Breeding biology and nest success of 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-years study on the breeding biology of the Short-tailed Antthrush, *Chamaeza campanisona* (Lichtenstein, 1823*)* in an Atlantic rainforest of northeastern Brazil (Alagoas/Pernambuco). We found a total of 38 nests, of which 19 failed, 11 succeeded and 8 had an unknown fate. The presence of most nests coincided with the arrival of rains in March/April but nests with eggs and/or chicks were found throughout the year, with no records in January only. Nests were placed inside natural tree cavities resulting from broken branches and trunks. Both parents fed the chicks and 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^2 revealed no differences on nest characteristics between successful and failed nests (*p-value*>0.05) and linear models showed that cavity entrance size and cavity entrance height from ground are the main nest characteristics influencing nesting success of *C. campanisona.*

Key words: Short-tailed Antthrush, Formicariidae, breeding biology, breeding season, nest success, nest characteristics.

Introduction

Four species of *Chamaeza* antthrushes are recorded in forested habitats in Brazil (Piacentini et al. 2015). Short-tailed Antthrush, *Chamaeza campanisona* occurs in the Atlantic rainforest with disjunct populations occurring 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 and its presence has been unnoticed in several fragments of northeastern Atlantic rainforests (Silveira et al. 2003).

Information about 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 or inexistent.

We present our results on breeding biology and nest characteristics over a time span of 30 years in Pedra Talhada forest. We also present the results of nest success for this species and the relation between nest characteristics and nest fate.

Material and methods

Study area

Bird observations were conducted in Pedra Talhada forest (09°14.00'S; 36°25.00'W), located at 90 km from the Atlantic coast, on the borderline of Alagoas and Pernambuco states in northeastern Brazil (Figure 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) became a reserve: "Reserva Biológica de Pedra Talhada" in 1989 (Diário Oficial Brasil 1989, Sousa et al. 2015)

Pedra Talhada forest is an Atlantic rainforest biome enclave and is considered as a submontane and montane semi-evergreen 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 its particular climate the altitude forest enclaves of these northeastern regions 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).

Nest search

Observations were carried out over a time span of 30-years from April 1986 to April 2016, with the exception of years 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 the year and nests were located either by observing conspicuous adult behavior (Martin and Geupel 1983) or active inspection of existing cavities by use of a mirror and a pocket lamp (Skutch 1945). When an active nest was found, it was visited every three to four days and every second day when near hatching and or fledging (Lara et al. 2012). If the exact date of nest fate could not be determined, we recorded the median date between the two last visits (Dudley and Saab 2003). Under adequate conditions, a leaf-camouflaged 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. For the cavity, we measured the height from ground (FG) to the entrance, the diameter of the entrance, its total size (width x height), and the depth from entrance to the nest located at the bottom of the cavity. For the nest, we measured its height FG, diameter and weight.

Moreover, the host tree species were identified. Other variables such as measures of eggs, clutch size, breeding season and reproductive success were documented too. Egg shape was determined as suggested by Baicich et al. (1997) and nest characterization according to Simon and Pacheco (2005). Incubation period was calculated from the complete laying of 2 eggs to the hatching date of the first egg and the nestling period ranged from hatching to 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 had not been witnessed, we assumed that they had been lost through predation.

Statistical analysis

A nest was considered to be successful when at least one nestling fledged and nest success was calculated using two different approaches: Mayfield (1975) method and MARK program (Dinsmore and Dinsmore 2007). The Mayfield (1975) method is an alternative to the apparent estimator (AE) of nest success (successful nests/total nests) in order to avoid the upward bias caused by 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 equation A and nest success during the whole nesting cycle (S) can then be calculated by equation B, where j is the average nesting period length for the given species (Mayfield 1975).

The nest-survival model in the MARK program is based on five assumptions for each nest: 1) nests are correctly aged when they are discovered; 2) nest fates are correctly determined; 3) nest discovery and subsequent nest checks do not influence survival; 4) nest fates are independent; 5) homogeneity of daily nest-survival rates (Dinsmore and Dinsmore 2007).

Both the incubation and nestling period were determined for this species during the study. This helped us to correctly determine the nest age for the model in MARK program. When we encountered nests during incubation, the age of the nest was determined by means of counting back the incubation days from the hatching date. When nests were found during nestling stage, we counted back the days from the fledging date. For the remaining cases, when nests were unsuccessful before hatching, we estimated the date that incubation began using the following formula (equation C, Martin et al. 1997).

Nests of which the fate was unknown were not included in MARK program.

Secondly, nest characteristics (cavity entrance height FG, nest height FG, cavity entrance size and cavity depth) were compared with the multivariate Hotelling's T^2 test to determine whether nests were structurally different between successful and failed nests. 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 avoid type I error in the results.

Finally, assuming that the daily survival rate (DSR) remains constant all over the year, we investigated the effects of 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). ΔAIC_i 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 forest between 1986 and 2016. All nests were found in the more conserved patches of the forest, in places where ground was covered by a thick foliage layer and tree trunks were rather spaced apart (Figure 2).

C. campanisona is a non-excavator bird and all observed nests were located inside natural tree cavities resulting from broken branches or trunks (Figure 2). According to Simon and Pacheco's (2005) nest classification, *C. campanisona* used cavity/with tunnel/low cup nests. These nests could be in either dead (n=2), living trees (n=32) or in dead parts of living trees (n=4). Nest heights from ground (NH) were in the higher (NH ≥2 m; n=11), middle (1m< NH >2m; n=9) or lower parts (NH ≥1m; n = 18) of the trunk. The nests were covered with a layer of leaves which were regularly renewed during the whole reproductive period (Figure 3). A total of 14 tree species from 11 botanic families were identified and only two dried trunks remained unidentified (Appendix 1).

In some cases, we observed that certain cavities had been reoccupied for a subsequent breeding attempt. For example, the cavity of nest n° 2 in *Psidium guineense* tree was reoccupied four years later (nest n°9); the cavity of nest n° 3 located in *Byrsonima sericea* tree was reoccupied three years later (nest n°7) and the cavity of nest n° 13 also in *Byrsonima sericea* tree was reoccupied six months later (nest n° 15). We could not verify in any case 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 the cavity. Cavity entrance size was on average 144.95 cm^2 ± 20.54 Standard Error (SE; extremes 48-360 cm^2). Cavity entrances were placed at an average height from ground of 235.08 cm ± 16.48 SE (extremes 80-436 cm) and nests were located at an average height from ground of 134.89 cm ± 15.19 SE (extremes 15-380 cm). Cavity depth was on average 93.87 cm ± 6.18 SE (extremes 25-190 cm; Appendix 1). Nest diameter was on average 12.06 cm ± 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 were white and short-oval shaped 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 (Figure 3). Egg size was on average 32.7x25.1mm (± 0.21 & ± 0.15 SE; n=30) and weight was on average 10.07g ± 0.22 (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 ± 0.49 SE: 19 days (n=2); 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 ± 0.49 SE.

Both parents participated on rising the chicks and 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 this species following army ants.

When approaching the nest, the adults walked zigzagging across the floor. Often one or both parents walked around the trunk before reaching the cavity entrance with a short flight and usually stopped there a moment, looking at the surroundings before descending into the nest. The adult came in and out of the nest 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 to the woods in horizontal line. Sometimes the adult flapped its wings two to three times at the nest entrance before flying away. The reason of this behavior could not be determined.

During several morning observations at five nests for periods of 5 hours between 06:30 to 11:30, we observed parent-offspring feeding behavior. Results showed that with nestlings aged between 5-10 days, parents fed the chicks with a frequency of 1-2 times/hour. From the age of 10 days onwards, visits were less frequent (0.5-1 time/hour) and adults brought a greater quantity of food at a time. In many cases wings and legs of insects dangled from the parents' beak (Figure 4). Adults usually arrived separately to the nest. When arriving together, one adult entered the nest cavity while the other one 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 heat 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 during the years 2000 and 2001. The presence of most nests coincided with 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 highest peak (Figure 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 in each month of the year, except January (Figure 5).

To calculate the duration of the breeding season all dataset 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.

Nest failure and potential predators

Out of the 38 nests, 19 failed, 11 were successful and 8 had an unknown fate (Appendix 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 the two nests in August (1995) when parents abandoned the cavity that had been flooded with rainwater.

We observed that predators usually arrived at night, however, in most cases the 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 $0.9716 \ d^{-1}$ and the nest success during the breeding period (b=30.75 days) was 31.87%. Following the MARK program, DSR was $0.9651 \ d^{-1} \pm 0.0078$ SE and nest success during the breeding period (b=30.75 days) was 24.09%.

Hotelling's T^2 test revealed no differences between successful and failed nests ($T^2 = 1.8952$, *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).

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

Nest variable[a]	n	Successful	Failed	t-test	df	*p-value*	*p-value*[b]
EH (cm)	38 (11,19)	301.18 ± 31.31	228.98 ± 21.69	1.90	19.42	0.0729	0.2916
NH (cm)	38 (11,19)	188.64 ± 34.33	130.31 ± 18.88	1.49	16.15	0.1559	0.6236
D (cm)	38 (11,19)	112.55 ± 12.59	86 ± 8.20	1.77	18.43	0.0938	0.3752
ES (cm)	21 (9,12)	118.22 ± 19.53	178.25 ± 34.07	-0.62	13.298	0.546	1.0000

[a] EH=Cavity entrance height from ground, NH =Nest height from ground, D=Cavity depth, ES=Cavity entrance size.
[b] *p-value* after Bonferroni corrections.

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).

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

Model[a]	df	*p-value*	Log-likelihood	AICc	ΔAIC_i	AIC_i *Weight*
F~EH+ES	4	0.014	-15.93	41.5	0	0.569
F~EH+D+ES	5	0.0204	-15.12	42.7	1.27	0.302
INTERCEPT	2	0	-20.67	45.8	4.32	0.066
F~EH+NH+D+ES	6	0.0471	-15.1	45.9	4.39	0.063

[a] F= Nest fate. See Table 1 for definitions of explanatory variables.

Discussion

Clutch sizes of 3 eggs were found by Maders and Matuchaka (2011) in Argentina and by Franz (2013) in southern Brazil. 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 2 eggs. These differences in clutch size may be attributed to the geographical variations of each study. 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 25-29ºS (Maders and Matuchaka 2011, Franz 2013, Bodrati et al. 2014, Maugeri 2014).

The eggs of *C. campanisona* are white, so as those 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) mentions them to be spherical shaped, Krabbe and Schulenberg (2003), Maders and Matuchaka (2011) and Bodrati et al. (2014) described them as oval shaped. Franz (2013) states that eggs are characterized for having "clearly unequal poles" and Maugeri (2014) defined them to be short subelliptical.

The nest characteristics here described 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 of advanced state of decomposition (Maugeri 2014). We found cavity entrances as high as 4.36 m above ground and Bodrati et al. (2014) found one at 9.6 m above 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 and Heine, 1860) and of sympatric antthrushes such as *Gymnopithys rufigula* (Boddaert, 1783) and *Formicarius analis* (d'Orbigny and Lafresnaye, 1837) are also placed in dead tree cavities (Oniki 1971, Sick 1997, Zyskowski 2015). Nest material is described to be 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). Nest diameter of *C. campanisona* was 12x12.06 cm (n=8) which is similar to the measures of 12x13 cm (n=1) indicated for this species by Maugeri (2014) and ca. 12cm (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 Bodrati et al. (2014) suggested. Bodrati et al. (2014) calculated a nestling period of 22-23 days and comparing with our results, we consider that the nestling period ranks 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).

Breeding seasons vary considerably throughout the different regions of Brazil and it is generally admitted that birds depend on food availability to raise their young, which in turn depends on beginning of rainfalls (Aguilar et al. 1999, Duca and Marini 2004, Hoffman and Rodrigues 2011, Marini et al. 2012). The northeastern region is considered a semi-arid ecosystem, where relations between bird reproduction and rainfall seasonality are strongly correlated (Scheuerlein and Gwinner 2002, Cavalcanti et al. 2016). This strong correlation clearly appears in Pedra Talhada forest as illustrated in Figure 5.

The northeastern region has been qualified as some of the most irregular and semiarid regions worldwide (Molion and Bernardo 2000) and where the influences of severe droughts, rainfall anomalies and El Niño phenomena are emphasized by many authors (Hastenrath and Heller 1977, Moura and Shukla 1981, Pontes da Silva et al. 2011). Even though this forest is situated in the northeastern region, Pedra Talhada forest escapes this harsh pattern and benefits from far more humidity than the adjacent regions (Tscharner et al. 2015). This irregularity of rainfalls could also signify a certain degree of adaptation by *C. campanisona* and may explain the extremely long time span of its breeding period (Figure 5).

Very long breeding periods for *C. campanisona* are not verified in other areas of its distribution range. One of the few long-term studies published on the breeding period of *C. campanisona* by Bodrati et al. (2014) suggests that it lasts from September to November. 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 this main breeding period.

This long-term study of the Short-tailed Antthrush allowed us to evaluate its success rate in Pedra Talhada forest using two different methods. For the MARK program it was necessary to know nest fate (Dinsmore and Dinsmore 2007), hence, nests with unknown fate had to be excluded from the analysis. This may be the cause of a negative bias, which led to an underestimation of the nest success. This result shows the advantage of using Mayfield (1975) method, due to its ability to include unknown fate nests to determine daily survival rate. 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 cavity entrance size and cavity entrance height from 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 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 mammalian predators. Thus, these birds may vary the height at which they build their nests in response of predators 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, the birds may not always be able to choose between cavities due to their 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 carry out breeding attempts in unsuited cavities (Martin and Li 1992, Martin 1995). This could also explain the reason why we found such variations in nest characteristics or the justification to reoccupy 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) and also turned out to be the main cause of nest loss for *C. campanisona* in Pedra Talhada forest.

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 Barnet 2003). It therefore matches the results from other studies that suggest that closed nests located in cavities present higher nest success than open nests (Oniki 1975, Gibbs 1991, Brawn et al. 2011, Studer 1994, 2015), an assumption that still has to be proven in Pedra Talhada forest.

Chamaeza campanisona appears 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 Mayfield (1975) method, this species still encounters adequate conditions for its survival in Pedra Talhada forest.

Acknowledgements

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Figure 1. Location of Pedra Talhada forest.

Figure 2. Detail of *C. campanisona* nest location (March 2009; A. Studer).

Figure 3. Nest and eggs of *C. campanisona* at cavity bottom (March 2009; A. Studer).

Figure 4. Adult of *C. campanisona* at nest entrance carrying a large quantity of arthropods (March 2009; A. Studer).

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