

ANDRÉS ROJAS VALLE

**E a chuva levou: efeitos negativos da precipitação sobre o sucesso reprodutivo dos machos em um aracnídeo construtor de ninhos**

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

SÃO PAULO

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Dissertação apresentada ao Instituto de Biociências da Universidade de São Paulo como parte dos requisitos para obtenção do título de Mestre em Ciências, na área de Ecologia de Ecossistemas Terrestres e Aquáticos.

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SÃO PAULO

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Aprovada em: \_\_\_\_\_

**Banca examinadora:**

\_\_\_\_\_

\_\_\_\_\_

\_\_\_\_\_

\_\_\_\_\_

(Orientador)

## Epígrafe

*“Un tronco podrido: qué tesoro!... Hongos negros y azules le han dado orejas, rojas plantas parásitas lo han colmado de rubíes, otras plantas perezosas le han prestado sus barbas y brota, veloz, una culebra desde sus entrañas podridas, como una emanación, como que al tronco muerto se le escapara el alma... Más lejos cada árbol se separó de sus semejantes... Se yerguen sobre la alfombra de la selva secreta, y cada uno de los follajes, lineal, encrespado, ramoso, lanceolado, tiene un estilo diferente, como cortado por una tijera de movimientos infinitos...”*

“El Bosque Chileno”

Pablo Neruda

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# Resumo

ROJAS VALLE, A. E a chuva levou: efeitos negativos da precipitação sobre o sucesso reprodutivo dos machos em um aracnídeo construtor de ninhos. 2018. Dissertação (Mestrado) – Instituto de Biociências, Universidade de São Paulo, SP.

Em espécies que constroem ninhos, a sobrevivência da prole e o sucesso reprodutivo dos indivíduos parentais são fortemente influenciados pela localização e qualidade dos ninhos. Portanto, quantificar a influência das condições abióticas sobre a integridade dos ninhos é importante para prever os efeitos que a variabilidade climática pode ter na sobrevivência da prole e no sucesso reprodutivo dos pais. Neste estudo, investigamos como a chuva influencia a integridade dos ninhos e como a integridade dos ninhos influencia a atratividade masculina e o tempo de posse do ninho. Nossa espécie de estudo foi o opilião *Quindina limbata*, em que os machos constroem ninhos de barro em troncos caídos e protegem os ovos contra predadores e infestação por fungos. Nosso conjunto de dados é baseado em 12 meses de inspeções regulares de mais de 150 ninhos em uma floresta tropical na Costa Rica. Descobrimos que 43% dos ninhos foram destruídos pela chuva. A força de arrasto promovida pela chuva na superfície dos troncos caídos influenciou negativamente a integridade dos ninhos, diminuindo o perímetro da parede e a área do piso. A intensidade de cobertura de fungos não foi explicada pela posição do ninho ou pela precipitação. O tamanho corporal dos machos não influenciou o ganho de ovos, mas ninhos com alta integridade receberam mais ovos do que ninhos com baixa integridade. Curiosamente, ninhos com altos valores de cobertura de fungos receberam mais ovos. Por fim, a integridade dos ninhos e a cobertura de fungos não influenciaram o tempo de posse do ninho, mas a probabilidade de os machos abandonarem seus ninhos aumentou com o tempo em que não receberam ovos em seus ninhos. Considerando que temporais ocorrem durante todo o ano em florestas tropicais, os melhores machos devem selecionar locais protegidos para construção dos seus ninhos a fim de diminuir as chances de destruição promovida pela chuva. Locais protegidos podem manter a estrutura do ninho melhor preservada, melhorar a sobrevivência da prole, atrair mais fêmeas e, finalmente, aumentar o sucesso reprodutivo dos machos.

**Palavras-chave:** abandono de ninho, atratividade masculina, condições abióticas, cuidado paternal, fenótipo estendido, fungo, integridade do ninho, opiliões, sucesso de acasalamento.

## Abstract

34 ROJAS VALLE, A. **Gone with the rain: negative effects of rainfall on male reproductive**  
35 **success in a nest-building arachnid.** 2018. Dissertação (Mestrado) - Instituto de Biociências,  
36 Universidade de São Paulo, SP.

37

38 In nest-building species, offspring survival and reproductive success of parental individuals  
39 are strongly influenced by nest location and quality. Thus, quantifying the influence of  
40 abiotic conditions on nest integrity is important to predict the effects that weather variability  
41 may have on offspring survival and parental reproductive success. Here we investigated  
42 how rainfall affects nest integrity and how nest integrity influences male attractiveness and  
43 nest tenure. Our study species was the harvestman *Quindina limbata*, in which males build  
44 cup-like mud nests on fallen logs and protect the eggs against predators and fungi  
45 infestation. Our dataset is based on 12 months of regular inspections of over 150 nests in a  
46 tropical rainforest from Costa Rica. We found that 43% of the nests were destroyed by  
47 rainfall. The drag force promoted by rainfall running on the log surface negatively affected  
48 nest integrity by decreasing the wall perimeter and the floor area. The intensity of fungi  
49 cover was not explained by nest position or by precipitation. No matter the body size of the  
50 owner males, nests with high integrity received more eggs than nests with low integrity.  
51 Curiously, nests with high values of fungi cover received more eggs. Finally, nest integrity  
52 and fungi cover did not affect nest tenure, but the probability of males abandoning their  
53 nests increased with time they did not receive eggs. Considering that intense rainfall occurs  
54 all year long in tropical forests, the best males can do to decrease the chances of nest  
55 destruction is to select protected places to build their nests. Protected sites may keep nest  
56 structure better preserved, improve offspring survival, attract more females, and ultimately  
57 increase male reproductive success.

58 **Key-words:** abiotic conditions, extended phenotype, fungi, harvestman, male attractiveness,  
59 mating success, nest abandonment, nest integrity, paternal care.

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

62

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## 72 **Introduction**

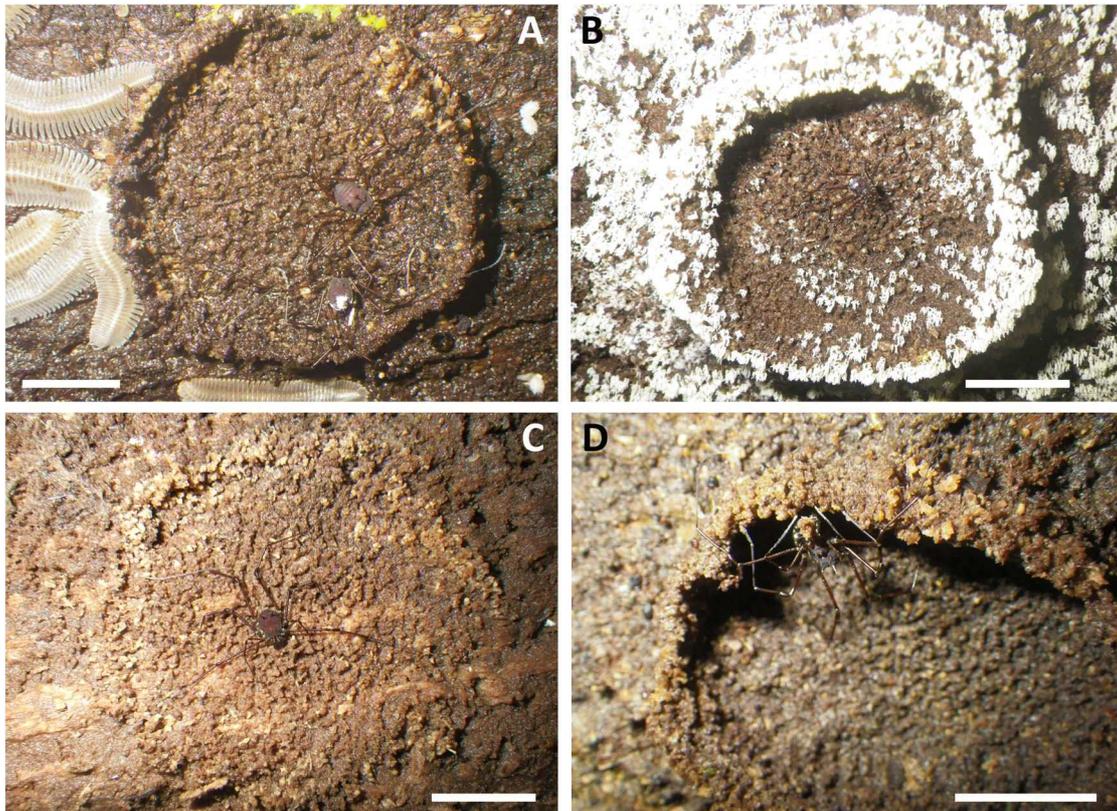
73 In species in which individuals build nests for their offspring, the location and quality of the  
74 nests are key components of offspring survival and reproductive success of parental  
75 individuals. Inadequate nesting sites may expose both the parents and the offspring to a  
76 wide range of unfavorable factors, including attacks of natural enemies and harsh abiotic  
77 conditions (reviewed in Refsnider and Janzen 2010). Abiotic conditions, in particular, can  
78 negatively affect nesting success in different ways. For instance, among aquatic organisms,  
79 such as fish, cold temperatures in the nest site may decrease egg development rate and larval  
80 growth speed (e.g. Osenberg et al. 1988), extending the caring period and increasing the  
81 probability of nest abandonment by the parents (e.g. Wrenn 1984). Among terrestrial species,  
82 such as birds, heavy, prolonged rainfall and cold temperatures may increase the probability  
83 of (i) nestling mortality due to exposure (e.g. Boersma and Rebstock 2014), (ii) nestling  
84 starvation due to reduced adult foraging efficiency (e.g. Dawson and Bortolotti 2000, Öberg  
85 et al. 2014), (iii) nest destruction promoted by rainfall (e.g. Thompson and Furness 1991), and  
86 ultimately (iv) nest abandonment by parental individuals (e.g. Griebel et al. 2007). Thus,  
87 quantifying the influence of abiotic conditions on offspring survival and reproductive  
88 success of parental individuals is important to predict the effects that weather variability  
89 may have on animal populations (Parmesan et al. 2000).

90 When males are the sole responsible for nest building and parental care, females are  
91 expected to make mating decisions based not only on morphological male traits, which may  
92 indicate the overall quality of a male as mating partner, but also on traits that indicate his  
93 parental abilities and the quality of his nest. Females that evaluate male parental abilities and  
94 nest quality may benefit indirectly through the inheritance of either good genes that increase  
95 offspring fitness (Tallamy 2001) or genes that will increase the attractiveness of the male  
96 offspring (Candolin 2003). In addition, females may also benefit directly because offspring

97 survival is expected to increase when they mate with males possessing well-built nests or  
98 nests in favorable locations. Indeed females select males based on male caring quality and  
99 also on particular nest traits, including location, size, shape, and ornamentation, in many  
100 species of fish (e.g. Lindström 1992, Forsgren 1997, Candolin and Reynolds 2001, Östlund-  
101 Nilsson and Holmlund 2003), frogs (e.g. Felton et al. 2006), and birds (e.g. Hoi et al. 1994,  
102 Quader 2006, Kleindorfer 2007). Therefore, any factor decreasing nest quality may have  
103 profound consequences for males' reproductive success because it may negatively affect both  
104 their mating success and offspring survival.

105       Even though exclusive paternal care has evolved at least 16 times independently  
106 among arthropods (Requena et al. 2013), nest-building by males is known to occur only in a  
107 small clade of harvestmen belonging to genus *Quindina* (Arachnida: Opiliones). Males of *Q.*  
108 *albomarginis* and *Q. limbata*, for instance, build cup-like nests made of mud on the surface of  
109 fallen logs that females visit to mate and lay eggs (Mora 1990, Fig. 1A). Nests are composed  
110 of a circular floor where females lay their eggs, surrounded by a wall 5-15 mm high (Fig. 1A).  
111 Eggs hatch in 20-25 days and nymphs may stay inside the nest during the first two or three  
112 instars. Nest-owner males stay on the same nest for several weeks or months, defending it  
113 from the invasion of conspecific males, protecting eggs and newly hatched nymphs from  
114 predators, removing fungi from eggs, and repairing the nest from physical damage  
115 (Rodríguez and Guerrero 1976, Mora 1990, Fig. 1B). Field experiments with *Q. albomarginis*  
116 and *Q. limbata* showed that male presence inside the nest is crucial for offspring survival  
117 because eggs in unattended nests may be attacked by fungi or consumed by predators, such  
118 as ants and conspecifics (Mora 1990; Quesada-Hidalgo et al. 2017). Moreover, females of both  
119 species seem to copulate exclusively with nest-owning males and carefully inspect nest  
120 structure before copulating and laying eggs (Mora 1990, Toscano-Gadea and Rojas 2014).

121 Therefore, nest possession and nest quality are likely to be important components of male  
122 reproductive success in these two species with exclusive male care.



123

124 **Figure 1.** Nests of the harvestman *Quindina limbata* built on the surface of fallen logs in a  
125 Costa Rican rainforest. (A) Intact nest with one male (marked with a white dot on the  
126 dorsum and on the last right leg) and one female (unmarked). Note that the nest wall is  
127 approximately 5 mm high and its texture is finely granulated. The nest floor is thick,  
128 completely circular, and have a spongy texture. Outside the nest there are several feather  
129 millipedes that are prevented from entering the nest by the intact walls. (B) Nest heavily  
130 covered with fungi. Although males can actively remove and consume hyphae, sometimes  
131 they cannot prevent fungi growth inside the nest. This seems to be the case of the nest in the  
132 photo. (C) Nest heavily damaged by rainfall. Note that both the wall and the floor are  
133 destroyed in some parts and considerably damaged in other parts. The general texture of the  
134 nest wall is roughly granulated, and the floor does not have the typical spongy texture. (D)  
135 Male repairing a damaged nest, adding debris mixed with saliva to the wall. In all photos,  
136 scale bars = 1 cm.

137 All *Quindina* species occur in Neotropical rainforests (Pinto-da-Rocha and Bragagnolo  
138 2017), where nests are subjected to intense rainfall. Males respond to extensive nest  
139 destruction by either repairing or abandoning their nests (Mora 1990, Figs 1B-D). However,  
140 the negative effects of rainfall on nest structure and male attractiveness have not been  
141 explored so far in any arthropod species with exclusive male care. Here, we investigate the  
142 effects of rainfall on nest integrity and male reproductive success using *Q. limbata* as our  
143 study species. In particular, we investigated how rainfall affects nest integrity and how nest  
144 integrity, in turn, influences male attractiveness and nest tenure. We expected that rainfall  
145 would have a direct negative effect on nest integrity washing away nest wall and nest floor.  
146 We also expected an indirect effect of rainfall on nest integrity because the higher the  
147 humidity, the higher the chance of fungi growth on the fallen logs (Griffin 1977) and  
148 consequently on the nests (Fig. 1C). Given that nest integrity is likely to be important for egg  
149 survival, we expected that males occupying well-preserved nests would be more attractive  
150 and receive more visits from females. Finally, the costs of nest maintenance and the benefits  
151 of female attraction should affect male nest tenure. Accordingly, the probability of nest  
152 abandonment would be higher in sites where nests are constantly damaged by rainfall and  
153 receive few visits by females. In these sites, the costs of nest maintenance should be higher  
154 than the benefits in terms of egg gaining by the males, thus nest tenure should be low.

155

## 156 **Methods**

### 157 **Study site and nest monitoring**

158 We studied a population of the harvestman *Q. limbata* found at Veragua Rainforest  
159 (9°55'35.7"N; 83°11'27.9"W; altitude 400 m a.s.l.), in the district of Las Brisas, province of  
160 Limón, Costa Rica. Local temperature varies from 17 to 33 °C during the year (mean = 27 °C)  
161 and, during the study period, annual precipitation was 2280.7 mm (monthly mean = 190

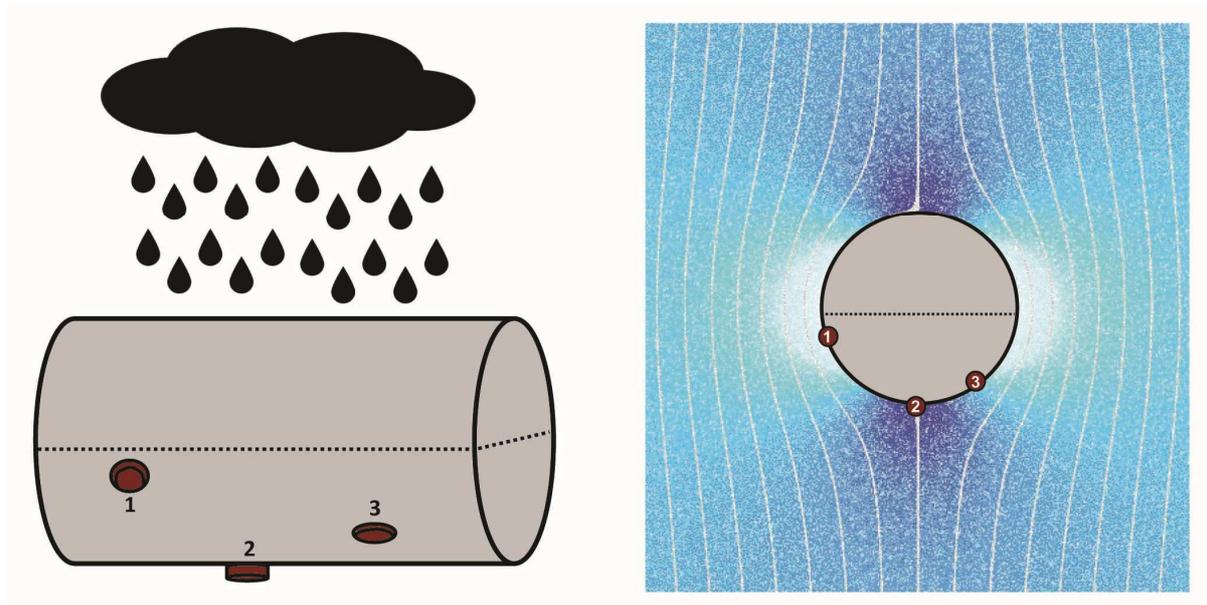
162 mm), with no clear seasonal variation in monthly precipitation. Between May 2012 and May  
163 2013, we followed all nests found in four fallen logs, which were 17, 19, 21, and 22 m long.  
164 During the entire study period, we visited each fallen log 41 times, with intervals from 6 to  
165 28 days between consecutive fieldtrips. In each fieldtrip we photographed all nests and their  
166 corresponding owner male. Moreover, we individually marked all males with enamel ink  
167 applied to their dorsal scute (carapace) and femora of their hind legs (following Requena and  
168 Machado 2015; see marked individual in Fig. 1A). Finally, we individually labeled all nests  
169 and measured the angle of each nest in relation to an imaginary line crossing the middle of  
170 the fallen log parallel to the ground (Fig. 2).

171

## 172 **Rainfall and drag**

173 We obtained daily rainfall values from a meteorological station located 21 km from the study  
174 site, in the district of Matina, Limón. We calculated accumulated rainfall between fieldtrips  
175 by adding the daily precipitation between two consecutive fieldtrips. When rain hits a fallen  
176 log, the direct impact is strong enough to completely destroy any nest exposed on the  
177 superior half of the log (Fig. 2). In turn, nests located on the inferior half of the fallen log are  
178 protected from the direct impact of raindrops. However, water flowing down on the log  
179 surface exerts a drag force on the nests that can produce damage to their structure or even  
180 wash them away. According to fluid dynamics theory, this force is proportional to the  
181 amount of flowing water and to the angle of the nest on the log surface (Batchelor 1967, Fig.  
182 2). Assuming that logs were approximately cylindrical, we used the following formula to  
183 calculate the drag force  $D_{i,t}$  of flowing water acting on nest  $i$  at time  $t$ :  $D_{i,t} = r_t \cdot \sin(\theta_i)$ , where  
184  $r_t$  is the accumulated rainfall between one fieldtrip (time  $t-1$ ) and the subsequent fieldtrip  
185 (time  $t$ ), which is a proxy of the total amount of water flowing on the log surface, and  $\theta_i$  is the  
186 angle of the nest on the log surface (Fig. 2). We used the values of  $D_{i,t}$  as the predictor

187 variable in the analysis of physical damage promoted by rainfall on the wall and floor of  
188 nests (see below).



189  
190 **Figure 2.** Scheme of the drag force promoted by rainfall running on a fallen log surface. (A)  
191 Lateral view of a fallen log (grey cylinder) showing three cup-like mud nests (brown circles)  
192 of the harvestman *Quindina limbata* at the inferior portion of the log. In this position, nests are  
193 protected from the direct impact of the rain. (B) Transversal view of the fallen log showing  
194 the angle of each nest (the numbers of the nests are the same as in A): (1) nearly 15°, (2) 90°,  
195 and (3) nearly 120°. The blue area around the log represents the drag force promoted by the  
196 water running on the surface of a cylinder. Darker shades of blue indicate areas with high  
197 values of drag force. According to fluid dynamics, nest 2 is subject to a higher drag force  
198 than nest 1, and thus has a higher chance of being washed away during intense rainfall.  
199

## 200 **Nest integrity**

201 When there is no physical damage promoted by rainfall, the nest wall usually is 5-15 mm  
202 high and its general texture is finely granulated (Fig. 1A). Moreover, the nest floor is a  
203 continuous, circular layer of mud with a spongy texture where females insert their eggs (Fig.  
204 1A). Upon physical damage promoted by rainfall, the height of nest wall is reduced and its  
205 general texture becomes roughly granulated (Fig. 1C). Also, whole sections of the wall may

206 be eroded, so that in damaged nests the floor may not be totally surrounded by walls.  
207 Depending on the damage intensity, the nest floor may also be partially or completely  
208 eroded, losing its circular shape and also its spongy texture (Fig. 1C). These features can be  
209 easily observed in the photographs taken from the nests in each fieldtrip, so we used these  
210 photographs to estimate the proportion of intact wall and the proportion of intact floor for  
211 each nest, in each fieldtrip, in the four fallen logs we followed during the study period. To  
212 estimate wall integrity, we divided the wall of each nest in 10 sections and visually inspected  
213 how many sections were intact (see Figs S1A-B in Supplementary Material). We used the  
214 proportion of intact wall sections as a proxy of wall integrity. In the case of nest floor, we  
215 divided the floor area in a grid of 24 squares, and considered the proportion of intact sections  
216 as a proxy of floor integrity (see Figs S1C-D in Supplementary Material).

217 We also used photographs to estimate the percentage of nest covered with fungi,  
218 which can be easily recognized due to the presence of white hyphae growing on the floor  
219 and/or the walls of the nest (Fig. 1B). We scored the percentage of fungi cover in each nest at  
220 each fieldtrip as a five-level ordinal variable, using the following categories: (0) no cover, (1)  
221 1-5% of the nest covered, (2) 6-10% of the nest covered, (3) 11-25% of the nest covered, and  
222 (4) 26-100% of the nest covered. Categories (3) and (4) comprise wider intervals because the  
223 number of nests with a high percentage of fungi cover was much lower than the number of  
224 nests in the lower categories.

225

## 226 **Reproductive success and nest tenure**

227 Recently laid eggs of *Q. limbata* are white and can be seen partially buried on the nest floor.  
228 Given that harvestman eggs get darker during embryonic development, and it takes 5-7 days  
229 for the white eggs of *Q. limbata* to become pale brown, we could use the photographs to  
230 identify and count recently laid white eggs inside each nest in each fieldtrip. Although some

231 eggs can be entirely buried in the spongy nest floor, and thus cannot be seen in the  
232 photographs, we assume that the higher the male reproductive success, the higher the  
233 number of recently laid eggs that can be seen in a photograph.

234 In the analysis of nest tenure (see below), we only included males that we observed  
235 building their own nests. We used this criterion because we know that *Quindina* males fight  
236 each other for the possession of nests, and that some owner males can be displaced from  
237 their nests by invader males (Mora 1990, A.V. Rojas personal observation). We considered  
238 that a nest was abandoned when its owner was not recorded inside it during at least two  
239 consecutive fieldtrips.

240

## 241 **Statistical analyses**

242 In all analyses described below, we used information from previous observations of a given  
243 nest to predict what would happen to this same nest in the following observations, so that  
244 our sampling units were always a given nest at a given time (i.e., fieldtrip). Because we have  
245 repeated observations of the same nests and their respective owner males on four fallen logs,  
246 in all analyses described below we included male identity and fallen log as random effects.  
247 We tested all our predictions using generalized linear mixed models (GLMM), adopting  
248 different distributions to best fit our data (Gelman and Hill 2006). Prior to model fitting, we  
249 standardized the continuous predictor variables to produce comparable effect sizes  
250 (Schielezeth 2010). We implemented all models using the *stan* probabilistic programming  
251 language (Carpenter et al. 2017), and fitted the models in a Bayesian approach using  
252 Markov-Chain Monte-Carlo (MCMC) optimization (Gelman et al. 2014). The Bayesian  
253 analyses were performed in the software R version 3.4.1 (R Core Team 2017) using the  
254 package *rstan* (Stan Development Team 2018). In all model fits we ran three MCMC chains

255 with 5,000 iterations plus 5,000 warm-up iterations and adopted the default *rstan* non-  
256 informative priors.

257

### 258 ***Nest floor and wall integrity analyses***

259 To test the prediction that exposure to intense rainfall would decrease the overall integrity of  
260 the nests we fit two models in which the predictor variable was the drag force ( $D_{i,t}$ ) and the  
261 response variables were the proportion of damaged wall (model 1) and the proportion of  
262 damaged floor (model 2) observed at each fieldtrip after the nest was first located on a fallen  
263 log. In both models 1 and 2 we adopted a beta distribution for the response variable, which is  
264 the most adequate for proportion data (Bolker 2008). Moreover, we allowed both the  
265 expected mean ( $\mu$ ) and the precision ( $\phi$ ) parameters of the beta distribution to vary as a  
266 function of the response variable, and adopted an inverse logit link function for  $\mu$  and an  
267 exponential link function to  $\phi$  (following Ferrari and Cribari-Neto 2004). Prior to model  
268 fitting, we transformed the proportions using the formula:  $y' = y \cdot (N - 1)/N$ , where  $y'$  is the  
269 transformed value,  $y$  is the observed proportion, and  $N$  is the total sample size. This  
270 transformation simply ensures that  $y'$  will not assume the values of exactly 0 or 1, which can  
271 cause problems during model fitting (Ferrari and Cribari-Neto 2004).

272

### 273 ***Fungi cover analysis***

274 To test the prediction that fungi cover on nests would increase after periods of intense  
275 rainfall, we used a multi-logit model, which is similar to a logistic regression model, but with  
276 multi-level categorical data as response variable (Gelman and Hill 2006). The fitted model  
277 contains one slope for each predictor variable and a number of intercepts equal to the  
278 number of categories in the response variable minus one. We used the level of fungi cover

279 (from 0 to 4) as the categorical response variable, and as predictor variables we used the  
280 accumulated rain between fieldtrips and the position (i.e., angle) of the nest on the log. We  
281 included the position of the nest because nests located at the inferior portion of the log (see  
282 nest 2 in Fig. 2) are more protected from wind and sunlight, and thus should stay humid for  
283 longer periods after rainfall, and thus more susceptible to fungi attack. Moreover, if we  
284 assume that a fallen log absorbs water from rainfall, nests at the inferior portion of the log  
285 should be more humid due to water percolation through the wood. Instead of using the  
286 angle of the nest directly in the analysis, we calculated an index of position of each nest as  
287  $p = (90 - A)/90$ , where  $p$  is the position index and  $A$  is the angle of the nest in degrees (see  
288 Fig. 2). Following this formula, nests at the inferior portion of the log have  $p = 1$ , whereas  
289 nests close to the lateral sides of the log have  $p \sim 0$ . Therefore, our expectation was to find a  
290 positive effect of  $p$  on fungi cover.

291

### 292 ***Reproductive success analysis***

293 To test the predictions that (1) nest integrity would increase the gain of eggs by males, and  
294 (2) fungi cover would decrease the gain of eggs, we used a model in which we adopted a  
295 gamma distribution for the response variable. The gamma distribution is a positive  
296 continuous distribution, adequate for data with high variance (Bolker 2008). The response  
297 variable was the number of newly laid eggs in the nest plus  $10^{-6}$ . We added a small value to  
298 all egg counts to prevent the presence of zeros in the data, which can be a problem during  
299 model fitting with gamma distribution (Bolker 2008). The predictor variables were an index  
300 of nest integrity calculated as the mean between floor and wall integrity, and the categorical  
301 level of fungi cover on the nest. To investigate the potential role of male size on his  
302 reproductive success, we also included male dorsal scute width, a standard measure of body  
303 size in harvestmen (see Buzatto et al. 2014), as a predictor variable in the model. Both nest

304 integrity and fungi cover level used in the analysis were those observed the fieldtrip prior to  
305 egg counting. Nest integrity and male's dorsal scute width were standardized prior to model  
306 fitting, whereas fungi cover was considered a five-level categorical variable. We adopted an  
307 exponential link function for the expected mean ( $\mu$ ) of the distribution and fit a single value  
308 for the shape parameter.

309

### 310 ***Nest tenure analysis***

311 To test the predictions that males would be more likely to remain in nests (1) that have  
312 maintained high integrity and low fungi cover throughout the time, and (2) where males  
313 have copulated recently, we used a binomial logistic model. In this model, the sampling  
314 units were all observations of each nest, except the one in which it was first found, until it  
315 was abandoned by the owner male. The binary response variable of tenure received a value  
316 of 1 if the male was still present in the nest in fieldtrip  $F$ , and 0 if he abandoned the nest at  
317 fieldtrip  $F$ . The predictor variables were the number of fieldtrips since the male last received  
318 eggs in his nest at fieldtrip  $F-1$ , as well as the mean nest integrity and mean level of fungi  
319 cover from the moment the nest was built until fieldtrip  $F-1$ . As in the previous analysis, nest  
320 integrity at each fieldtrip was calculated as the mean between wall and floor integrity. In this  
321 analysis, we considered fungi cover as a continuous variable because we used mean values  
322 of fungi level, and standardized all predictor variables prior to model fitting.

## 323 **Results**

### 324 **General description of the data**

325 We found 181 nests during our study, from which 132 nests were monitored from the  
326 construction until the moment they were destructed or permanently abandoned by the  
327 owner male. The mean ( $\pm$  SD) time males were recorded inside their nests was  $49 \pm 55$  days  
328 (min. - max. = 1 - 267 days). A total of 78 nests were completely destroyed during the study  
329 period: 65 (83%) by rainfall, 9 (11%) by fungal attack, and 4 (6%) by damages promoted by  
330 fallen branches. In all these cases, the owner males abandoned their nests after destruction.  
331 Additionally, 54 nests that were not completely destroyed were abandoned by their owner  
332 males. From the 78 males that abandoned their nests after complete destruction, 16 were later  
333 found on the same fallen log, with ( $n = 9$ ) or without a new nest ( $n = 7$ ). The remaining 62  
334 males were never observed again on the same fallen log.

335

### 336 **Effect of rainfall on nest integrity**

337 The drag force promoted by rainfall running on the log surface affected nest integrity by  
338 decreasing the wall perimeter and the floor area (Fig. 3). High drag values promoted more  
339 damage to nest walls than to nest floor (Table 1). The variance in nest wall and nest floor  
340 integrity increased with the drag. In general, when the drag was low, mean nest integrity  
341 was high and the variance of nest integrity was low (Table 1, Fig. 3). In turn, when the drag  
342 was high, mean nest integrity was low and the variance of nest integrity increased,  
343 indicating that for the same drag value some nests were heavily damaged whereas others  
344 remained almost intact (Fig. 3). Finally, both log identity and male identity had a relatively  
345 large effect on the variation in the integrity of both nest wall and floor (Tables 1-2).

346 **Effect of rainfall on fungal attack**

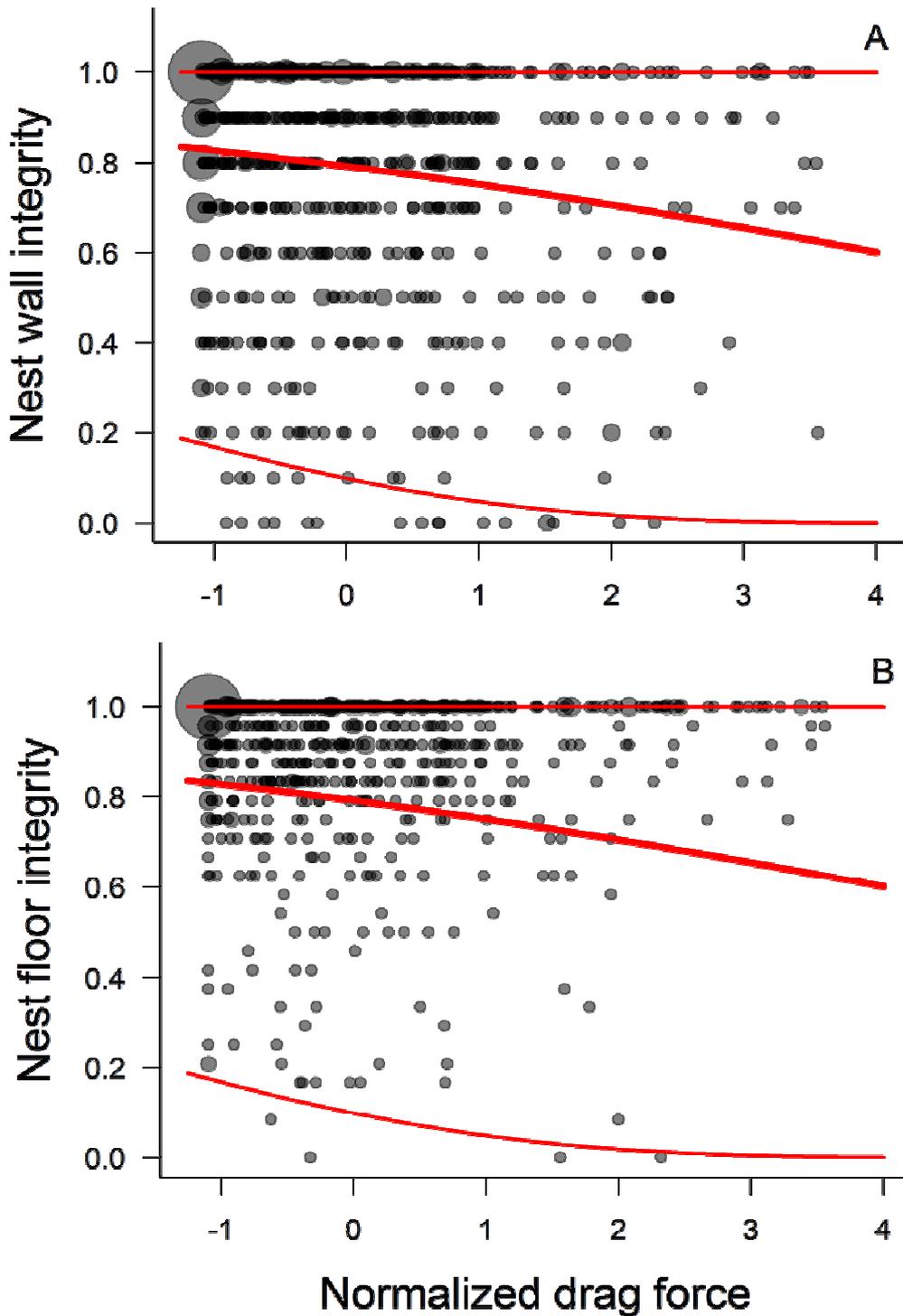
347 The intensity of fungi cover was not explained by nest position or by the precipitation  
 348 accumulated between consecutive fieldtrips (Table 2, Fig. 4). Nonetheless, both log identity  
 349 and male identity had a strong effect on the variation in fungi cover (Table 3).

350

351 **Table 1.** Summary of the statistical models used to explain nest floor and nest wall integrity  
 352 (response variables) in the harvestman *Quindina limbata*. The predictor variable was the drag  
 353 force, which was estimated based on the accumulated rainfall between fieldtrips and the  
 354 position of the nest on the fallen log surface. We employed a beta distribution and allowed  
 355 both the mean ( $\mu$ ) and the precision ( $\varphi$ ) to vary in function of the response variable. We  
 356 included both nest identity and log identity as random variables. The results are presented as  
 357 median estimate and 95% credible interval (CI). We also present the standard deviation (SD)  
 358 of the random effects, which represents how much of the variance in the data is explained by  
 359 variation between logs and between males.

360

Parameter	Nest floor		Nest wall	
	Median	95% CI	Median	95% CI
<i>Mean (<math>\mu</math>)</i>				
Intercept	2.133	1.476 to 2.771	1.336	0.99 to 1.714
Drag force (slope)	-0.149	-0.262 to -0.037	-0.231	-0.33 to -0.131
<i>Precision (<math>\varphi</math>)</i>				
Intercept	0.98	0.852 to 1.102	0.274	0.164 to 0.382
Drag force (slope)	-0.18	-0.293 to -0.068	-0.166	-0.257 to -0.076
<i>Random effects (SD)</i>				
Log identity	0.318	0.085 to 1.918	0.157	0.013 to 1.027
Male identity	0.446	0.317 to 0.589	0.444	0.295 to 0.602

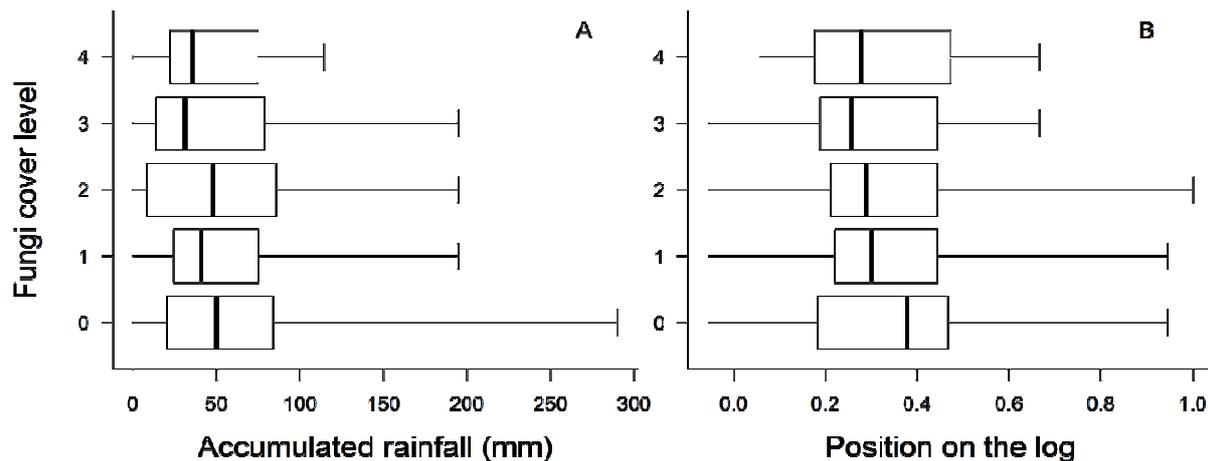


361

362 **Figure 3.** Effect of the drag force promoted by rainfall running on the log surface on the  
 363 integrity of (A) nest wall and (B) nest floor. In both graphics, 0 indicates that the wall or the  
 364 floor of a nest is completely destroyed by rainfall and 1 indicates that they are intact. Bubble  
 365 area is proportional to the number of superimposed data points. The thick red line represents  
 366 the mean and the thin red lines represent the 95% confidence interval expected by the  
 367 adjusted model (see Table 1).

368 **Table 2.** Summary of the model of fungi cover on the nests of the harvestman *Quindina*  
369 *limbata*. The response variable was a categorical measure of fungi cover from zero (no fungi)  
370 to four (more than 25% of fungi cover) per nest in each fieldtrip. The predictor variables were  
371 the accumulated rainfall between fieldtrips and an index of nest position on the fallen log,  
372 according to which higher values indicate nests closer to the underside of the log (see Fig. 2).  
373 We used a multi-logistic model in which the intercepts represent thresholds between  
374 categories of the response variable. Fungi cover effects were calculated using fungi cover 0 as  
375 baseline. We included both nest identity and log identity as random variables. The results  
376 are presented as median estimate and 95% credible interval (CI). We also present the  
377 standard deviation (SD) of the random effects, which represents how much of the variance in  
378 the data is explained by variation between logs and between males.  
379

<b>Parameter</b>	<b>Median</b>	<b>95% CI</b>
Rainfall (slope)	0.154	-0.166 to 0.477n
Nest position (slope)	-0.74	-2.721 to 1.254
<i>Intercepts (thresholds)</i>		
Fungi cover — level 1	0.74	-1.558 to 3.754
Fungi cover — level 2	2.191	-0.059 to 5.258
Fungi cover — level 3	3.362	1.090 to 6.400
Fungi cover — level 4	4.778	2.499 to 7.791
<i>Random effects (SD)</i>		
Log identity	1.417	0.413 to 7.567
Male identity	1.932	1.534 to 2.423



380

381 **Figure 4.** Effect of (A) accumulated rainfall and (B) position (angle of the nest) on the  
 382 intensity of fungi cover according to the following classes: (0) no cover, (2) 1-5% of the nest  
 383 covered, (2) 6-10% of the nest covered, (3) 11-25% of the nest covered, and (4) 26-100% of the  
 384 nest covered. The central line represents the median, the box represents the central quartiles  
 385 (25% to 75%), and whiskers represent the minimum and maximum observed data.

386

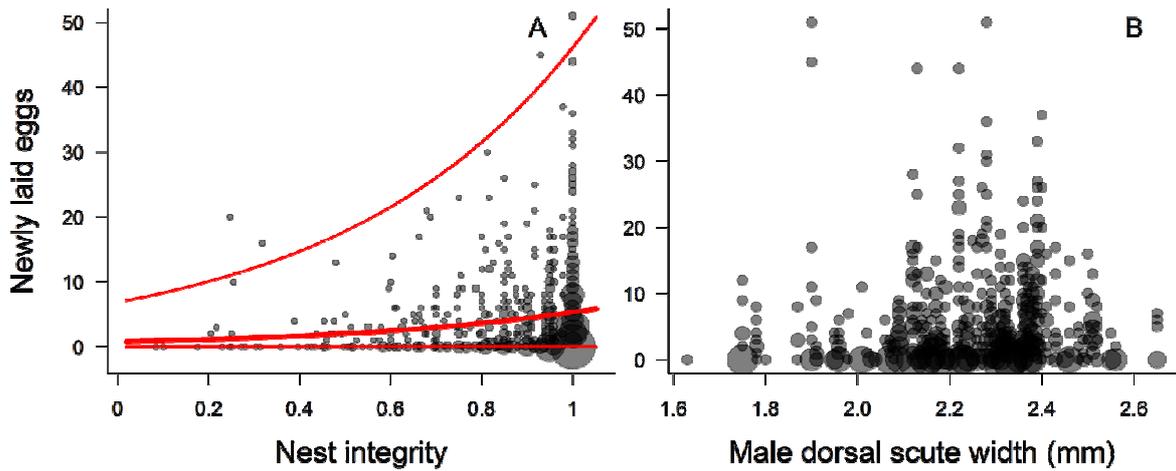
### 387 **Effect of nest integrity and fungi cover on reproductive success**

388 Irrespective of the body size of the owner males, nests with high integrity received more  
 389 eggs than nests with low integrity (Fig. 5). Low to moderate fungi cover did not affect the  
 390 number of eggs received in the nests (Table 3). However, nests with high values of fungi  
 391 cover received more eggs (Table 3). Both log identity and male identity had a strong effect on  
 392 the variation in fungi cover (Table 3).

393

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

395 Nest integrity and fungi cover did not affect nest tenure, but the recent mating success of the  
 396 owner males did (Fig. 6). We found that the probability of males abandoning their nests  
 397 increased with time they did not receive eggs. Once more, both log identity and male  
 398 identity had a strong effect on the variation in nest tenure (Table 4).

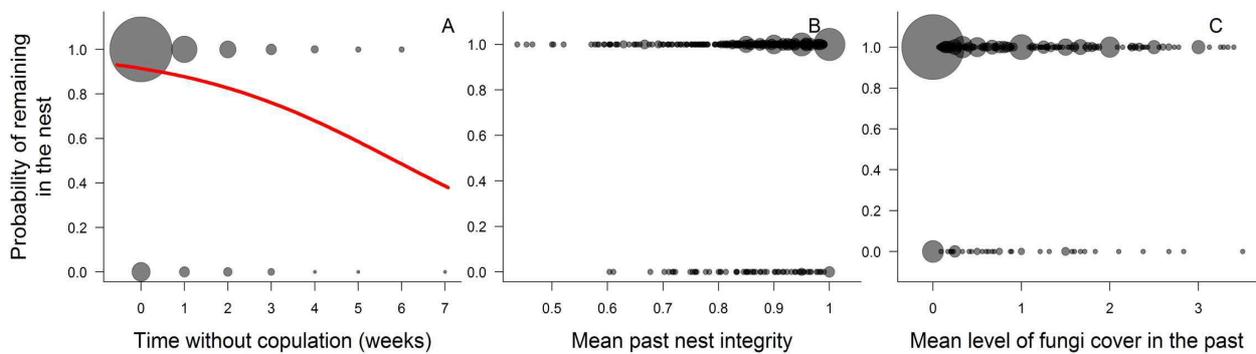


399

400 **Figure 5.** Effect of (A) nest integrity and (B) male body size (measured as dorsal scute width)  
 401 on the number of recently laid eggs found inside a nest. In (A), 0 indicates that the a nest is  
 402 completely destroyed and 1 indicates that a nest is intact. The thick red line represents the  
 403 mean and the thin red lines represent the 95% prediction interval according to the adjusted  
 404 model (see Table 3). In both graphics, bubble area is proportional to the number of  
 405 superimposed data points.

406

407



408

409

410 **Figure 6.** Effect of (A) reproductive success (measured as the time without gaining eggs), (B)  
 411 past nest integrity, and (C) past fungi cover on nest tenure. In (A), the thick red line  
 412 represents the mean expected by the adjusted model (see Table 4). In all graphics, bubble  
 413 area is proportional to the number of superimposed data points.

414

415 **Table 3.** Summary of the statistical model used to explain egg gain by males of the  
416 harvestman *Quindina limbata*. The response variable was the number of new eggs observed  
417 in each nest per male in each fieldtrip. The predictor variables were male dorsal scute width  
418 (body size), nest integrity, and fungi cover (which is a categorical variable with five levels,  
419 from 0 to 4). We adopted a gamma distribution and fit a single shape parameter. Fungi cover  
420 effects were calculated using fungi cover 0 as baseline. We added male identity and log  
421 identity as random effects in the model. The results are presented as median estimate and  
422 95% credible interval (CI). We also present the standard deviation (SD) of the random effects,  
423 which represents how much of the variance in the data is explained by variation between  
424 logs and between males.  
425

<b>Parameter</b>	<b>Median</b>	<b>95% CI</b>
Intercept	1.262	0.768 to 1.794
Shape parameter	0.142	0.131 to 0.153
Nest integrity (slope)	0.324	0.112 to 0.521
Dorsal scute width (slope)	0.169	-0.068 to 0.397
<i>Fungi cover effects</i>		
Fungi cover – level 1	0.27	-0.272 to 0.864
Fungi cover – level 2	0.255	-0.379 to 0.992
Fungi cover – level 3	0.818	0.057 to 1.774
Fungi cover – level 4	0.899	-0.133 to 2.279
<i>Random effects (SD)</i>		
Log identity	0.193	0.012 to 1.326
Male identity	0.295	0.025 to 0.659

426 **Table 4.** Summary of the nest tenure of males of the harvestman *Quindina limbata*. The  
 427 binary response variable was male presence inside his nest at fieldtrip *F*. The response  
 428 variables were estimated at the previous fieldtrip (*F-1*). Mean past nest integrity and mean  
 429 past fungi cover were calculated from nest building to *F-1*. We added male identity and log  
 430 identity as random effects in the model. The results are presented as median estimate and  
 431 95% credible interval (CI). We also present the standard deviation (SD) of the random effects,  
 432 which represents how much of the variance in the data is explained by variation between  
 433 logs and between males.

434

Parameter	Median	95% CI
Intercept	2.186	0.439 to 3.806
Past nest integrity (slope)	0.192	-0.096 to 0.461
Past fungi cover (slope)	0.061	-0.237 to 0.385
Time without copulation (slope)	-0.412	-0.647 to -0.189
<i>Random effects (SD)</i>		
Log identity	0.757	0.129 to 5.723
Male identity	0.367	0.061 to 0.958

435

436

## 437 Discussion

438 Here we followed a large number of nests of the harvestman *Quindina limbata* to evaluate  
 439 how rainfall could influence nest integrity and consequently males' reproductive success.  
 440 Severe damages caused by rainfall lead to nest abandonment by males in almost 50% of the  
 441 nests we monitored since the moment they were built. Moreover, the higher the drag force  
 442 experienced by a nest, the higher the damages on its floor and wall. However, rainfall had no  
 443 effect on fungal growth inside the nests. As we expected, nest integrity had a positive effect  
 444 on males' reproductive success, so that males with well-preserved nests received more eggs.

445 Surprisingly, the intensity of fungal attack also had a positive effect on reproductive success,  
446 so that males with nests showing extensive fungi cover also received more eggs. Finally, nest  
447 tenure was influenced only by reproductive success: males that received eggs recently had a  
448 lower chance of abandoning their nests than males that had not received eggs in a long time.  
449 In what follows, we will integrate these findings and discuss their implications to our  
450 understanding on how abiotic conditions may affect the reproductive success of males in a  
451 species in which they are the sole responsible for nest building and maintenance.

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

470 Male capacity to repair nest damages may also explain part of the variance we found in  
471 the effect of rainfall on nest integrity. Although there is no study on the energetic costs of  
472 nest building and maintenance in *Q. limbata*, these activities are known to be energetically  
473 demanding in fish (Hinch and Nicholas 1991) and birds (Mainwaring and Hartley 2013). We  
474 know, however, that males of *Q. limbata* take on average one month to build a nest, which  
475 represents a great part of their adult lifetime, estimated to be no more than 12 months (A.V.  
476 Rojas unpublished data). Thus, we argue that only males in good body condition (i.e., those  
477 with enough energy reserves) should be able to pay the costs of repairing frequent nest  
478 damages promoted by rainfall. Nests exposed to low drag force produced by water running  
479 on the log surface would demand low maintenance effort, and males in both poor and good  
480 condition should be able to keep their nests intact, generating low variance in nest integrity  
481 (as shown in Fig. 3). In turn, nests exposed to high drag force would demand high  
482 maintenance effort, and only males in good body condition should be able to keep their nests  
483 intact. If we assume that males in poor and good condition differ in the ability to repair  
484 extensive nest damages, variance in nest integrity should increase in response to higher  
485 values of drag force (as shown in Fig. 3). As in the case of log identity, male identity also  
486 explained a great part of the variation in data of nest integrity (Table 1). This finding  
487 suggests that in places where nests are subject to intense drag force, nest integrity may be an  
488 indicator of male condition that can be used by females to select the best mating partners, as  
489 already suggested for some fish (e.g. Barber et al. 2001, Olsson et al. 2009).

490 Fungal attack was also a major source of nest destruction, and males abandoned their  
491 nests after extensive fungus infestation in nearly 10% of the nests we monitored since the  
492 moment they were built. Contrary to our prediction, rainfall and the angle of the nests on the  
493 log did not influence the intensity of fungal attack. The fungi that attack *Quindina* nests are  
494 clearly associated with the decomposition of the fallen logs where the nests are built because

495 they occur not only inside the nests, but also on the bark (Fig. 1B). Considering that our  
496 study site is a tropical rainforest with no clear seasonal variation in precipitation, moisture is  
497 consistently high, and we argue that this creates good conditions for fungal growth  
498 throughout the entire year (Chapin et al. 2002). This finding differs from what happens with  
499 clutches of the cave harvestman *Acutisoma longipes* that may also be covered with fungi. In  
500 this species, fungal attack on clutches is highly seasonal because the river that crosses the  
501 cave suffers great reduction in water volume during the dry season. Only 17% of the clutches  
502 are attacked by fungi during the dry season, whereas 50% of them are attacked during the  
503 wet season (Machado and Oliveira 1998). Although parental individuals (females) of *A.*  
504 *longipes* are unable to prevent extensive fungal infestation (Machado and Oliveira 1998),  
505 parental individuals (males) of *Quindina* can feed on the hyphae and control fungal attack to  
506 a certain degree (Mora 1990). However, there may be high variation in males' ability to  
507 remove fungi and/or high variation in the potential for fungi growth among nest sites  
508 because male identity explained a great part of the variation in the data of fungal attack  
509 (Table 2). Moreover, the risk of fungal attack varies between fallen logs, because log identity  
510 also explained a great part of the variation in data of fungal attack (Table 2). Taken together,  
511 our findings suggest that the risk of fungal attack is homogeneous through time, but highly  
512 heterogeneous in the space, reinforcing the importance of nest site selection.

513         There is evidence that nest quality is correlated with female attraction in fish species  
514 with exclusive paternal care (e.g. Lindström 1992, Candolin and Reynolds 2001, Östlund-  
515 Nilsson and Holmlund 2003, Olsson et al. 2009). To the best of our knowledge, this study is  
516 the first to show that nest traits also influence female attraction in arthropods. Males of *Q.*  
517 *limbata* owning high-integrity nests had higher reproductive success than males owning low-  
518 integrity nests, which suggests that females are choosing mates based on nest quality. In fact,  
519 detailed behavioral data on *Q. albomarginis* show that females carefully inspect nest structure

520 before any physical contact with the owner male, and that after this inspection, some females  
521 may leave the nest without mating (Mora 1990). As we mentioned above, nest integrity may  
522 be positively related to male body condition in sites where nests are subject to high drag  
523 force (such as nest 2 in Fig. 2). Moreover, damages to the nest may increase offspring  
524 mortality due to exposure to predation, as reported for some fish (e.g. Whoriskey and  
525 FitzGerald 1985). In the case of *Q. limbata*, high nest walls may prevent the entrance of some  
526 egg predators, such as flat-backed millipedes (Fig. 1A). Moreover, given that females insert  
527 their eggs in pores of the spongy nest floor, a damaged floor may make the eggs more  
528 exposed and vulnerable to predatory attacks. Thus, females that select males based on nest  
529 integrity may acquire both indirect benefits related to male body condition and direct  
530 benefits related to increased offspring survival.

531 Females of *Q. limbata* also based their mating decisions on the fungi cover inside the  
532 nests. However, contrary to our prediction, they selected nests with extensive fungi cover  
533 instead of avoiding them. In several groups with exclusive paternal care, including  
534 arthropods (e.g. Mora 1990), fish (Okuda et al. 2002), and frogs (e.g. Simon 1983), fungi are a  
535 major source of egg mortality. To our knowledge, though, there is no experimental evidence  
536 that females in these groups avoid nests infested by fungi. The results found here are  
537 puzzling because females preferred nests infested by fungi, despite the fact that severe  
538 fungal infestation leads to nest destruction and that eggs infested by fungi may die. Two  
539 non-exclusive explanations may account for the positive relationship between fungi cover  
540 and male reproductive success. Previous studies with *Q. albomarginis* showed that male body  
541 condition does not decrease during the caring period, probably because males feed on small  
542 arthropods found close to their nests and also on the fungi growing inside their nests  
543 (Requena and Machado 2015). If fungi is an important food source for owner males, allowing  
544 them to keep good body condition during the caring period, females may select nests with

545 more fungi cover because in these nests males may provide better care to their eggs.  
546 Additionally, if fungi grow preferentially in wetter sites, females may use fungi cover as a  
547 clue to the substrate moisture, which could offer better growing conditions for the eggs.

548 Nest tenure by owner males was influenced exclusively by their reproductive success,  
549 so that males that did not attract females and did not receive eggs tended to abandon their  
550 nests. The nests built by *Q. limbata* males, as well by males of many fish and bird species, can  
551 be regarded as an extended phenotype with a double function: female attraction and egg  
552 protection (Schaedelin and Taborsky 2009). As in the case of other extended phenotypes that  
553 are immobile structures, such as the pits built by antlion larvae (e.g. Scharf and Ovadia 2006),  
554 the decision to keep investing or abandoning a nest should depend on the current benefits of  
555 remaining and the costs involved in finding a new site and building a new nest. As should  
556 be expected, unsuccessful males abandoned their nests more frequently than successful  
557 males. Moreover, some of the males that abandoned their nests built a new nest in other part  
558 of the logs, which suggests that they were indeed relocating their nests. Although we did not  
559 find a direct effect of nest integrity on nest tenure, it is important to note that nest integrity  
560 was the most important predictor of male reproductive success (Table 3). Thus, we argue  
561 that nest integrity has an indirect effect on nest tenure because well-preserved nests attract  
562 more females, decreasing the chances of nest abandonment by the owner males.

563 Studies on the effects of abiotic factors on the breeding biology of ectotherms are  
564 traditionally focused on aquatic species, such as waterbugs (Belostomatidae) and fish, in  
565 which water temperature, oxygen concentration, and salinity are known to affect male  
566 attractiveness, offspring survival, and the costs of parental care (e.g. St Mary et al. 2001, 2004,  
567 Lissåker et al. 2003, Green 2004, Hale and St Mary 2007, Munguía-Steyer et al. 2008; but see  
568 Delia et al. 2013). Here we explored how rainfall, an important abiotic factor in tropical  
569 forests, may affect nest integrity and male reproductive success in a terrestrial arthropod

570 with exclusive paternal care. Our findings indicate that intense rainfall has a major negative  
571 effect on male reproductive success, mostly caused by nest destruction. Considering that  
572 storms occur all year long in many tropical forests and that they are unpredictable in time,  
573 the best males can do to decrease the chances of nest destruction is to select protected places  
574 to build their nests and to perform nest maintenance continuously. This way, males can  
575 ensure that their nests remain better preserved, improving their offspring survival, attracting  
576 more females, and ultimately increasing male reproductive success.

577

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586

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589 manuscript.

590

591 *Permits* — No permit is required to conduct field observations with invertebrates in Costa  
592 Rica.

593 **References**

- 594 Barber, I. et al. 2001. Nests as ornaments: revealing construction by male sticklebacks. —  
595 Behav. Ecol. 12: 390–396.
- 596 Batchelor, G. K. 1967. An introduction to fluid dynamics. — Cambridge Univ. Press.
- 597 Bellrose, F. C. et al. 1964. Relative value of natural cavities and nesting houses for wood  
598 ducks. J. Wild. Manag. 28: 661–676.
- 599 Boersma, P. D. and Rebstock, G. A. 2014. Climate change increases reproductive failure in  
600 Magellanic penguins. — PLoS One 9: e85602.
- 601 Bolker, B. M. 2008 Ecological models and data in R. — Princeton Univ. Press.
- 602 Buzatto, B. A. et al. 2014. Correlated evolution of sexual dimorphism and male dimorphism  
603 in a clade of neotropical harvestmen. — Evolution 68: 1671–1686.
- 604 Candolin, U. 2003. The use of multiple cues in mate choice. — Biol. Rev. 78: 575–595.
- 605 Candolin, U. and Reynolds, J. D. 2001. Sexual signaling in the European bitterling: females  
606 learn the truth by direct inspection of the resource. — Behav. Ecol. 12: 407–411.
- 607 Carpenter, B. et al. 2017. Stan: A probabilistic programming language. — J. Stat. Softw. 76: 1-  
608 32.
- 609 Chapin, F. S. III et al. 2002. Principles of terrestrial ecosystem ecology. Springer-Verlag.
- 610 Consolmagno, R. C. et al. 2016. Costs and benefits of temporary egg desertion in a rocky  
611 shore frog with male-only care. — Behav. Ecol. Sociobiol. 70: 785–795.
- 612 Dawson, R. D. and Bortolotti, G. R. 2000. Reproductive success of American Kestrels: the role  
613 of prey abundance and weather. — Condor 102: 814–822.
- 614 Delia, J. R. et al. 2013. Parents adjust care in response to weather conditions and egg  
615 dehydration in a Neotropical glassfrog. — Behav. Ecol. Sociobiol. 67: 557–569.
- 616 Felton, A. et al. 2006. Multiple mate choice criteria and the importance of age for male mating  
617 success in the microhylid frog, *Cophixalus ornatus*. — Behav. Ecol. Sociobiol. 59: 786–795.

618 Ferrari, S. L. P. and Cribari-Neto, F. 2004. Beta regression for modelling rates and  
619 proportions. — J. Appl. Stat. 31: 799–815.

620 Forsgren, E. 1997. Female sand gobies prefer good fathers over dominant males. — Proc. R.  
621 Soc. Lond. B 264: 1283–1286.

622 Gelman, A. and Hill, J. 2006. Data analysis using regression and multilevel/hierarchical  
623 models. — Cambridge Univ. Press.

624 Gelman, A. et al. 2014. Bayesian data analysis, 3rd edition. — Chapman & Hall.

625 Green, B. S. and McCormick, M. I. 2005. O<sub>2</sub> replenishment to fish nests: males adjust brood  
626 care to ambient conditions and brood development. — Behav. Ecol. 16: 389–397.

627 Griebel, R. L. et al. 2007. Factors influencing burrowing owl reproductive performance in  
628 contiguous shortgrass prairie. — J. Raptor Res. 41: 212–221.

629 Griffin, D. M. 1977. Water potential and wood-decay fungi.— Annu. Rev. Phytopathol. 15:  
630 319–329.

631 Hale, R. E. and St Mary, C. M. 2007. Nest tending increases reproductive success, sometimes:  
632 environmental effects on paternal care and mate choice in flagfish. — Anim. Behav. 74:  
633 577–588.

634 Hinch, S. G. and Nicholas, C. C. 1991. Importance of diurnal and nocturnal nest defense in  
635 the energy budget of male smallmouth bass: insights from direct video observations. —  
636 Trans. Am. Fish. Soc. 120: 657–663.

637 Hoi, H. et al. 1994. Female mate choice and nest desertion in penduline tits, *Remiz pendulinus*:  
638 the importance of nest quality. — Anim. Behav. 48: 743–746.

639 Kleindorfer, S. 2007. Nesting success in Darwin's small tree finch, *Camarhynchus parvulus*:  
640 evidence of female preference for older males and more concealed nests. — Anim. Behav.  
641 74: 795–804.

642 Lindstrom, K. 1992. Female spawning patterns and male mating success in the sand goby  
643 *Pomatoschistus minutus*. — Mar. Biol. 113: 475–480.

644 Lissåker, M. et al. 2003. Effects of a low oxygen environment on parental effort and filial  
645 cannibalism in the male sand goby, *Pomatoschistus minutus*. — Behav. Ecol. 14: 374–381.

646 Machado, G. and Oliveira, P. S. 1998. Reproductive biology of the neotropical harvestman  
647 (*Goniosoma longipes*) (Arachnida, Opiliones: Gonyleptidae): mating and oviposition  
648 behaviour, brood mortality, and parental care. — J. Zool. 246: 359–367.

649 Mainwaring, M. C. and Hartley, I. R. 2013. The energetic costs of nest building in birds. —  
650 Avian. Biol. Res. 6: 12–17.

651 Mallory, M. L. et al. 2009. Influence of weather on reproductive success of northern fulmars  
652 in the Canadian high Arctic. — Polar Biol. 32: 529–538.

653 Mora, G. 1990. Paternal care in a neotropical harvestman, *Zygopachylus albomarginis*  
654 (Arachnida, Opiliones: Gonyleptidae). — Anim. Behav. 39: 582–593.

655 Munguía-Steyer, R. et al. 2008. Brood pumping modulation and the benefits of paternal care  
656 in *Abedus breviceps* (Hemiptera: Belostomatidae). — Ethology 114: 693–700.

657 Öberg, M. et al. 2014. Decomposing the seasonal fitness decline. — Oecologia 174: 139–150.

658 Okuda, N. et al. 2002. Female spawning strategy in *Rhinogobius* sp. OR: how do females  
659 deposit their eggs in the nest? — Ichthyol. Res. 49: 371–379.

660 Olsson, K. H. et al. 2009. Relative costs of courtship behaviours in nest-building sand gobies.  
661 — Anim. Behav. 77: 541–546.

662 Osenberg, C. W. et al. 1988. Growth patterns in bluegill (*Lepomis macrochirus*) and  
663 pumpkinseed (*L. gibbosus*) sunfish: environmental variation and the importance of  
664 ontogenetic niche shifts. — Can. J. Fish. Aquat. Sci. 43: 17–26.

665 Östlund-Nilsson, S. and Holmlund, M. 2003. The artistic three-spined stickleback  
666 (*Gasterosteus aculeatus*). — Behav. Ecol. Sociobiol. 53: 214–220.

667 Parmesan, C. et al. 2000. Impacts of extreme weather and climate on terrestrial biota. — Bull.  
668 Am. Meteorol. Soc. 81: 443–450.

669 Pinto-da-Rocha, R. and Bragagnolo, C. 2017. Cladistic analysis of the family Nomoclastidae  
670 with descriptions of a new genus and eight new species (Opiliones, Laniatores). — *Invert.*  
671 *Syst.* 31: 91–123.

672 Quader, S. 2006. What makes a good nest? Benefits of nest choice to female Baya weavers  
673 (*Ploceus philippinus*). — *Auk* 123: 475–486.

674 Quesada-Hidalgo, R. et al. 2017. The good fathers: efficiency of exclusive paternal care and  
675 the role of foster parents as egg protectors in a Neotropical arachnid. — Submitted  
676 manuscript.

677 R Core Team 2017. R: A language and environment for statistical computing. R Foundation  
678 for Statistical Computing, Vienna, Austria. Available from: <https://www.R-project.org/>.

679 Refsnider, J. M. and Janzen, F. J. 2010. Putting eggs in one basket: ecological and  
680 evolutionary hypotheses for variation in oviposition-site choice. — *Ann. Rev. Ecol. Evol.*  
681 *Syst.* 41: 39–57.

682 Requena, G. S. and Machado, G. 2015. Lack of costs associated with nest-related behaviors in  
683 an arachnid with exclusive paternal care. — *Oikos* 124: 372–380.

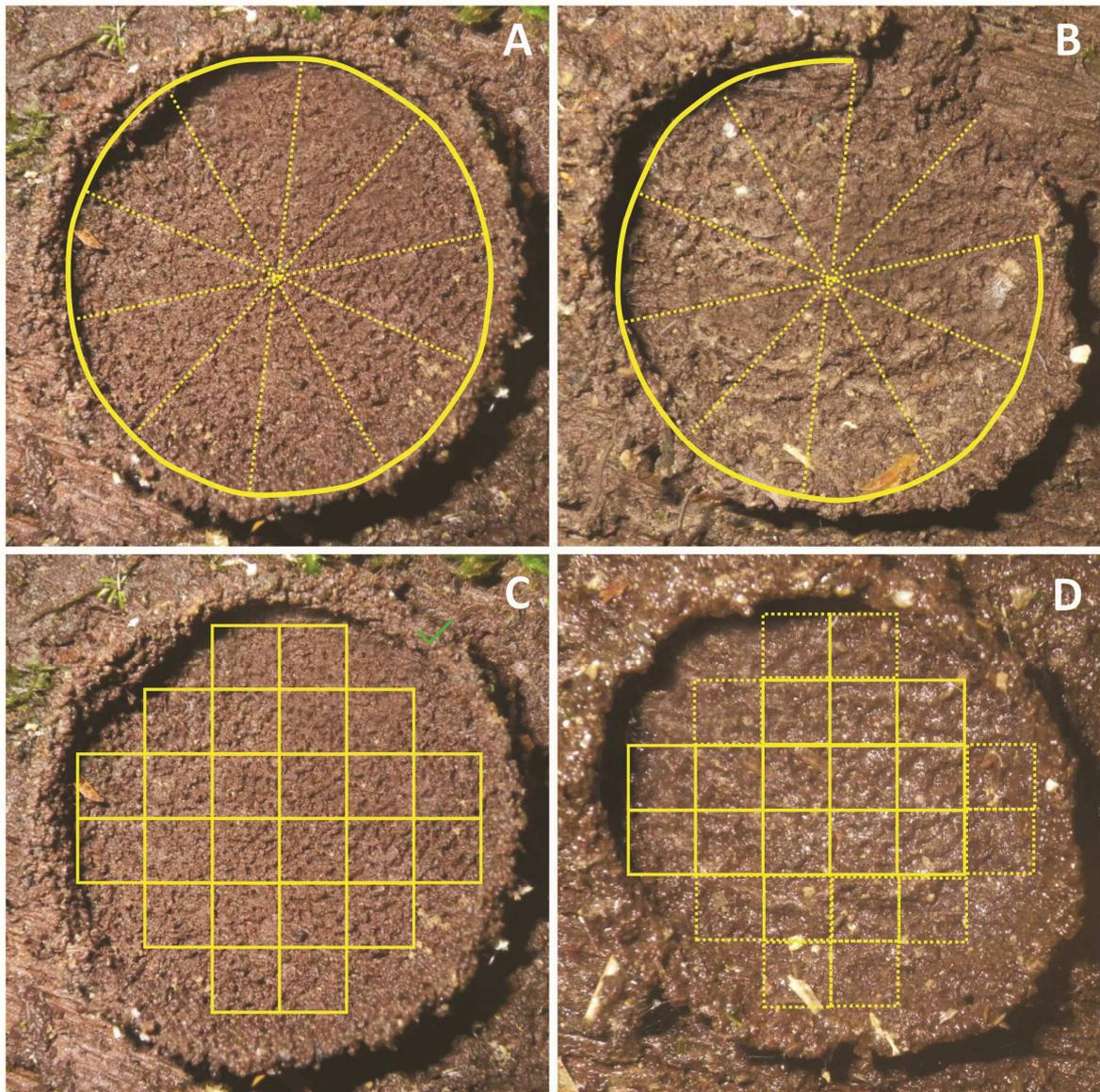
684 Requena, G. S. et al. 2013. Parental care and sexual selection in arthropods. In: *Sexual*  
685 *selection: perspectives and models from the Neotropics* (Macedo, R. H. and Machado, G.,  
686 eds.).— Elsevier Acad. Press, pp. 201–222.

687 Rodríguez, C. A. and Guerrero, S. 1976. La historia natural y el comportamiento de  
688 *Zygopachylus albomarginis* (Chamberlin) (Arachnida: Opiliones: Gonyleptidae). —  
689 *Biotropica* 8: 242–247.

690 Schaedelin, F. C. and Taborsky, M. 2009. Extended phenotypes as signals. — *Biol. Rev.* 84:  
691 293–313.

692 Scharf, I. and Ovadia, O. 2006. Factors influencing site abandonment and site selection in a  
693 sit-and-wait predator: a review of pit-building antlion larvae. — *J. Insect Behav.* 19: 197–  
694 218.

- 695 Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. —  
696 Methods Ecol. Evol. 1: 103–113.
- 697 Simon, M. P. 1983. The ecology of parental care in a terrestrial breeding frog from New  
698 Guinea. — Behav. Ecol. Sociobiol. 14: 61–67.
- 699 St Mary, C. M. et al. 2001. Environmental effects on male reproductive success and parental  
700 care in the Florida flagfish *Jordanella floridae*. — Ethology 107: 1035–1052.
- 701 St Mary, C. M. et al. 2004. Environmental effects on egg development and hatching success in  
702 *Jordanella floridae*, a species with parental care. — J. Fish Biol. 65: 760–768.
- 703 Stan Development Team 2018. RStan: the R interface to Stan. R package version 2.17.3.  
704 Available from: <http://mc-stan.org/>.
- 705 Tallamy, D. W. 2001. Evolution of exclusive paternal care in arthropods. — Ann. Rev.  
706 Entomol. 46: 139–165.
- 707 Thompson, K. R. and Furness, R. W. 1991. The influence of rainfall and nest-site quality on  
708 the population dynamics of the Manx shearwater *Puffinus puffinus* on Rhum. — J. Zool.  
709 225: 427–437.
- 710 Toscano-Gadea, C. A. and Rojas, A. 2014. Posible inversión parcial de roles sexuales en el  
711 opilión neotropical *Poassa limbata* (Arachnida: Opiliones). In: IV Congreso  
712 Latinoamericano de Aracnología. Morelia, Mexico.
- 713 Whoriskey, F. G. and FitzGerald, G. J. 1985. Nest sites of the threespine stickleback: can site  
714 characters alone protect the nest against egg predators and are nest sites a limiting  
715 resource? — Canad. J. Zool. 63: 1991–1994.
- 716 Wrenn, W. B. 1984. Smallmouth bass reproduction in elevated temperature regimes at the  
717 species' native southern limit. — Trans. Am. Fish. Soc. 113: 295–303.



719

720 **Figure S1.** Procedure used to quantify nest integrity. (A-B) To estimate wall integrity, we  
 721 divided nest wall in 10 sections and counted how many sections were intact (solid line  
 722 around the nest). In (A), the wall is intact and completely surrounds the nest, but in (B), there  
 723 are two sections in which the wall is destroyed. (C-D) To estimate floor integrity, we divided  
 724 the floor area in a grid of 24 squares and counted how many squares were intact (solid lines).  
 725 In (C), the floor is intact because its texture is spongy in all squares, but in (D), there are parts  
 726 of the floor that have lost this spongy texture.