



## **RESEARCH ARTICLE**

# The breeding biology and nest success of the Short-tailed Antthrush Chamaeza campanisona (Aves: Formicariidae) in the Atlantic rainforest of northeastern Brazil

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ABSTRACT. We present the results of a 26-year study on the breeding biology of the Short-tailed Antthrush, *Chamaeza campanisona* (Lichtenstein, 1823) in an Atlantic rainforest remnant of northeastern Brazil (Alagoas/Pernambuco). We followed the fate of 38 nests, of which 19 failed, 11 succeeded and 8 had an unknown fate. The presence of most nests coincided with the beginning of the rainy season in March/April but nests with eggs and/or chicks were found throughout the year, with no records only in January. Nests were placed inside natural tree cavities that result from broken branches and trunks. Both parents were engaged in feeding the chicks, their diet consisted mainly of insects, spiders, and some unidentified berries. All nests had a clutch size of two eggs. Incubation took 19 days and the mean nestling period was 20.75 days. Mayfield (1975) showed a survival rate of 31.87% and MARK 24.09%. Hotelling's T<sup>2</sup> revealed no differences in nest characteristics between successful and failed nests (p-value > 0.05). Linear models showed that the size of the entrance of the cavity and its height from ground are the main nest characteristics influencing the nesting success of *C. campanisona*.

KEY WORDS. Breeding season, breeding success, cavity-nesting, nest characteristics, Mayfield, linear model.

### **INTRODUCTION**

Four species of *Chamaeza* Vigors, 1825 antthrushes have been recorded from forested habitats in Brazil (Piacentini et al. 2015). Disjunct populations of the Short-tailed Antthrush, *Chamaeza campanisona* (Lichtenstein, 1823), occur in the Atlantic rainforest in the states of Ceará, Alagoas and Bahia, down to Santa Catarina (Krabbe and Schulenberg 2003, Grantsau 2010, Piacentini et al. 2015). This species inhabits the forest floor, particularly in primary vegetation areas (Sick 1997). It is a rare species that has been overlooked in several fragments of northeastern Atlantic rainforests (Silveira et al. 2003).

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Information about the breeding biology of *C. campanisona* is scarce (Krabbe and Schulenberg 2003). Recent studies have been published on nests, eggs and nestlings in Brazil, in the state of Rio Grande do Sul (Franz 2013) and in Argentina (Maders and Matuchaka 2011, Bodrati et al. 2014, Maugeri 2014). However, in northeastern Brazil, studies on this species are rare.

We present our results on the breeding biology and nest characteristics of *C. antthrushes*, collected over a time span of 30 years in a forest known as Pedra Talhada. We also present the results of the nest success of this species and the relationship between nest characteristics and nest fate.

## MATERIAL AND METHODS

Observations on the bird *C. campanisona* were conducted at Pedra Talhada forest (09°14.00'S; 36°25.00'W), located 90 km from the Atlantic coast, on the border between the states of Alagoas and Pernambuco, northeastern Brazil (Fig. 1). The forest's surface area comprises ca. 5,000 ha situated on a granitic multi-convex relief hill reaching 883 m above sea level. Most of this forest (4,469 ha) has become a reserve: "Reserva Biológica de Pedra Talhada" in 1989 (Brazil 1989, Sousa et al. 2015).

Pedra Talhada forest is an Atlantic rainforest biome enclave and is considered as a submontane and montane semi-evergreen





Figure 1. Location of Pedra Talhada forest.

seasonal forest, regionally called "brejo de altitude", far more humid than the surrounding lowland areas. These favorable climatic conditions are a consequence of the Borborema Plateau, which sweeps the oceanic winds and captures, by condensation, the humidity of the air that returns in form of rainfall. It is believed that, due to their particular climate, the altitude forest enclaves of the Brazilian Northeast can cope with the dry season (Tscharner et al. 2015).

The vegetation of Pedra Talhada forest includes rupicolous forests, slope forests and plain forests with sempervirens and deciduous trees up to 35 m high, as well as open vegetation areas such as rocky outcrops, clearings and marshes (Nusbaumer et al. 2015). This range of habitats hosts 255 species of birds, which are part of the total 2,100 plant and animal species recorded in Pedra Talhada, including new, endemic and endangered species (Studer et al. 2015).

We observed the nests of *C. campanisona* birds for 30-years from April 1986 to April 2016, with the exception of 2010–2013, totaling 26 years of fieldwork. Nest search was carried out on an irregular day-schedule from one to four times a month, throughout each year. The nests were located either by observing conspicuous adult behavior (Martin and Geupel 1983) or by active inspection of existing cavities using a mirror and a pocket lamp (Skutch 1945). When we found an active nest, we visited it every three to four days and every second day when near hatching and or fledging (Lara et al. 2012). When the exact date of fledging could not be determined, we recorded it as the median date between the two last visits (Dudley and Saab 2003). Under adequate conditions, a hide was installed 10 m away from nest, providing a good view of its surroundings. Observations were made with binoculars and images were recorded with video cameras.

Several parameters of the cavity and nest were recorded. We measured the height from the ground (FG) to the entrance of the cavity, and the following cavity dimensions: diameter of entrance, total size (width x height), and depth from the entrance to the nest located at the bottom of the cavity. We measured the height FG, diameter and weight of the nest.

We also identified the host tree species. Other variables such as egg dimensions, clutch size, breeding season and reproductive success were also documented. Egg shape was determined as suggested by Baicich et al. (1997) and nest characterization according to Simon and Pacheco (2005). The incubation period was calculated from the time when two eggs had been laid to the date when the first hatched egg was detected. The nestling period ranged from the time the egg hatched to the day of fledging (Oniki 1975). When nest failure was observed, the reason for it was identified according to three categories: predation, abandonment or adverse climatic conditions. When eggs or chicks disappeared from the nest before the normal incubation or nestling period, and the event leading to it could not be determined, we assumed that predation had taken place.

A nest was considered successful when at least one nestling fledged, and nest success was calculated using two different approaches: the Mayfield (1975) method and with program MARK (Dinsmore and Dinsmore 2007). The Mayfield (1975) method is an alternative to the apparent estimator (AE) of nest success (successful nests/total nests) that avoids the upward bias caused by the AE. This bias is avoided in the Mayfield (1975) method with the exposure days factor, which is the total number of observation days for all nests in the sample. The daily survival estimate (*p*) is calculated by the equation: p = 1 - (failed nests/exposure days), and nest success during the whole nesting cycle (*S*) can then be calculated by the equation:  $S = p^j$ , where *j* is the average duration of the nesting period for the given species (Mayfield 1975).

The nest-survival model in the MARK program is based on five assumptions for each nest: 1) the age of the nests were correctly estimated when they were discovered; 2) the fate of the nests were correctly determined; 3) discovering and checking the nests did not influence survival; 4) nest fates are independent; 5) daily nest-survival rates are homogenous (Dinsmore and Dinsmore 2007).

Both the incubation (19 days) and nestling (20.75 days) periods were determined for *C. campanisona* during the study. This helped us to correctly determine the nest age for the model in the MARK program (assumption 1). When we encountered nests with eggs already being incubated, we determined the age of the nest by back-aging the mean incubation period from the hatching date. For example if a nest hatched 5 days after discovery, it meant it was 14 days old when we first encountered it. When nests were found during the nestling stage, we back-aged the mean breeding period from the fledging date. In the remaining cases, when nests were unsuccessful before hatching, we estimated the date when incubation began using the following equation: *First day of incubation = date found – (incubation period – number of days observed/2)* (equation C, Martin et al. 1997).

Nests with unknown fate were not included in the analysis with the MARK program.

Nest characteristics (cavity entrance height FG, nest height FG, cavity entrance size and cavity depth) were compared with the multivariate Hotelling's T<sup>2</sup> test to determine whether successful and failed nests were structurally different. Afterwards,



we conducted univariate comparisons (t-tests) in order to detect which nest characteristics were remarkably different between successful and failed nests. Bonferroni corrections were applied to prevent type I error.

Finally, assuming that the daily survival rate (DSR) remains constant throughout the year, we investigated the effects of the above-mentioned nest characteristics on nest fate. We created a set of linear models combining the different explanatory variables and a stepwise model selection was carried out by calculating Akaike's information criterion (AIC).  $\Delta$ AIC<sub>i</sub> and AIC weight were taken into account for model selection (Burnham and Anderson 2002). These statistical analyses were run out in RStudio Desktop 1.0.136 program (RStudio 2016).

## RESULTS

#### Nest description and breeding behavior

A total of 38 nests were observed in Pedra Talhada between 1986 and 2016. All nests were found in the more conserved patches of the forest, in places where the ground was covered by a thick layer of foliage and tree trunks were rather spaced apart (Fig. 2).

*Chamaeza campanisona* is a non-excavator bird. Consistent with that, all nests observed by us were located inside natural tree cavities resulting from broken branches or trunks (Fig. 2). According to the nest classification of Simon and Pacheco' (2005), *C. campanisona* uses cavity/with tunnel/low cup nests. These nests are either on dead trees (n = 2), living trees (n = 32) or in dead parts of living trees (n = 4). Nest heights from the ground (NH) were in the higher (NH  $\ge$  2 m, n = 11), middle (1 m < NH > 2 m, n = 9) or lower parts (NH  $\ge$  1 m, n = 18) of the trunk. The nests were covered with a layer of leaves that were regularly renewed during the reproductive period (Fig. 3). A total of 14 tree species from 11 botanic families were identified and only two dried trunks remained unidentified (Suppl. material 1).

In some cases, we observed that certain cavities had been reoccupied for a subsequent breeding attempt. For example, the cavity of nest #2 in *Psidium guineense* tree was reoccupied four years later (nest #9); the cavity of nest 3, in a *Byrsonima sericea* tree, was reoccupied three years later (nest #7) and the cavity of nest #13 also in *Byrsonima sericea* tree was reoccupied six months later (nest #15). We were not able to verify if the same breeding pair had reoccupied the cavities.

Birds flew to the entrance of the cavity and stepped down to reach the nest that was placed at the bottom of it. Cavity entrance size was on average 144.95 cm<sup>2</sup>  $\pm$  20.54 Standard Error (SE, extremes 48–360 cm<sup>2</sup>). Cavity entrances were placed at an average height from ground of 235.08 cm  $\pm$  16.48 SE (extremes 80–436 cm) and nests were located at an average height from ground of 134.89 cm  $\pm$  15.19 SE (extremes 15–380 cm). Cavity depth was on average 93.87 cm  $\pm$  6.18 SE (extremes 25–190 cm; Suppl. material 1). Nest diameter was on average 12.06 cm  $\pm$  0.54 SE. Nests weighed 80 g (n = 1) and 110 g (n = 1) and contained, respectively, 110 and 130 green leaves of 4–10 cm size.

Eggs are white and short-oval according to Baicich et al. (1997). Once the eggs were laid they were subsequently impregnated with dirt from the legs of the incubating adult. By the end of the incubation period the eggs acquired a greenish hue due to the decomposition of the leaves lining the nest (Fig. 3). Egg size was on average  $32.7 \times 25.1$ mm ( $\pm 0.21 \times \pm 0.15$  SE, n = 30) and egg weight was on average  $10.07 \text{ g} \pm 0.22$  SE (n = 12). Every nest had a clutch size of two eggs: thirty-four nests were discovered during the incubation period and four during the nestling period.

When hatched, the nestlings were fully covered with fine grey-violet down feathers and squeezed together forming a dark sphere, so that one could only distinguish the different parts of the bodies when handling the chicks. The bill was light purple with white flanges. The throat was slightly pink with greenish nuances; tibias, tarsus and digits were light violet with tiny white nails. When leaving the nest, even though it had a greenish-brown tone, the fledgling resembled the final adult plumage.

The incubation period lasted 19 days (n = 2) and the nestling period averaged 20.75 days  $\pm$  0.49 SE: 19 days (n = 2);



Figures 2–4. (2) Detail of *C. campanisona* nest location; (3) nest and eggs of *C. campanisona* at cavity bottom; (4) adult of *C. campanisona* at nest entrance carrying a large quantity of arthropods. All photos by A. Studer on March 2009.

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20 days (n = 1); 21 days (n = 3); 22 days (n = 1); 23 days (n = 1). Therefore, we estimated that the total breeding period lasted 39.75 days  $\pm$  0.49 SE.

Both parents participated in raising the chicks and their food consisted mostly of insects (crickets, grasshoppers, praying mantis, beetles, ants and caterpillars), several spider species and some unidentified berries. Even though we observed the parents bringing ants to the nest, we rarely saw them following army ants.

When approaching the nest, the adults zigzagged across the floor. Often one or both parents walked around the trunk before reaching the entrance of the cavity with a short flight and usually stopped there for a moment, looking at the surroundings before descending into the nest. The adults came in and out of the nests by climbing the interior walls. In some nests, we noticed that the walls became smooth from the many comings and goings of the birds. After feeding the chicks, the adults usually stopped again for a few seconds at the entrance of the cavity looking in all directions before flying away in a horizontal line. Sometimes the adult flapped its wings two to three times at the nest entrance before flying away. We were not able to determine the reason for this behavior.

During several morning observations of five nests for periods of five hours between 06:30 to 11:30 am, we observed parent-offspring feeding behavior. Our results show that parents fed 5–10 day old chicks 1–2 times/hour. Chicks that were 10 days old or older were fed less frequently (0.5–1 time/hour) and adults brought a greater quantity of food in each visit. In many cases, wings and legs of insects dangled from the parents' beak (Fig. 4). Adults usually arrived separately to the nest. When arriving together, one adult entered the nest cavity while the other waited, often singing on a distant branch. Once its mate left the nest, it entered to feed the chicks or just accompanied the mate flying away. During the first 15 days the adults took turns staying a few minutes with the chicks, supposedly to warm them up. After this period adults usually quit this behavior and flew away quickly after feeding. Both adults carried fecal sacs away from the nest.

#### Breeding season

The breeding periods were very irregular from one year to another and no nests were found in 2000 and 2001. The presence of most nests coincided with the beginning of the rainy season and most active nests with eggs or young were discovered between March and June, mainly in April, right before the rainy season reaches its peak (Fig. 5). A smaller peak with active nests was also found in November and December, a period that corresponds to a weaker peak of rainfalls. Despite these two peaks, active nests with eggs and/or chicks were present each month of the year, except January (Fig. 5).

To calculate the duration of the breeding season all data was pooled together (1986–2016). The first nest was found during incubation on February 17 and the last nest succeeded on December 28, representing a period of 315 days.



Figure 5. Cumulative number of active nests between 1986–2016 and the average precipitation in Quebrangulo (Agência Nacional de Águas 2009).

Nest failure and potential predators

Out of the 38 nests, 19 failed, 11 were successful and eight had an unknown fate (Suppl. material 1). Predation was the main cause of nest failure (89.5%; n = 17), followed by adverse climatic conditions (10.5%; n = 2). In this last case, we found two nests in August (1995) being abandoned because the cavity had been flooded with rainwater.

We observed that predators usually arrived at night. However, in most cases, the predation timing could not be determined and therefore no general patterns were identified. In two cases we discovered a White-eared opossum, *Didelphis albiventris* (Lund, 1840), sleeping in the nest, probably after consuming the eggs which had disappeared the same morning (February 1997).

#### Nest success

Following the Mayfield (1975) method, we counted a total of 670 exposure days, of which 170 had an unknown fate. The daily survival rate (DSR) was 0.9716 d<sup>-1</sup> and the nest success during the breeding period (b = 30.75 days) was 31.87%. Following the MARK program, DSR was 0.9651 d<sup>-1</sup> ± 0.0078 SE and nest success during the breeding period (b = 30.75 days) was 24.09%.

Hotelling's T<sup>2</sup> test revealed no differences between successful and failed nests (T<sup>2</sup> = 1.8952, p-value: 0.1552). Successful nests appeared to have greater cavity entrance heights FG, deeper cavities, greater nest heights FG and smaller cavity entrances, although based on individual tests these differences were not statistical significant (Table 1).

Of all candidate models, the model including cavity entrance height and cavity entrance size had the highest explanatory power (Table 2). The only explanatory variable that was significant was cavity entrance size (p-value: 0.0392).



Nest variable	n	Successful	Failed	t-test	df	p-value	p-value
EH (cm)	38 (11, 19)	301.18 ± 31.31	$228.98 \pm 21.69$	1.90	19.420	0.0729	0.2916
NH (cm)	38 (11, 19)	188.64 ± 34.33	$130.31 \pm 18.88$	1.49	16.150	0.1559	0.6236
D (cm)	38 (11, 19)	112.55 ± 12.59	86.00 ± 8.20	1.77	18.430	0.0938	0.3752
ES (cm)	21 (9, 12)	118.22 ± 19.53	178.25 ± 34.07	-0.62	13.298	0.5460	1.0000

Table 1. t-tests between successful and failed nests (mean ± SE), n: number of observations (successful, failed).

(EH) cavity entrance height from ground, (NH) nest height from ground, (D) cavity depth, (ES) cavity entrance size. p-value after Bonferroni corrections.

Table 2. Ranking of models considered to explain *C. campanisona* nest fate.

Modelª	df	p-value	Log-likelihood	AICc	$\Delta \text{AIC}_{i}$	AIC <sub>i</sub> Weight
F~EH+ES	4	0.0140	-15.93	41.5	0.00	0.569
F~EH+D+ES	5	0.0204	-15.12	42.7	1.27	0.302
INTERCEPT	2	0.0000	-20.67	45.8	4.32	0.066
F~EH+NH+D+ES	6	0.0471	-15.10	45.9	4.39	0.063

(EH) cavity entrance height from ground, (F) nest fate, (NH) nest height from ground, (D) cavity depth, (ES) cavity entrance size.

## DISCUSSION

Clutch sizes of three eggs were found by Maders and Matuchaka (2011) in Argentina and by Franz (2013) in southern Brazil, for *C. campanisona*. Clutch sizes of 2-3 eggs were found by Bodrati et al. (2014) and Maugeri (2014) in Argentina. These results contrast with ours since we found clutch sizes of only two eggs. These differences in clutch size may be attributed to the geography. Many authors support the hypothesis that clutch sizes increase in higher latitudes (Moreau 1944, Klomp 1970, Ricklefs 1970, Jetz et al. 2008, Bianucci and Martin 2010) and according to Moreau (1944), this fact would be significant only with clutch size differences of less than half an egg. The latitude of Pedra Talhada is 9°S, whereas the previous studies are placed between 25-29°S (Maders and Matuchaka 2011, Franz 2013, Bodrati et al. 2014, Maugeri 2014).

The eggs of *C. campanisona* are white, consistent with the color of the eggs of most cavity-nesting birds (Rice 2005). Egg shape appears to match that of previous studies even though descriptions vary slightly among authors. Sick (1997) described them as spherical, whereas Krabbe and Schulenberg (2003), Maders and Matuchaka (2011) and Bodrati et al. (2014) described them as oval. Franz (2013) stated that eggs are characterized by having "clearly unequal poles" and Maugeri (2014) defined them to be short subelliptical.

The nest characteristics described here resemble in many ways the descriptions from previous studies of *C. campanisona* (Maders and Matuchaka 2011, Franz 2013, Bodrati et al. 2014, Maugeri 2014). Nests have also been found in living trees (Bodrati et al. 2014) or in trees at advanced state of decomposition (Maugeri 2014). We found cavity entrances as high as 4.36 m above the ground and Bodrati et al. (2014) found one at 9.6 m above the ground, which is very high for a bird that forages and moves predominantly on the ground (Krabbe and Schulenberg

2003). Nests of *Chamaeza ruficauda* (Cabanis & Heine, 1860) and of the sympatric antthrushes such as *Gymnopithys rufigula* (Boddaert, 1783) and *Formicarius analis* (d'Orbigny & Lafresnaye, 1837) are also placed in dead tree cavities (Oniki 1971, Sick 1997, Zyskowski 2015). Nest material has been described as only leaves for *Formicarius analis* (Sick 1997) or a wide range of plant material such as bamboo leaves, leathery tree leaves, fungal rhizomorphs and grass for *C. ruficauda* (Zyskowski 2015). The diameter of the nest of *C. campanisona* in our data was 12×12.06 cm (n = 8), which is similar to the measurements of 12×13 cm (n = 1) indicated for this species by Maugeri (2014) and ca. 12 cm (n = 1) by Zyskowski (2015) for *C. ruficauda*.

Franz (2013) estimated the nestling period of *C. campanisona* to be 16–19 days. However, he did not witness fledging, and nestlings may have been depredated as suggested by Bodrati et al. (2014). Bodrati et al. (2014) calculated a nestling period of 22-23 days and, compared with our results, we consider that the nestling period ranges between 19 to 23 days. Bodrati et al. (2014) calculated an incubation period of 18 days (n = 2), which does not considerably differ from our result of 19 days (n = 2).

Bird breeding seasons vary considerably throughout the different regions of Brazil. It is generally acknowledged that birds depend on food availability to raise their young, which in turn depends on beginning of rainfalls, resulting on larger quantities of food (Aguilar et al. 1999, Duca and Marini 2004, Hoffman and Rodrigues 2011, Marini et al. 2012). The northeastern region is a semi-arid ecosystem where bird reproduction and rainfall seasonality are strongly correlated (Scheuerlein and Gwinner 2002, Cavalcanti et al. 2016). This strong correlation has been observed in our study in Pedra Talhada, as illustrated in Fig. 5.

The northeastern region has been qualified as one of the most irregular and semiarid regions worldwide (Molion and Bernardo 2000), where the influence of severe droughts, rainfall anomalies and El Niño phenomena are strong (Hastenrath and Heller 1977, Moura and Shukla 1981, Pontes da Silva et al. 2011). Even though Pedra Talhada is situated in the Northeast, the climate there is not so harsh, owing to higher humidity levels than in adjacent regions (Tscharner et al. 2015). The irregular rainfalls of the Northeast might be reflected in a certain degree of adaptation by *C. campanisona* and may explain the extremely long time span of its breeding period (Fig. 5).

In other areas within the distribution range of *C. campanisona* the breeding period of this bird is not as long. One of the few long-term studies published on this subject (Bodrati et al. 2014) suggests



that *C. campanisona* birds breed from September to November based on the fact that nest search only happens during this period. However, these authors state *that nest search* was carried out only from September to December and it would therefore be possible that *C. campanisona* also breeds outside that breeding period.

This long-term study of the Short-tailed Antthrush allowed us to evaluate the breeding success of *C. campanisona* in Pedra Talhada using two different methods. Analyses in the MARK program required that nest fate was known (Dinsmore and Dinsmore 2007); consequently, nests with unknown fate had to be excluded from the analysis. This may have been responsible for a negative bias, which led to an underestimation of nest success. Since the Mayfield (1975) method allows the inclusion of nests whose fate is unknown, we deem this method more appropriate in this study to determine daily survival rates. As the level of uncertainty is relative high in this study, 107 nest days out of 670 have an unknown fate, the Mayfield (1975) method allows us to include information that otherwise would be lost.

According to our analyses, nest success can be predicted by the size of the entrance of the nets' cavity and height of cavity entrance from the ground. It has been largely established that nest failure due to predation or harsh climatic conditions is closely related to nest location, height, structure, shape and environment (Klomp 1970, Conway and Martin 2000, França et al. 2009, Borges and Marini 2010, Brawn et al. 2011). According to Mainwaring et al. (2014), greater height of nests from the ground can influence positively or negatively nest predation rates, which would be higher if avian predators are the main risk, or lower in case of mammal predators. Thus, these birds may vary the height at which they build their nests in response of predatory behavior (Li and Martin 1991). In this hypothesis, if *C. campanisona* could choose between cavities, it would look for high cavities with narrow entrances to increase protection for eggs and chicks against predation.

However, *C. campanisona* birds may not always be able to choose their cavities due to limited availability (Vazquez and Renton 2015). As tree cavities are rare in forests, they become a limiting factor for cavity-nesting birds and couples may try to breed in cavities that are unsuited for the purpose (Martin and Li 1992, Martin 1995). This could also explain the reason why we found wide variations in nest characteristics, and birds reoccupy-ing the same cavities, even after unsuccessful nesting attempts.

Predation is usually the primary source of nest mortality for both open- and cavity-nesting birds (Lack 1947, Li and Martin 1991, Lahti 2009, Martin et al. 2000). Consistent with this, predation turned out to be the main cause of nest loss for *C. campanisona* in Pedra Talhada. On the other hand, with a nest success of 31.87% as per Mayfield (1975) method, *C. campanisona* falls inside the limits indicated for other cavity/enclosed nesting birds occurring in the tropics, which ranges between 27%–50% as per Brawn et al. (2011). Moreover, *C. campanisona* has a greater success rate when compared to other sympatric species from the same locality, such as the Thamnophilidae *Myrmoderus* (*Myrmeciza*) *ruficauda* (Wied, 1831) or *Dysithamnus mentalis* (Temminck, 1823; pers. obs.), which construct open nests (Lill and Ffrench 1970, Buzzetti and Barnett 2003). Therefore our results match those from other studies, which suggest that closed nests located in cavities present greater nest success than open nests (Oniki 1975, Gibbs 1991, Brawn et al. 2011, Studer 1994, 2015), a hypothesis that still has to be tested in Pedra Talhada forest.

*Chamaeza campanisona* birds appear to depend on well-preserved forests with old, decaying trees for hosting the bird's offspring (Maders and Matuchaka 2011, Franz 2013, Bodrati et al. 2014) and we consider that with a nest success of 31.87% as per the Mayfield (1975) method, this species still encounters adequate conditions for its survival in Pedra Talhada's forest.

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## LITERATURE CITED

- Agência Nacional de Águas (2009) Inventário das estações pluviométricas. Agência Nacional de Águas, SGH, Brasília, 2<sup>nd</sup> ed., 495 pp.
- Aguilar TM, Leite LO, Marini MÃ (1999) Biologia de nidificação de Lathricus euleri (Cabanis, 1968) (Tyrannidae). Em fragmentos de mata em Minas Gerais. Ararajuba 7: 125–133.
- Bianucci L, Martin TE (2010) Can selection on nest size from nest predation explain the latitudinal gradient in clutch size. Journal of Animal Ecology 79: 1086–1092. https://doi.org/10.1111/ j.1365-2656.2010.01720.x
- Baicich PJ, Harrison JO, Harrison CJ (1997) A guide to the nests, eggs and nestlings of North American birds. Academic Press, San Diego, 416 pp.
- Bodrati A, Cokle KL, Di Sallo FG (2014) Nesting of the short-tailed antthrush (*Chamaeza campanisona*) in the Atlantic Forest of Argentina. Ornitologia Neotropical 25: 421–431.
- Borges FJA, Marini MÃ (2010) Birds nesting survival in disturbed and protected Neotropical savannas. Biodiversity and Conservation 19: 223–236. https://doi.org/10.1007/s10531-009-9718-z
- Brawn JD, Angehr G, Davros N, Robinson WD, Styrsky JN, Tarwater CE (2011) Sources of variation in the nesting success of understory tropical birds. Journal of Avian Biology 42: 61–68. https:// doi.org/10.1111/j.1600-048X.2010.04897.x
- Brazil (1989) Decreto 98.524 de 13 de dezembro de 1989, cria a reserva Biológica de Pedra Talhada. Imprensa Nacional, Diário Oficial da União, República Federativa do Brasil, Brasília, Seção 1, 23067 pp.



- Burnham KP, Anderson DR (2002) Model selection and multimodel inference. Springer-Verlag, New York, 6731 pp.
- Buzzetti DRC, Barnett JM (2003) Description of the nest and eggs of two *Myrmeciza* antbirds endemic to the Atlantic Forest of Brazil. Cotinga 20: 89–93.
- Cavalcanti LMP, Paiva LV, França LF (2016) Effects of rainfall on bird reproduction in a semi-arid Neotropical region. Zoologia 33: e20160018. https://doi.org/10.1590/s1984-4689zool-20160018
- Conway CJ, Martin TE (2000) Evolution of passerine incubation behavior; influence of food, temperature, and nest predation. Evolution 54: 670–685. https://doi.org/10.1554/0014-3820(2 000)054[0670:EOPIBI]2.0.CO;2
- Dinsmore SJ, Dinsmore JJ (2007) Modelling avian nest survival in program MARK. Studies in Avian Biology 34: 73–83.
- Duca C, Marini MÃ (2004) Aspectos da nidificação de *Cacicus haemorrhous* (Passeriformes, Icterinae) no sudeste do Brasil. Ararajuba 12: 23–30.
- Dudley J, Saab V (2003) A field protocol to monitor cavity-nesting birds. Rocky Mountain Research Station, 16 pp. https://doi. org/10.2737/RMRS-RP-44
- França LF, Sousa NOM, Santos LR, Duca C, Gressler DT, Borges FJA, Lopes LE, Manica LT, Paiva LV, Medeiros RCS, Marini MÃ (2009) Passeriformes: nest predators and prey in a Neotropical savannah in central Brazil. Zoologia 26: 799–802. https://doi.org/10.1590/S1984-46702009000400028
- Franz I (2013) On the nest, eggs and nestlings of the Short-tailed Antthrush (*Chamaeza campanisona*). Revista Brasileira de Ornitologia 21: 101–104.
- Gibbs JP (1991) Avian nest predation in tropical wet forest: an experimental study. Oikos 60: 155–161. https://doi. org/10.2307/3544861
- Grantsau R (2010) Guia completo para a identificação das aves do Brasil. Vento Verde, São Carlos, 1249 pp.
- Hastenrath S, Heller L (1977) Dynamics of climatic hazards in northeast Brazil. Quarterly Journal of the Royal Meteorological Society 103: 77–92. https://doi.org/10.1002/qj.49710343505
- Hoffmann D, Rodrigues M (2011) Breeding biology and reproductive success of *Polystictus superciliaris* (Aves: Tyrannidae), an uncommun Tyrant flycatcher endemic to the highlands of eastern Brazil. Zoologia 28: 305–311. https://doi.org/10.1590/ S1984-4670201100030000
- Jetz W, Sekercioglu CH, Böhning-Gaese K (2008) The worldwide variation in avian clutch size across species and space. PLOS Biol 6: 2650–2657. https://doi.org/10.1371/journal.pbio.0060303
- Klomp H (1970) The determination of clutch-size in birds a review. Ardea 58: 1–121. https://doi.org/10.5253/arde.v58.p1
- Krabbe NK, Schulenberg TS (2003) Family Formicariidae (Ground-Antbirds). In: del Hoyo J, Elliott A, Christe, DA (Eds) Handbook of the Birds of the World, Broadbills to Tapaculos. Lynx Edicions, Barcelona, 682–731.
- Lack D (1947) The significance of clutch-size. Ibis 89: 23–45. https://doi.org/10.1111/j.1474-919X.1947.tb04155.x

- Lahti DC (2009) Why we have been unable to generalize about bird nest predation. Animal Conservation 12: 279–281. https://doi.org/10.1111/j.1469-1795.2009.00286.x
- Lara K, Pinho J, Silveira R (2012) Biologia reproductiva de *Taraba major* (Aves, Thamnophilidae) na Região do Pirizal, Porção Norte do Pantanal, Mato Grosso, Brasil. Papéis Avulsos de Zoologia 52: 349– 359. https://doi.org/10.1590/S0031-10492012021000001
- Li P, Martin TE (1991) Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages. The Auk 108: 405–418.
- Lill A, Ffrench RP (1970) Nesting of the Plain Antvireo *Dysithamnus mentalis andrei* in Trinidad, West Indies. Ibis 112: 267–268. https://doi.org/10.1111/j.1474-919X.1970.tb00104.x
- Maders CJ, Matuchaka V (2011) Descripción de nido, huevos y pichones de la Tovaca común (*Chamaeza campanisona tshororo*). Nuestras Aves 56: 10–11.
- Mainwaring MC, Hartley IR, Lambrechts MM, Deeming DC (2014) The design and function of bird's nests. Ecology and Evolution 4: 3909–3928. https://doi.org/10.1002/ece3.1054
- Marini MÃ, Borges FJA, Lopes LE, Sousa NOM, Gressler DT, Santos LR, Paiva LV, Duca C, Manica LT, Rodrigues SS, França LF, Costa PM, França LC, Heming NM, Silveira MB, Pereira ZP, Lobo Y, Medeiros RCS, Roper JJ (2012) Breeding biology of birds in the Cerrado of central Brazil. Ornitologia Neotropical 23: 385–405.
- Martin TE (1995) Avian Life History Evolution in relation to nest sites, nest predation and food. Ecological Monographs 65: 101–127. https://doi.org/10.2307/2937160
- Martin TE, Li P (1992) Life history traits of open- vs. cavity-nesting birds. Ecology 73: 579–592. https://doi.org/10.2307/1940764
- Martin TE, Paine C, Conway CJ, Hochachka WM, Allen P, Jenkins W (1997) BBIRD Field protocol. Biological Resources Division. Montana Cooperative Wildlife Research Unit 406: 243–5372.
- Martin TE, Scott J, Menge C (2000) Nest predation increases with parental activity; separating nest site and parental activity effects. Proceedings of the Royal Society 267: 2287–2293. https://doi.org/10.1098/rspb.2000.1281
- Martin TH, Geupel GR (1983) Nest-Monitoring Plots: Methods for locating nests and monitoring success (Métodos para localizar nidos y monitorear el éxito de estos). Journal of Field Ornithology 64: 507–519.
- Maugeri FG (2014) Nuevo registro del nido y de los huevos de la Tovaca común (*Chamaza campanisona*; Passeriformes; Formicariidae) para la provincia de Misiones, Argentina. Acta Zoológica Lilloana 58: 243–249.
- Mayfield HF (1975) Suggestions for calculating nest success. The Wilson Bulletin 87: 456–466.
- Molion, LCB, Bernardo SDO (2000) Dinâmica das chuvas no Nordeste Brasileiro. In: Anais do XI Congresso Brasileiro de Meteorologia. Sociedade Brasileira de Meteorologia, Rio de Janeiro, 1–5 [CDROM].
- Moura AD, Shukla J (1981) On the dynamics of droughts in northeast brazil: observations, theory and numerical experiments with a general circulation model. American Meteorological So-



ciety 38: 2653–2675. https://doi.org/10.1175/1520-0469(198 1)038<2653:OTDODI>2.0.CO;2

- Moreau RE (1944) Clutch-size: A comparative study, with special reference to African birds. Ibis 86: 286–347. https://doi.or-g/10.1111/j.1474-919X.1944.tb04093.x
- Nusbaumer L, Barbosa MRV, Thomas WW, Alves MV, Loizeau PA, Spichiger R (2015) Flora e vegetação da Reserva Biológica de Pedra Talhada. In: Studer A, Nusbaumer L, Spichiger R (Eds) Biodiversidade da Reserva Biológica de Pedra Talhada. Alagoas-Pernambuco, Boissiera, 59–83.
- Oniki Y (1971) Parental care and nesting in the Rufous-throated Antbird, *Gymnopithys rufigula*, in Amapá, Brazil. The Wilson Bulletin 83: 347–351.
- Oniki Y (1975) The behavior and ecology of Slaty Antshrikes (*Tham-nophilus punctatus*) on Barro Colorado Island, Panama Canal Zone. Annalss of the Brazilian Academy of Sciences 47: 471–515.
- Piacentini VQ, Aleixo A, Agne CE, Nachtigall GM, Pacheco JF, Bravo GA, Brito GRR, Naka LN, Olmos F, Posso S, Silveira LF, Betini GS, Carrano E, Franz I, Lees AC, Lima LM, Pioli D, Schunck F, Amaral FR, Bencke GA, Cohn-haft M, Figueiredo LFA, Straube FC, Cesari E (2015) Annotated checklist of the birds of Brazil by the Brazilian Ornithological Records Committee/Lista comentada das aves do Brasil pelo Comitê Brasileiro de Registros Ornitológicos. Revista Brasileira de Ornitologia 23: 91–298.
- Pontes da Silva BF, Fedorova N, Levit V, Peresetsky A, Brito BM (2011) Sistemas Sinóticos associados às precipitações intensas no estado de Alagoas. Revista Brasileira de Meteorologia 26: 323–338. https://doi.org/10.1590/S0102-77862011000300001
- Rice NH (2005) Further evidence for paraphyly of the formicariidae (Passeriformes). The Condor 107: 910–915. https://doi. org/10.1650/7696.1
- Ricklefs RE (1970). Clutch size in birds: outcome of opposing predator and prey adaptations. Science 168: 599–600. https://doi. org/10.1126/science.168.3931.599
- RStudio (2016) Open source and enterprise-ready professional software for R. Available online at: https://www.rstudio.com [Accessed: 01/11/2016]
- Scheuerlein A, Gwinner E (2002) Is food availability a circannual zeitgeber in tropical birds? A field experiment on Stonechats in tropical Africa. Journal of Biological Rhythms 17: 171–180. https://doi.org/10.1177/074873002129002465
- Sick H (1997) Ornitologia brasileira. Nova Fronteira, Rio de Janeiro, 862 pp.
- Silveira LF, Olmos F, Long AJ (2003) Birds in Atlantic forest fragments in North-East Brazil. Cotinga 20: 32–46.
- Simon EJ, Pacheco S (2005) On the standardization of nest descriptions of neotropical birds. Revista Brasileira de Ornitologia 13: 143–154.
- Skutch AF (1945) Incubation and nestling periods of birds. The Auk 62: 8–37. https://doi.org/10.2307/4079958
- Sousa MC, Cusimano E, Vedovotto N, Studer A (2015) Histórico da Reserva Biológica de Pedra Talhada. In: Studer A, Nusbaumer L, Spichiger R (Eds) Biodiversidade da Reserva Biológica de Pedra Talhada. Alagoas-Pernambuco, Boissiera, 766–778.

- Studer A (1994). Analysis of nest success in Brazilian nests. Journal für Ornithologie 135: 298.
- Studer A (2015) Aves da Reserva Biológica de Pedra Talhada. In: Studer A, Nusbaumer L, Spichiger R (Eds) Biodiversidade da Reserva Biológica de Pedra Talhada. Alagoas-Pernambuco, Boissiera, 376–405.
- Studer A, Nusbaumer L, Spichiger R (2015) Biodiversidade da Reserva Biológica de Pedra Talhada. Alagoas-Pernambuco, Boissiera, 818 pp.
- Tscharner T, Duda GP, Oliveira VP, Silva CMS, Nusbaumer L, Silva-Filho AF (2015) Parâmetros abióticos da Reserva Biológica de Pedra Talhada. In: Studer A, Nusbaumer L, Spichiger R (Eds) Biodiversidade da Reserva Biológica de Pedra Talhada. Alagoas-Pernambuco, Boissiera, 39–57.
- Vazquez L, Renton K (2015) High density of tree-cavities and snags in tropical dry forest of western Mexico raises questions for a latitudinal gradient. PlosS One 10: e0116745. https://doi. org/10.1371/journal.pone.0116745
- Zyskowski K (2015) First description of a nest of the Rufous-tailed Antthrush *Chamaeza ruficauda*. Revista Brasileira de Ornitologia 23: 5–8.

## Supplementary material 1

## Nests of Chamaeza campanisona found during the study period (1986–2016) with their respective characteristics Authors: Anita Studer, Marcelo Cardoso de Sousa, Begoña Barcena-Goyena

Data type: species data

Explanation note: Date of encounter could be of nests either with eggs (e) or with nestlings (n). Fate is given as: (F) failed, (S) successful, and (U) unknown. Exposure days refer to the observation period of each nest according to Mayfield (1975). Means and standard errors (SE) and lower-upper limits for every nest characteristic can be found at the end of the table.

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