

Lack of costs associated with nest-related behaviors in an arachnid with exclusive paternal care

Gustavo S. Requena and Glauco Machado

G. S. Requena (*gs.requena@gmail.com*) and G. Machado, *Depto de Ecologia, Inst. de Biociências, Universidade de São Paulo, Rua do Matão, trav. 14, no. 321, Cidade Universitária, 05508-900, São Paulo, SP, Brazil. Present address for GSR: Dept of Ecology and Evolutionary Biology, Yale Univ., 165 Prospect Street, New Haven, CT 06520, USA.*

Nest-related behaviors may benefit males by increasing offspring survival and their attractiveness to females, but may also limit males' foraging activity, increase their metabolic expenses, and expose them to increased mortality during nest attendance. Although intensively studied among birds and ectothermic vertebrates, the costs of nest-related behaviors in arthropods remain poorly explored. Females of the Neotropical harvestman *Zygopachylus albomarginis* (Arachnida: Opiliones) lay eggs exclusively inside mud nests that are built, repaired, cleaned and defended by males, which may remain stationary and associated with the nest for up to five months. To assess energetic and survival costs of nest-related behaviors in this arthropod species, we measured body condition of nesting and non-nesting males and conducted a field capture-mark-recapture study to estimate their survival rates. Despite the long period of nest attendance, nesting males sustained good body conditions and presented higher survival rates than non-nesting males and females. Two ecological conditions may play an important role modulating the costs of nest attendance in the species. First, high food supply in tropical rainforests may provide males with frequent access to food in the vicinity of their nests, reducing or eliminating the costs related to limited foraging opportunities. Second, predation pressure seems to be directly mostly to vagrant individuals, so that the more they move, the more likely they are to be singled out by predators. Taken together, our findings indicate that nest and offspring defense in *Z. albomarginis* provide numerous benefits, surprisingly imposing no evident cost to the males.

Nest defense and maintenance are behaviors widespread across several animal groups, often associated with mate attraction and/or parental care (Soler et al. 1998, Wells 2007, Coleman and Jones 2011, Requena et al. 2013). In many species of fishes, amphibians and arthropods, male care as well as nest defense and maintenance are so tightly related that they commonly involve a similar set of behaviors. For instance, when a nesting male chases away a conspecific competitor that attempts to take over his nest, he is simultaneously defending the ownership of his nest and protecting the offspring against a potential predator, since egg cannibalism is particularly common in these animal groups (DeMartini 1987, Mora 1990, Summers 1990). Moreover, nest maintenance requires males to remove debris and prevent fungal growth inside the nest, actions that also contribute to protect eggs against infection (Mora 1990, Giacomello et al. 2006, Walke et al. 2011). Therefore, although nest defense, nest maintenance, and offspring protection contribute to different components of males' fitness, they are performed concomitantly and entail similar behaviors. This makes difficult the assessment of the specific costs associated with each of these nest-related activities.

One of the main costs of nest-related behaviors is the reduction of males' body condition as a consequence of either decreasing foraging activity (Simon 1983, Marconato et al.

1993) or increasing metabolic expenses associated with nest defense, nest repair, and protection of the offspring against predators and adverse abiotic conditions (Sabat 1994, Hinch and Collins 1991). Furthermore, individuals may incur increased mortality risks due to the long-term detrimental effects of the energetic costs or increased exposure to predation during the period of nest attendance (reviewed by Wells 2007, Santos and Nakagawa 2012). Moreover, at least among most bird species, nest-related behaviors cannot be performed simultaneously with female attraction, compromising male opportunities to gain additional matings (Magrath and Komdeur 2003). Among fishes, amphibians and arthropods, however, nest possession is usually crucial for female attraction (Mora 1990, Barber et al. 2001, Wells 2007) and the presence of eggs inside the nest may even increase male attractiveness (Ridley and Rechten 1981, Forsgren et al. 1996, Nazareth and Machado 2010). Such conditions attenuate the tradeoff between mating and parental efforts associated with nest attendance. Consequently, it is not surprising that most of the studies on these animal groups have focused only on survival and energetic costs, ignoring the so-called promiscuity costs associated with nest and offspring defense (but see Townsend 1986).

Exclusive paternal care has independently evolved in at least 15 lineages of arthropods, and in five of them females

lay eggs inside nests that are either natural cavities or structures constructed by the males (reviewed by Requena et al. 2013). Here, we evaluated the survival and the energetic costs of nest and offspring defense in *Zygopachylus albomarginis* (Arachnida: Opiliones), a Neotropical harvestman with exclusive paternal care. Males of this species build a cup-like mud nest that may be visited by several females during the breeding season (Fig. 1A; Rodríguez and Guerrero 1976, Mora 1990). Males may start building their nests early-mid June and remain attending them for up to five months (mean \pm SD = 49.1 \pm 39.7 days; range = 3–150 days; Mora 1990, 1991). During nest attendance, a male actively repairs the walls of his nest, remove fungus hyphae growing inside the nest (Fig. 1B), and protect it from the invasion of conspecific males, sometimes engaging in intense contests (Rodríguez and Guerrero 1976, Mora 1990). Most of the time males remain attending their nests, they are also engaged in parental activities, which include defending the offspring against predation by conspecifics (both males and females) and ants, and against fungal infection (Mora 1990). Therefore, potentially costly activities, such as chasing conspecifics off and preventing fungal infection, are performed by nesting males

as a form of both nest maintenance for female attraction (mating effort) and offspring protection (parental effort).

Nesting males of *Z. albomarginis* may spend several months building, repairing, cleaning and defending their mud nests, when their activities are mainly constrained to a small area close to the nest (Mora 1991). Therefore, it is likely that their foraging opportunities are limited, and their prolonged and elaborated nest-related behaviors increase males' metabolic expenses. In this sense, the energetic costs of nest/offspring defense in this harvestman species should be high, and we predict that body condition of nesting males should deteriorate during the breeding season. Nest-related behaviors are also expected to increase mortality risks, either because males are likely to be more exposed to injuries when attacking nest intruders (Montgomerie and Weatherhead 1988) or because staying stationary within a conspicuous nest would increase predator attention (Gilbert et al. 2010). Consequently, we predict that mortality rates of nesting males should be higher than other conspecific adults that do not attend nests, including vagrant males and females.

Material and methods

Study site

We conducted this study on Barro Colorado Island (09°09'N, 79°51'W), Panama, a reserve administered by the Smithsonian Institution with a total area of 1500 ha that was isolated from the surrounding mainland in 1914. The most important seasonal change is associated with fluctuations in rainfall, which are responsible for two seasons: a dry season, between late December and early May, when the cumulative rainfall is usually less than 120 mm, and a rainy season, between mid May and early December, when nearly 90% of yearly rainfall occurs, totaling 1100 mm (Windsor 1990).

We sampled individuals in a plot approximately 80 m long and 20 m wide located in the plateau area of the island, between Wheeler and Drayton trails. In a previous extensive work with *Zygopachylus albomarginis*, Mora (1991) identified that both nests and individuals were highly concentrated in this plateau area, which is covered by old forest that has been maintained undisturbed for the last 400–500 years (Windsor 1990). We carried out the fieldwork between mid-September and mid-November 2009, encompassing the mid-breeding season of *Z. albomarginis*, when individuals present their peak of reproductive activity (Mora 1991).

Capture–mark–recapture study

To estimate the potential survival costs associated with nest-related behaviors in *Z. albomarginis*, we conducted a capture–mark–recapture study that dissociates apparent survival probabilities from recapture probabilities (Lebreton et al. 1992; see also Supplementary material Appendix 1). Before beginning this study, we individually identified three fallen logs and 81 trees in our plot, ignoring small trees with diameter at breast height < 10 cm, where the occupancy by *Z. albomarginis* individuals is very low (Mora 1991). During this preliminary search, we carefully scanned logs and trees

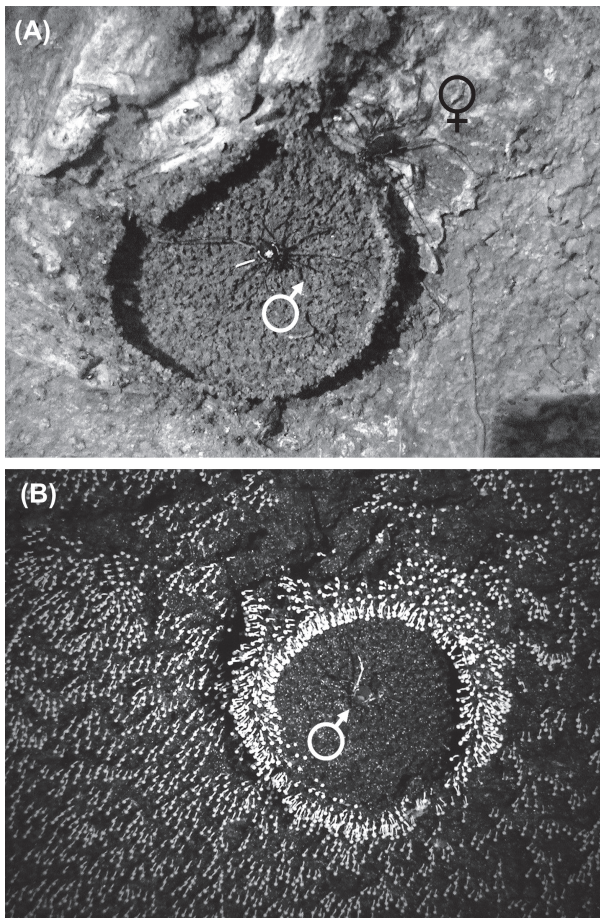


Figure 1. (A) Marked male of the harvestman *Zygopachylus albomarginis* inside his cup-like mud nest while a female approaches him. (B) Fungal infestation on a log on which a *Z. albomarginis* male has built his nest. Note that the only clean area is inside the nest because the male is constantly cleaning the nest and the eggs inside it. This behavior prevents infection of the offspring and, at the same time, provides food resources for the nesting male.

to flag all occupied nests. We inspected each log and tree for 2 min, from the ground to the height of 2 m, twice a day (afternoon: from 13:00 to 18:00 h; evening: from 20:00 to 01:00 h) for two consecutive days. Given that storms were common during the study, the sampling periods varied, but they always included night sampling. We considered the two-day period as our primary sampling occasion, which we repeated six times with regular intervals of 10 days in between (additional details in Supplementary material Appendix 1).

All individuals captured for the first time received an individual mark with enamel colored paint (following Mora 1990), and after manipulation, we released them at the same place where they were captured. This procedure has already been used in other mark–recapture studies with Neotropical harvestmen, and there is no evidence that the disturbance imposed by catching and marking individuals promotes a change in their behavior or increases their chance of migration (Gnaschini 1996, Buzatto et al. 2007, 2011, Requena et al. 2012). Particularly for *Z. albomarginis*, previous behavioral studies have also used the same marking procedure used here, and the authors were able to follow the same individuals (both males and females), in the same sites (usually fallen logs) throughout the entire breeding season (Rodríguez and Guerrero 1976, Mora 1990).

In each survey, we actively searched for *Z. albomarginis* adults, recording the identity of the tree or log where they were found, their sex, and, in the case of males, whether or not they were associated with a nest. Because females insert their eggs into the nest floor and cover them with debris (Rodríguez and Guerrero 1976, Mora 1990, Requena unpubl.), it was difficult to visually assess whether a nest contained eggs or not without manipulating and damaging the nest structure. To avoid such disturbance, which could have interfered with the mark–recapture study, we classified males only as: (a) nesting individuals if they were resting inside the nest, performing any nest-related behavior (such as, maintenance of the walls, cleaning, or parental care) or wondering at the vicinity (ca 30 cm) of an empty nest; or (b) non-nesting individuals if they were resting or wondering far from any empty nest (more than 60 cm), or in the vicinity of a nest occupied by other male. Despite the differences in nest-ownership state, the dorsal scute length, which is a measure of structural body size commonly used for harvestmen, does not differ between nesting and non-nesting males (nesting \times non-nesting; $F_{1,63} = 0.964$, $p = 0.33$). Therefore, we argue that any difference on mortality risk and body condition between nesting and non-nesting males is more likely related to nest-ownership state than to body size.

To assess the potential mortality risks associated with nest-related behaviors in *Z. albomarginis*, we analyzed the capture–mark–recapture data using Huggins closed robust design multi-state models implemented in the program MARK (White and Burnham 1999). The robust design involves two or more primary sampling occasions and several (usually more than two) secondary sampling occasions within each primary occasion (Pollock et al. 1990, Kendall et al. 1995). The interval between primary sampling occasions needs to be sufficiently long that gains (birth and immigration) and losses (death and emigration) to the population can occur. On the other hand, the interval between secondary sampling occasions needs to be sufficiently short

that the population can be assumed to be closed to gains and losses while the samples are being taken (for more details on the method see the Supplementary material Appendix 1). As we stated above, we defined a 10-day interval between primary sampling occasions and concentrated four secondary sampling occasions during two consecutive days. This decision is in accordance to previous mark–recapture studies with other harvestman species exhibiting parental care, in which adult lifespan under field conditions ranges from 6 to 24 months (Buzatto et al. 2007, 2011, Requena et al. 2012).

Using the robust design, we are able to decompose the probability of re-encountering an individual as the product of two independent events: (a) the probability of surviving since the marking procedure, and (b) the probability that we have detected this individual, conditional on being alive (Lebreton et al. 1992; see also Supplementary material Appendix 1). Although the effect of permanent emigration is still confounded into the estimates of the models (Kendall et al. 1995, 1997), we claim that this effect is negligible in our study because we focused our searching on fallen logs and at the base of large trees, where nests are built and where adults move, forage, and rest (Mora 1991, Requena unpubl.). Therefore, even if vagrant individuals (males and females) visit small trees, the canopy, or the leaf litter (specific places that were not sampled), these visits are likely to be short because they spend most of the breeding season in the area where nests are present (places that were sampled), either trying to usurp them or ovipositing on them (Mora 1990, Requena unpubl.). Moreover, we consider that permanent emigration is unlikely in the time frame of our study, and that occasional short visits to non-sampled sites within our plot probably constitute events of temporary emigration (sensu Kendall et al. 1997; Supplementary material Appendix 1). Thus, any variation in the apparent survival probability may be interpreted as the result of differential mortality (Loison et al. 1999, Gilbert et al. 2010, Potti et al. 2013).

Our models estimated three different probabilities. The first was the apparent survival probability (ϕ) of females, nesting and non-nesting males between consecutive primary sampling occasions. The second was the recapture probability (ρ) of females, nesting and non-nesting males within primary sampling occasions, assuming no temporal variation between secondary sampling occasions (additional details in Supplementary material Appendix 1). Given that *Z. albomarginis* nesting males may abandon their nests or be displaced by intruders, and that non-nesting males may build a nest, occupy an empty nest, or displace nesting males from their nests (Mora 1990), the models also estimated the transition probabilities (ψ) between nest-ownership states between consecutive primary sampling occasions (Brownie et al. 1993). We fixed the value of ψ between males and females at zero because males do not change into females or vice versa. The analytical procedure that we used combines the advantages of closed capture models to estimate ρ within primary sampling occasions with the advantages of the Cormack–Jolly–Seber live recapture model to estimate ϕ and ψ between consecutive primary sampling occasions (Supplementary material Appendix 1).

We assessed the fit of the fully parameterized global model based on the goodness-of-fit test for multi-state

models, performed in the program U-CARE (Choquet et al. 2009). In the global model, ϕ and ρ depended on the interaction between: (a) individual category, i.e. females, nesting or non-nesting males; and (b) time, which is a categorical variable with 6 or 5 levels corresponding, respectively, to the number of primary sampling occasions (for estimating ρ) or to the number of intervals between consecutive primary sampling occasions (for estimating ϕ). The parameter ψ , which applies only to males, depended on the interaction between nest-ownership state on the previous sampling occasion and time. Because the global model fitted the capture–recapture data well (goodness-of fit adherence test for the JMV model: $\chi^2 = 54.5$, $DF = 69$, $p = 0.899$), we proceeded to the model selection approach. To avoid the comparison of all 605 possible models in a single analysis, we used the step-down approach (Lebreton et al. 1992, Doherty et al. 2012, Supplementary material Appendix 2), which has been previously employed to assess survival costs of paternal care in the harvestman *Iporangaia pustulosa* (Requena et al. 2012). First, we used the same structure of ϕ and ρ as in the global model (i.e. interaction between individual category and time), and built alternative models that considered ψ as follows: 1) constant and not dependent on nest-ownership state; 2) dependent on time; 3) dependent on nest-ownership state; 4) dependent on the additive effects of time and nest-ownership state; and 5) dependent on the interaction between time and nest-ownership state. We ranked the alternative models using the small sample size bias-corrected version of the Akaike information criterion (AIC_c) and computed the difference in the AIC_c values between the best-ranked model and all other models in the ranking (Burnham and Anderson 2002). We selected all models in which the difference in the AIC_c was less than 2 as the models containing the most plausible structure for ψ to explain the data.

In the second step, we used the structure of ψ as observed in the selected model(s), retained the structure of ϕ as in the global model (i.e. interaction between individual category and time), and built a new set of alternative models that considered ρ as follows: 1) constant and not dependent on individual category; 2) dependent on time; 3) dependent on individual category; 4) dependent on the additive effects of time and individual category; 5) dependent on the interaction between time and individual category; 6) dependent on sex (i.e. all males together versus females); 7) dependent on the additive effects of time and sex; 8) dependent on the interaction between time and sex; 9) dependent on nest-ownership state (i.e. nesting males vs. non-nesting males and females together); 10) dependent on the additive effects of time and nest-ownership state; and 11) dependent on the interaction between time and nest-ownership state. In the third and final step, we used the structure of ψ and ρ obtained in the best model(s) selected in the first and second steps, and then we built the same set of 11 alternative models described above for the effect on ϕ , repeating the model selection procedure.

Male body condition

During the capture–mark–recapture study, we repeatedly measured with an electronic caliper (precision of 0.01 mm) the following structures of males every time we recaptured

them: dorsal scute length (DSL), dorsal scute width (DSW), total body length (TBL), and body height (BH). Although linear body measurements and body volume have been broadly used as proxies for body condition, they actually have a great disadvantage of being correlated with structural body size (Moya-Laraño et al. 2008). Among harvestmen, the dorsal scute is a rigid structure that does not change in size after individuals molt into adults and, for this reason, both DSL and DSW can be classified as structural body size measures. On the other hand, because the last five opisthosomal tergites are only connected by an elastic membrane that allows body expansion after feeding, both TBL and BH are linear measures of body size that change with current condition. Therefore, we used body volume (V) and body mass as two different proxies to assess males' body condition. To remove the effect of the structural body size, we used DSL as a mandatory co-variable in every analysis. This procedure is suggested by Moya-Laraño et al. (2008) in their review on measures of body condition, and has been previously used for other harvestman species (Requena et al. 2012). Since *Z. albomarginis* adults' body is round, we assumed it approximates the ellipsoid shape and estimated V following the formula: $V = \frac{4\pi}{3} \times \frac{TBL}{2} \times \frac{DSW}{2} \times \frac{BH}{2}$.

In a first analysis aiming to evaluate how male body condition varied between consecutive sampling occasions, we built linear mixed models in which repeated measures of body volume of *Z. albomarginis* males depended on: 1) only DSL (as a co-variable accounting for structural body size); 2) the additive effects of DSL and male nest-ownership state; 3) the additive effects of DSL and the interval between sampling occasions (in days); 4) DSL and the additive effects of male nest-ownership state and the interval between sampling occasions; and 5) DSL and the interaction between male nest-ownership state and the interval between sampling occasions. Because we used repeated data only from males that we encountered and measured at least twice in different primary sampling occasions (17 nesting and six non-nesting males), all models included male identity as a random variable. If nest-related activities impose energetic costs to *Z. albomarginis* males, we would expect nest-ownership state to be included in the selected model, predicting worse body conditions for nesting males than for non-nesting males. Moreover, if energetic costs are cumulative, the best model fitted to the data should consider the interaction between nest-ownership state and time, indicating that body condition of nesting males deteriorates over the course of the breeding season when compared to non-nesting males.

On the last sampling occasion, we collected eight nesting males and nine non-nesting males in the field, brought them to the laboratory, and measured their body mass using an electronic scale (precision of 0.001 g). Considering individual body mass and body volume as two separate proxies for body condition, we conducted independent analyses to assess their relationship with male nest-ownership state. We built alternative linear models in which body condition proxies depended only on DSL (used again as a co-variable to account for structural body size), as well as its additive or interaction effect with nest-ownership state. If males incur energetic costs when performing nest-related activities, we expect that nest-ownership state should affect male

body condition, so that nesting males should be consistently at worse conditions when compared to non-nesting males.

In all of the analyses described above, we used the AIC_c to rank alternative models fitted to the data and applied a model selection approach to simultaneously compare different biological hypotheses (Burnham and Anderson 2002). We built, fit, and selected models using the packages ‘bbmle’ (Bolker 2011) and ‘lme4’ (Bates et al. 2011) in the program R 2.13.

Results

Survival costs

Between September and November 2009, we sampled 107 adults of *Zygopachylus albomarginis* (59 males and 48 females), recording a total of 468 captures and recaptures. Among the males captured in the study area, 56% were recorded only in non-nesting state ($n = 33$), 25% were recorded only in nesting state ($n = 15$), and 19% changed nest-ownership state during the study ($n = 11$). After applying the step-down model selection procedure to determine the best structures for the transition probabilities between male nest-ownership states (Ψ) and the recapture probabilities (ρ), the two equally plausible selected models considered the estimates for the apparent survival probabilities (ϕ) to depend only on nest-ownership state. In Table 1, we present the results of the third-step of the model selection procedure,

and the results of the intermediate steps can be found in the Supplementary material Appendix 2. Because parameter estimates from both best-ranked models differed only in the third or fourth digit (data not shown), for the sake of simplicity, we report here the estimates and the 95%CI values only for the best supported model, i.e. $\Psi_{(\text{male nest-ownership state})} \rho_{(\text{temporal variation} + \text{individual category})} \phi_{(\text{nest-ownership state})}$. The estimates obtained from this model showed that Ψ from nesting to non-nesting state was lower than Ψ from non-nesting to nesting state (Fig. 2). Higher recapture probabilities (ρ) and apparent survival probabilities (ϕ) were always estimated for nesting males compared to both non-nesting males and females (Fig. 2).

Energetic costs

Through repeated measurements of the same set of individuals over subsequent sampling occasions, the body volume accounting for structural body size (DSL) of *Z. albomarginis* males was not affected by nest-ownership state or by the interval between sampling occasions (Table 2). In the same way, both male body mass and male body volume measured once at the last sampling occasion did not depend on nest-ownership state, with the best models selected including only the effect of the co-variable used to account for structural body size (Table 3, Fig. 3). These results indicate that there was no difference in body condition between males in different states and that their body condition did not consistently decrease over time.

Table 1. Summary of the third step of the step-down model selection procedure for the capture–recapture analysis investigating the influence of time, sex, nest-ownership state, and the individual category on the apparent survival probability (ϕ) for *Zygopachylus albomarginis*. Models are ranked by the increasing order of their AIC_c , with the best models indicated in bold.

Parameter structure	AIC_c	K	ΔAIC_c	Weight
Nest-ownership state^A	1351.6	12	0.0	0.446
Nest-ownership state^B	1352.8	11	1.2	0.244
Individual category ^A	1353.7	13	2.1	0.0155
Individual category ^B	1354.8	12	3.2	0.089
Sex ^A	1358.2	12	6.6	0.016
Sex ^B	1358.7	11	7.1	0.013
Constant and not dependent on any category ^A	1358.9	11	7.3	0.012
Temporal variation + nest-ownership state ^A	1359.3	16	7.7	0.009
Temporal variation + nest-ownership state ^B	1360.5	15	8.9	0.005
Constant and not dependent on any category ^B	1360.7	10	9.1	0.005
Temporal variation + individual category ^A	1361.5	17	9.9	0.003
Temporal variation + individual category ^B	1362.6	16	11.0	0.002
Temporal variation + sex ^A	1366.1	16	14.5	<0.001
Temporal variation \times nest-ownership state ^A	1366.3	20	14.7	<0.001
Temporal variation + sex ^B	1366.5	15	14.9	<0.001
Temporal variation ^A	1366.6	15	15.0	<0.001
Temporal variation \times nest-ownership state ^B	1367.4	19	15.8	<0.001
Temporal variation ^B	1368.1	14	16.5	<0.001
Temporal variation \times sex ^A	1370.7	20	19.1	<0.001
Temporal variation \times sex ^B	1371.2	19	19.6	<0.001
Temporal variation \times individual category ^A	1373.1	25	21.5	<0.001
Temporal variation \times individual category ^B	1374.4	24	22.8	<0.001

Note: nest-ownership state is a categorical variable with two levels (nesting and non-nesting); individual category is a categorical variable with three levels (females, nesting and non-nesting males); the symbols + and \times represent additive and interaction effects, respectively. A = Models using the structure of the best ranked model in the second step, in which ρ depends on the additive effects of temporal variation and individual category (Supplementary material Appendix 2). B = Models using the structure of the second best ranked model in the second step, in which ρ depends on the additive effect of temporal variation and nest-ownership state (Supplementary material Appendix 2).

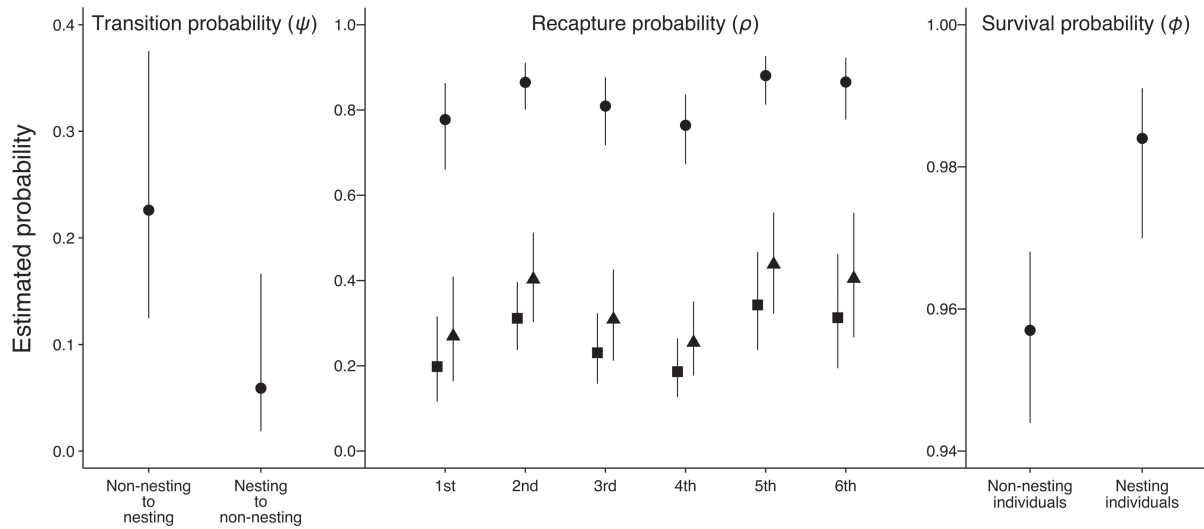


Figure 2. Estimated probability rates for individuals of the harvestman *Zygopachylus albomarginis* during the peak of their reproductive season. The left panel shows estimates for the transition probabilities from one male nest-ownership state to another, the mid panel shows estimates for the recapture probabilities, and the right panel shows estimates for the apparent survival probabilities. In the mid panel, circles represent estimates for nesting males, triangles represent estimates for non-nesting males, and squares represent estimates for females. Vertical lines represent the 95%CI of the estimates in the corresponding sampling occasions. The values were obtained from the best-ranked model (Table 1).

Discussion

Nest-related activities in the harvestman *Zygopachylus albomarginis* involve construction, maintenance, cleaning, and defense of the nest, as well as offspring protection against predation and fungi attack (Mora 1990). Given that males can be continuously associated with their nests for periods that can last up to five months (Mora 1991), we predicted that they would experience both high energetic costs and high mortality risks. Our results, however, do not support these predictions and show that nesting males can sustain body conditions at levels as good as non-nesting males and that nesting males present higher survival probability than non-nesting individuals (including non-nesting males and females). In the following topics, we discuss the broad implications of our findings, exploring how ecological factors can modulate the costs and benefits of nest-related behaviors.

Costs of nest-related behaviors

The theoretical prediction of energetic costs associated with nest-related behaviors (including paternal care) is based on tradeoffs that are particularly important among

birds, in which nests can be extremely elaborate and males intensively provide food to the young (Montgomerie and Weatherhead 1988). However, even among ectotherms, such as arthropods, amphibians, and fishes, males' body condition may deteriorate during nest attendance, either because they are food deprived (Simon 1983, Hinch and Collins 1991, Marconato et al. 1993, Nazareth and Machado 2010) or because they present high energetic expenditure while attending their nests (Hinch and Collins 1991, Cooke et al. 2006). Therefore, even among organisms with low basal metabolic rates, males may incur high energetic costs when they are associated with the nests for long periods, being somewhat limited to their access to food while doing it and/or performing activities that are energetically expensive. On the other hand, when males engage in nest-related behaviors only for short periods, during which they have frequent access to food and/or exhibit relatively inexpensive activities, they are likely to incur low energetic costs. Examples are rare in the literature, but short periods of nest association in the frog *Eleutherodactylus coqui* seems to cause only small losses in body mass of males, which keep calling for additional mates while attending nests containing eggs (Townsend 1986).

Table 2. Summary of the model selection approach applied to investigate the effect of male nest-ownership state and the interval between sampling occasions on male body volume in the harvestman *Zygopachylus albomarginis*. Models are ranked by the increasing order of their AIC_c , with the best models indicated in bold.

Predictor variables	AIC_c	K	ΔAIC_c	Weight
Dorsal scute length	109.0	4	0.0	0.767
Dorsal scute length + male nest-ownership state	111.6	5	2.6	0.210
Dorsal scute length + sampling interval	116.4	5	7.4	0.019
Dorsal scute length + male nest-ownership state + sampling interval	119.2	6	10.2	0.005
Dorsal scute length + male nest-ownership state \times sampling interval	128.3	7	19.2	<0.001

Note: male nest-ownership state is a categorical variable with two levels (nesting males and non-nesting males); the symbols + and \times represent additive and interaction effects, respectively.

Table 3. Summary of the model selection approach applied to compare the effect of male nest-ownership state and the structural body size measures on two body condition proxies in the harvestman male *Zygopachylus albomarginis*. Models are ranked by the increasing order of their AIC_c , with the best models indicated in bold.

Predictor variables	AIC_c	K	ΔAIC_c	Weight
Body mass				
DSL	61.8	3	0.0	0.773
DSL + male nest-ownership state	64.6	4	2.8	0.195
DSL \times male nest-ownership state	68.2	5	6.4	0.032
Body volume				
DSL	43.2	3	0.0	0.783
DSL + male nest-ownership state	46.2	4	3.0	0.175
DSL \times male nest-ownership state	49.0	5	5.8	0.042

Note: male nest-ownership state is a categorical variable with two levels (nesting males and non-nesting males); the symbols + and \times represent additive and interaction effects, respectively.

Despite the presumably expensive activities exhibited by *Z. albomarginis* males during the prolonged association with their nests, our results show no evidence of decline in body condition of nesting males over time or differences in body condition when compared to non-nesting males. Males of several fish species and at least one assassin bug are able to maintain good body condition while caring for the offspring because they usually engage in filial cannibalism (Manica 2002, Gilbert et al. 2010). Contrary to these species, *Z. albomarginis* males have never been observed eating eggs within their own nests (Mora 1990). Anecdotal observations, however, indicate that nesting males may feed on items found close to their nests, such as carcasses of dead arthropods, fruits, and insect larvae (Mora 1991), and may also spend several days eating fungal hyphae growing inside their nests (Mora 1990; Fig. 1B). If those items represent the main component of the diet of *Z. albomarginis* adults, feeding activities of stationary nesting males would not be severely constrained when compared to vagrant individuals.

In this case, we suggest that frequent access to food during nest attendance may compensate for energetic expenses associated with nest-related behaviors, explaining why nesting males are able to exhibit such activities for long periods.

Theory also predicts increased mortality risks to nesting males as a result of increased exposure to predation (Montgomerie and Weatherhead 1988). Among birds with biparental care, nesting males generally incur mortality costs associated to increased nest defense and parental provisioning (Santos and Nakagawa 2012). Although scarce, the information available for amphibians indicates that nesting males can be killed or severely injured by predators and competitor males while defending their nests and offspring (see examples in Wells 2007). For *Z. albomarginis*, the apparent survival probability of nesting males was consistently higher than that of non-nesting individuals of both sexes. Similar results have been recently reported for the harvestman *I. pustulosa*, in which males care for eggs laid on the vegetation, but defend no nest (Requena et al. 2012). Non-caring individuals (both males and females) of *I. pustulosa* cover longer distances on the vegetation than caring males, which remain stationary close to their clutches most of the time. While nesting males of *Z. albomarginis* remain stationary in the close vicinity of their nests, naturalistic observations obtained during our mark-recapture study show that all individuals recaptured on different trees or logs ($n = 4$ males and 4 females) were in the non-nesting state, suggesting an association between nest-ownership and individual movement patterns. Vagrant individuals that walk among trees have to cross the leaf litter, where they can encounter a wide range of potential predators, including both vertebrates (e.g. terrestrial marsupials, insectivorous rodents, and anurans) and invertebrates (e.g. spiders and ants, Cokendolpher and Mitov 2007). In at least two beetle species, males that are constantly moving seeking receptive mates are more frequently captured by predators than sedentary females (McCauley and Lawson 1986, Polis et al. 1998). Therefore, it seems that the more individuals move,

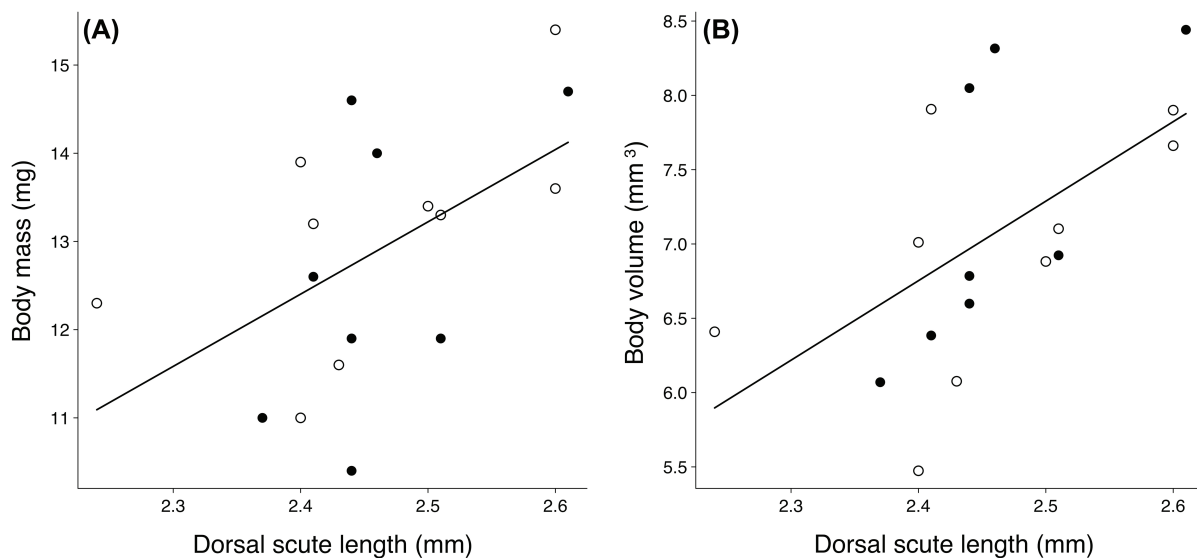


Figure 3. Relationship between the structural body size measures in the harvestman *Zygopachylus albomarginis* and our proxies of male body condition: (A) body mass and (B) body volume. Although male nest-ownership state was not associated with any body condition proxy, we distinguish nesting males (solid circles) from non-nesting males data (open circles).

the more likely they are to be captured by predators, which may explain the higher survival rates of stationary males among arthropods.

Why are there males without nests?

A non-nesting male of *Z. albomarginis* has three ways to become a nesting male: to build his own nest, to occupy an empty nest, or to aggressively attack a nesting male and take over his nest. In turn, nesting males may become non-nesting males if their nests are destructed or abandoned, or if they are displaced by rival males (Mora 1990). Given that complete nest destruction was rare during our study (Requena unpubl.), the transition from the nesting state to the non-nesting state provides a rough approximation of the combined probability of nest displacement and nest abandonment, estimated between 0.06 and 0.17 day⁻¹ (Fig. 2). On the other hand, the transition probability from the non-nesting state to the nesting state represents the combined effect of nest takeover, empty nest occupation, and nest construction, and it was estimated between 0.13 and 0.38 day⁻¹ (Fig. 2). Although the probability of nest acquisition is higher than the probability of nest loss, a great proportion of *Z. albomarginis* males in the population do not own a nest (Mora 1991, this study).

Considering that *Z. albomarginis* females mate and leave their eggs exclusively inside nests, nest ownership is of vital importance for males' reproductive success (Mora 1990). Moreover, as we discussed above, nesting males do not starve while attending their nests and have higher survival rates than non-nesting males. If performing nest-related behaviors is so profitable, why do not all males have a nest? There are at least three non-exclusive hypotheses to explain the high abundance of non-nesting males in *Z. albomarginis*. First, the arrival of sexually active adults in the population is likely to be highly asynchronous due to the long breeding season (Buzatto et al. 2013), and individuals without nests would thus represent recently molted adults. Second, nesting sites greatly vary in quality (Mora 1991) and males that have been displaced from their nests may take some time to find proper places to build another nest. Finally, nest construction may be the most expensive activity performed by males, so that only males in good body condition could be able to invest in this activity. Mora (1991) speculated, for instance, that salivary secretions, which are added to the mud at the moment males build their nests, may be costly. High costs of nest construction is generally argued to explain why some individuals rely on usurpation as an alternative reproductive tactic to acquire nests among solitary wasps and bees (reviewed by Field 1992), and it could also explain why some individuals do not build nest in *Z. albomarginis*.

Concluding remarks

Contrary to general predictions about costs paid by males when performing nest-related behaviors (Montgomerie and Weatherhead 1988), we report here that nesting males of the harvestman *Z. albomarginis* do not incur either survival or energetic costs. We argue that site fidelity may be responsible for the decreased mortality of nesting male, because the less they move, the lower their chances of being

singled out by predators. We also suggest that the high productivity of tropical rainforests may provide nesting males with frequent access to food while attending their nests, reducing the energetic unbalance of long-term nest-related behaviors. The high food supply of tropical rainforests may additionally increase the lifetime fecundity and the potential reproductive rate of females (Wheeler 1996), creating constant mating opportunities to nesting males (Maynard Smith 1977). The role of ecological factors in modulating the costs and benefits of parental care has been receiving increasing attention (Wong et al. 2013), and our findings indicate that nest and offspring defense in *Z. albomarginis* provide numerous benefits in terms of mate attraction and egg survival, surprisingly imposing no evident cost to nesting males.

Acknowledgements – Author contributions: GSR and GM conceived and designed the sampling procedure. GSR collected the data and performed the statistical analyses. GSR and GM wrote the manuscript. We thank the staff of the Smithsonian Tropical Research Institute (STRI) and of the Barro Colorado Nature Monument for logistical support. We are especially grateful to R. Munguía-Steyer and E. G. Martins for helping in the methodological design, and A. Aisenberg, J. E. Carvalho, P. I. K. L. Prado, L. Wedekin and K. Fritzsche for helpful comments on early versions of the manuscript. GSR had a short-term fellowship from STRI, a PhD fellowship from Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP, 08/50466-8), and is currently funded by the program 'Ciências Sem Fronteiras' from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq). GM has research grants from CNPq and FAPESP (2008/54833-5, 2012/50229-1).

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Supplementary material (available online as Appendix oik.01641 at <www.oikosjournal.org/readers/appendix>). Appendix 1.