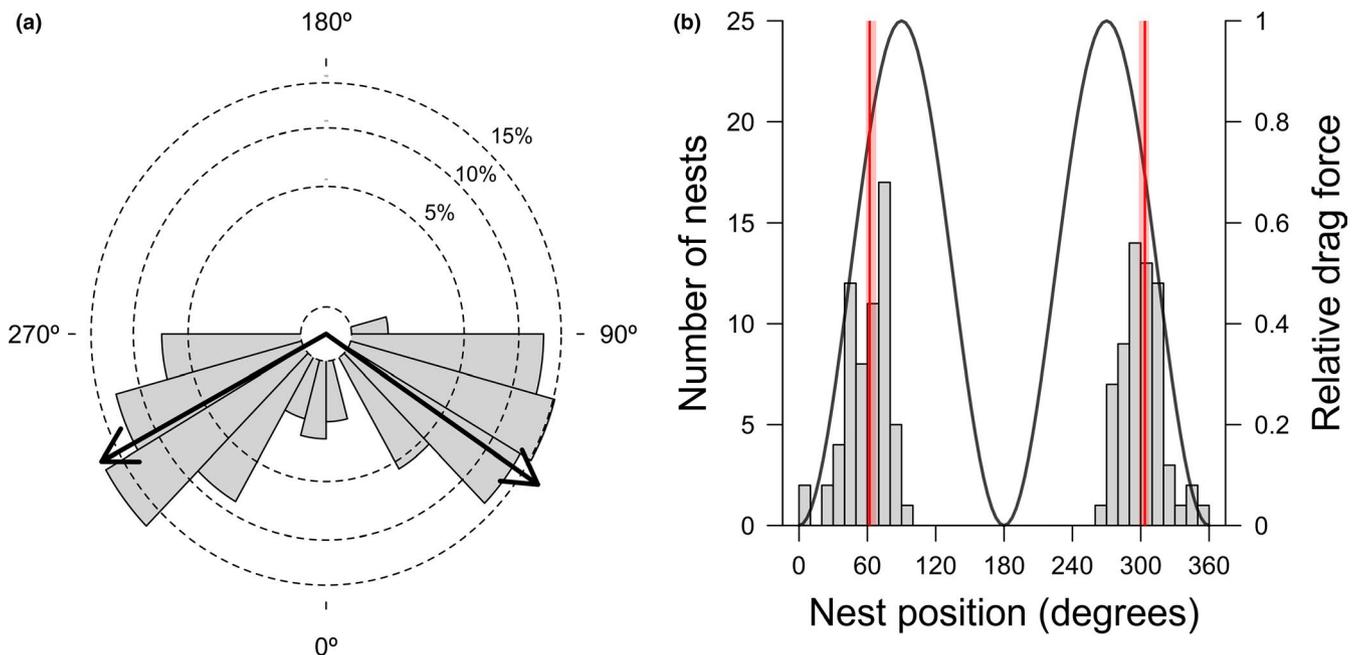
that were destroyed by rainfall, and not by fungal attack or damage caused by fallen branches. Because the nests take some weeks to be built and our field trips occurred within short intervals, the great majority of the nests were found during the building process. Therefore, we are confident that we recorded all nests built by the males in the four fallen logs and that no nest was destroyed before being recorded.

## 2.4 | Statistical analyses

To test the hypothesis that *Q. limbata* nests should be concentrated on the two optimum nesting sites (Figure 2), we used circular statistics, which allows us to work with angular data. According to our hypothesis, the angles of the nests should follow a bimodal distribution because they should be present mainly on the optimum nesting sites located on the lower half of the fallen logs, but not on the lowest part (Figure 2) or the laterals of the fallen logs (Figure 2). For this analysis, we used only the first nest built by the males ( $n = 125$ ) and fitted four alternative models to the data, comparing them using the Akaike information criterion (Burnham & Anderson, 2002). In all models, we adopted the von Mises circular distribution, which has two parameters: mean  $\mu$  and concentration  $\kappa$  (higher  $\kappa$  values represent lower variance, Mardia & Jupp, 2009). The first model was the null model, in which we assumed angles to follow a unimodal distribution and no difference between fallen logs. In the second model,

we still assumed a unimodal distribution but, because we collected data in four fallen logs, we included fallen log identity as a categorical predictor variable. In the third and fourth models, we assumed a bimodal distribution of angles using a mixture model of two von Mises distributions (McLachlan & Peel, 2004). In the third model, we assumed no difference between fallen logs, whereas in the fourth model we included fallen log identity as a categorical predictor of the means of angle distribution. In all models, we used a single concentration ( $\kappa$ ) value (similar to an ANOVA) because a visual inspection of the data indicated that this assumption was plausible. We fitted all models using the packages *bbmle* (Bolker & R Development Core Team, 2017) and *CircStats* (Lund & Agostinelli, 2018) in the software R 3.5.3 (R Core Team, 2019).

To test the hypothesis that males that had their nests destroyed by heavy rainfall should build their next nests closer to the optimum nesting sites, we considered the modal angles in which nests were concentrated in each side of the fallen logs (see Figure 3) as proxies of the optimum position to build a nest. Thus, for each male observed building a second nest, we calculated the absolute difference between the position (angle) of his nest and the closest modal angle (i.e., right or left modal angle in each fallen log). This difference represents the distance to the optimum position in degrees. Although three males constructed a third ( $n = 1$ ) and a fourth nest ( $n = 2$ ), we used in this analysis only the second nest built by the males ( $n = 13$ ). Our prediction was that males would build this second nest closer to the optimum position, so that the difference (in degrees) between



**FIGURE 3** Distribution of angles in which nests of the harvestman *Quindina limbata* were built on four fallen logs in a Costa Rican rainforest. (A) Circular histogram representing the distribution of nest angles; the thick arrows represent the estimated means of the two modes of the distribution. The peaks of the two distributions are located at the optimum nesting site zone (see Figure 2). (B) Regular histogram of nest angle distribution. The red lines represent the two modes of the distribution, and the shaded red area delimits the 95% confidence interval of these modes. The dark curve shows the expected relative drag force produced by flowing rainwater. According to fluid dynamics theory, the drag force produced by a fluid flowing over a cylindrical surface is proportional to the flow rate multiplied by  $\sin(\text{angle})^2$ . Thus, the dark curve depicts  $\sin(\text{angle})^2$  as a proxy of how strong is the drag force produced by flowing rainfall on the surface of the fallen log. Notice that the modes of the distribution do not overlap the peaks of the relative drag force [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

the second nest and the optimum position should be smaller than the difference between the first (destroyed) nest and the optimum position. To compare the values between the first and second nests built by the males, we used a paired *t* test performed in the software R 3.5.3 (R Core Team, 2019).

### 3 | RESULTS

We measured the angles of 139 *Q. limbata* nests in the four fallen logs we inspected. These nests occurred almost exclusively on the lower half of the fallen logs and were concentrated around two zones close to the laterals (Figure 3a). The models with a bimodal distribution of angles showed higher fit than the models with a unimodal distribution (Table 1). The best model (Akaike weight = 0.97) was the bimodal model without difference between fallen logs, so that the four fallen logs we sampled did not differ in the angles that concentrated most nests. In the best fitted model, the means of the two modes of angle distribution were 63° (CI95% = 57°–67°) and 303° (CI95% = 298°–308°) (Figures 2 and 3a–b), the concentration parameter  $\kappa$  was 10.03 (CI95% = 7.79 – 12.68), and the proportion of nests at each side of the fallen logs was very similar (right = 0.49; left = 0.51). The means of the two modes do not coincide with the areas of maximum drag force (Figure 3b).

We observed 13 males that had a nest destroyed by heavy rainfall and built another nest afterward on the same fallen log. Two males that built the first (destroyed) nest very far from the modal nest angles relocated their second nest to a place much closer to it (Figure 4). The other males, however, showed no clear pattern, and whereas four relocated their second nest to a place slightly closer to the modal nest angles, two males built the second nest at the same distance from the modal angle and the other six males relocated their nests to a place slightly further from the modal nest

**TABLE 1** Summary of the model selection performed to investigate whether the distribution of angles in which males of the harvestman *Quindina limbata* build nests on four fallen logs follows a uni- or bimodal distribution

Model description	$\Delta$ AIC	<i>df</i>	Akaike weight
Bimodal <b>without difference</b> between fallen logs	0	4	0.983
Bimodal <b>with difference</b> between fallen logs	8.1	10	0.017
Unimodal <b>with difference</b> between fallen logs	142.6	5	<0.001
Unimodal <b>without difference</b> between fallen logs (null model)	149.1	2	<0.001

Note:  $\Delta$ AIC: difference between the Akaike information criterion (AIC) of each model and that of the most plausible one (lower values indicate more plausible models). *df*: degrees of freedom (number of parameters). The Akaike weight is an additional measure of model plausibility, so that the higher the weight of a model, the stronger is the evidence supporting that model.

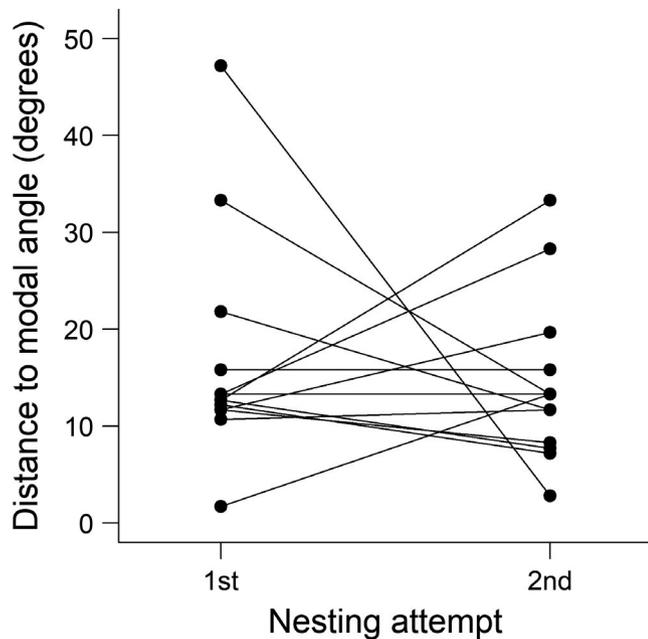
angles (Figure 4). Males did not build their second nest consistently closer to the modal nest angles (mean  $\pm$  SD absolute difference to the modal angle  $-2.4 \pm 16.6$ ,  $t = 0.52$ ,  $df = 12$ ,  $p = .61$ , Figure 4).

### 4 | DISCUSSION

Here, we investigate nest-site selection by an arachnid species for which we know important *proximate cues* that could be used by males to select where to build their nests, and also the possible *adaptive meaning* of nest-site selection for both males and offspring. As we hypothesized, nests are concentrated on the zones we called “optimal nesting sites,” on the lower half of the fallen log, but not exactly on the lateral sides (90° and 270°) nor directly on the underside of the log (0°). Nests were concentrated on angles approximately 60° above 0° on each side of the fallen logs (see Figures 2 and 3). At this position, the peak of nest occurrence is not coincident with the peak of drag force caused by rainwater flowing down the fallen log (Figure 3b), and is also far from the position where soaking of the nest floor is most likely to occur (Figure 2). Contrary to what we expected, however, males that had a nest destroyed by heavy rainfall did not build their next nests closer to the modal nest position, which we infer to represent the optimum nest angle.

Males of *Q. limbata* do not build their nests on the upper side of a falling log (between 90° and 270°), most likely because nests in this region would be exposed to direct impact of raindrops and falling debris from the canopy. Males also avoided lateral zones of the fallen log where water flowing down exerts a high drag force that can damage or even destroy the mud nests. At least for fish and birds, nest destruction usually imposes energetic costs to the parents because they need to repair the nest or rebuild it in another place (Mainwaring & Hartley, 2013; Wisenden et al., 2009). In *Q. limbata*, we do not have quantitative information on the energetic costs paid by males to build and repair their nests. However, we know that males may take as much as 1 month to build a nest, and this period represents a great part of their adult lifetime, estimated to be no more than 12 months under natural field conditions (A. Rojas, unpublished data). Thus, it is reasonable to suppose that complete nest destruction may represent a great energetic cost to males.

Among birds, all eggs can be lost if the nest is destroyed by abiotic factors, such as high tide or heavy rainfall (e.g., Fisher et al., 2015; Frederick, 1987; Thompson & Furness, 1991). This is also the case of *Q. limbata* because water flowing on the fallen log surface can wash the nest away, probably killing all eggs inside it and imposing high fitness costs to the males (Rojas et al., 2019). Moreover, as observed in several fish species showing exclusive paternal care (e.g., Barber et al., 2001; Candolin & Voigt, 2001; Kvarnemo, 1995; Olsson et al., 2009), nest integrity is a key component of males' reproductive success in *Q. limbata*, because females evaluate nest structure to select their mating partners (Rojas et al., 2019). According to our field observations, males without a nest do not copulate and are deprived from access to receptive females. Thus, besides the putative energetic costs related to nest rebuilding discussed above, nest



**FIGURE 4** When comparing the position of the first and second nests of *Quindina limbata* males that had their first nest destroyed by rainfall, we found no difference in the distance between the nests and the closest modal angle (i.e., the peak of the nest angles distribution). In the plot, we show the distance to the modal angle for the first and second nesting attempts of 13 males. The values for the two nesting attempts of the same male are connected by a line for comparison

destruction also removes a male from the mating pool for at least 2 weeks, which is the minimum time required to build another nest. This represents a high reproductive cost to males that do not select a protected nesting site where the risk of nest destruction is low. Additionally, given that fallen log identity did not affect the pattern of nest occurrence in the fallen logs we inspected, we suggest that protected nesting sites are predictable, allowing males to select the best places even if they move from one fallen log to another. In the future, it would be interesting to investigate what are the precise cues used by males to identify places (i.e., angles) where their nests are more protected from destruction and eggs safer from mortality by anoxia.

Although males avoid lateral zones with high drag, the most marked avoidance occurs in the lowest part of the fallen log, where we found only few nests. In a previous study, we showed that heavy rainfall causes a decrease in the intensity of fungal attack on eggs, but only in the lowest part of the fallen logs, where water velocity is close to zero and percolation is high, especially if the fallen logs are parallel to ground (Rojas et al., 2019). In the lower part of the fallen logs, wood probably gets frequently saturated with water, inhibiting the growth of wood-decay fungi (Griffin, 1977; Schmidt, 2006). Thus, egg anoxia by water saturation may impose higher fitness costs than the risk of nest destruction by the drag force of running water. In insects, eggs are overly sensitive to low levels of oxygen (Hoback & Stanley, 2001). In species in which eggs are submerged in water, such as giant water bugs (Belostomatidae),

males have to actively aerate the eggs placed by females on their backs. They do that exposing the eggs periodically at the air–water interface and performing movements with their hind legs to generate water flow and oxygen diffusion through the egg membrane (Smith, 1997). Females of the intertidal beetle *Bledius spectabilis* (Carabidae) lay their eggs in burrows that can be flooded by the tide (Wyatt, 1986). To keep the burrow dry and eggs safe from anoxia, females block the burrow entrance once the tide comes in and open it once the tide goes out (Wyatt, 1986). Unlike giant water bugs and intertidal beetles, males of *Q. limbata* are unable to actively protect the eggs from anoxia, and the best way to minimize the risk of nest flooding may be to avoid building their nests in zones where the wood gets highly saturated in water, that is, the lowest part of the fallen logs.

Despite energetic and reproductive costs associated with nest destruction, males that had their first nest destroyed by heavy rainfall did not build the second nest in a more protected place. There are at least two possible explanations to this unexpected pattern. *First*, positive experiences in the destroyed nest may influence the male to rebuild the second nest close to the first one. These positive experiences could be (a) high mating success (i.e., a great number of female visits to the nest) or (b) proximity to a reliable food source, such as a termite nest, which allows the male to feed while caring for the offspring. Thus, males with high mating success or abundant food resources close to the destroyed nest could rebuild the second nest close to the first one. In the spider *Argiope keyserlingi* (Araneidae), for instance, intense web damages are not costly enough to make individuals relocate their webs to a distant place if feeding success is high (Chmiel et al., 2000). *Second*, males could find zones protected from rainfall moving longitudinally on the fallen log, without changing the angle of the second nest. In a previous study on nest integrity in *Q. limbata*, we suggested that the negative effects of rainfall are not necessarily the same along the fallen log because the canopy cover is not homogeneous, the fallen logs are neither perfectly cylindrical nor parallel to the ground, and the surface has irregularities that may obstruct the water flow creating small protected pockets (Rojas et al., 2019). It is worth noting that while 50% of the nests are destroyed by rainfall (Rojas et al., 2019), only a small fraction of the males built a second nest in the same fallen log. Thus, it is possible that the most frequent tactic of nest relocation adopted by the males involves moving to another fallen log nearby. Given that males can also occupy abandoned nests in the same fallen log (Quesada-Hidalgo et al., 2019), an interesting question is whether empty nests located in more protected zones are reoccupied faster than empty nests located in less protected zones.

In conclusion, our findings suggest that males of the harvestman *Q. limbata* show a complex pattern of nest-site selection that responds to at least three proximate cues: the direct impact of raindrops on the upper half of the fallen log, the drag force caused by flowing water on the laterals of the fallen log surface, and the water saturation on the lowest part of the fallen log. These selective pressures create a clear bimodal pattern of nest distribution on the lower half of the fallen logs. The peaks of this distribution occur in places

where the nests are protected from the direct impact of raindrops, the drag force caused by flowing water is not the highest, and the risk of the nest getting saturated with water is low. Therefore, the possible adaptive meaning of nest-site selection is to minimize nest damage by rainfall and egg mortality by anoxia. Males that built their nests in protected sites may enjoy decreased energetic costs with nest maintenance, increased mating success, and increased offspring survival.

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