

Breeding biology of Pale-breasted Thrush *Turdus leucomelas* (Turdidae) in the north of Atlantic Forest, Brazil

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ABSTRACT: Reproduction is a key process in the life of organisms and represents high-energy cost to the parents, and often a tradeoff between survival and reproductive success. The breeding biology is an important aspect to be studied, which has inspired theories about bird life history evolution, such as the latitudinal gradient in the clutch size related to different survival rates between the temperate and tropical regions. To contribute with the knowledge of breeding ecology of tropical birds we monitored two reproductive periods of the Pale-breasted Thrush *Turdus leucomelas* in the northeastern Brazil. The breeding period in the studied area occurred from December through April. We found the nests mainly on Facheiro cactus (Cactaceae) at 1.43 ± 0.35 m above the ground. They were composed by roots, mosses, fungus mycelium, leaves, twigs, and a mix of fragmented vegetal material with soil and sand at the base. We found clutch sizes of three ($n = 9$), two ($n = 3$) and one ($n = 1$) eggs. The eggs ($n = 21$) had mass of 5.1 ± 0.9 g and measured 26.6 ± 1.3 mm by 19.5 ± 0.5 mm. We observed 12 days of incubation and 14 days of nestling period. The Mayfield nest success in 2013 was 7.3% and in 2014 it was 4.5%, lower during the nestling period than during the incubation in both years. Our results show that *T. leucomelas* breeds in the area in the beginning of rainy season, when the frequency of occurrence of the migrant *Turdus amaurochalinus* is low. In addition, the low nest success observed may be a consequence of the localization of the studied area in the periphery of the species range, where limited resources probably result in reduced fitness.

KEY-WORDS: breeding success, egg, Mayfield, nest, northeastern Brazil, predation.

INTRODUCTION

The breeding knowledge of many tropical species remains poorly understood, where we do not know many basic aspects, such as breeding season, nest characteristics, and clutch size (Martin 1996, Stutchbury & Morton 2000). In addition, accurate estimates of nest success are necessary for improving our understanding of life-history strategies of tropical birds, and how those strategies may differ among regions of the tropics and, also, from temperate zones. Reproduction is an important life history trait, which affects both parental fitness and population persistence (Berl *et al.* 2014). It is regulated basically by a density-dependent feedback of adult population (Ricklefs 1997), area-dependent changes (Hoover *et al.* 1995), habitat structure (Zanette & Jenkins 2000), predator assemblages (Thompson-III 2007, Klassen *et al.* 2012), food availability (Norris *et al.* 2013), weather conditions (Collister & Wilson 2007) and nest parasitism (Budnik *et*

al. 2000). Basically, breeding depends on environmental and ecological circumstances throughout the annual cycle, necessitating the integration of these components to understand it (Sherry *et al.* 2015).

Density-dependent feedback is not restricted to the same population, sometimes the increase of competitor presence can be an important driver of nesting. Interspecific competition can reduce breeding opportunities for subordinate species, resulting in lower fledgling rates and breeding density (Brazill-Boast *et al.* 2011, Edworthy 2016). Competition-mediated habitat selection is widely believed to change the range of habitats or resources exploited by different species (Sherry & Holmes 1988, Dhondt 2012). The dominance is a primary factor in determining the realized niche among species and the community structure of an area (Dhondt 2012, Thornton *et al.* 2015). Thus, the seasonal variation in the frequency of occurrence of possible competitors may influence the breeding biology of a resident species.

Additionally, different predator assemblages can change in distinct ways the reproductive success of the species. Predators are widely accepted as one of the main cause of breeding loss in tropical bird populations (Lack 1954, Nice 1957, Ricklefs 1969, Oniki 1979, Skutch 1985, Martin 1993). Nest predation influences reproductive strategies and nest-site selection (Martin 1995, Fontaine & Martin 2006). Consequently, nests are not randomly spread across the environment, they are generally hidden in the habitat or in places difficult to access (Klopfer 1963, Cink 1976, Ricklefs 1984, Sonnerud 1985, Martin & Roper 1988). Nest concealment is known to improve nest survival for a variety of open-cup avian species (Berl *et al.* 2014). The mechanism for this is linked to the effect of vegetative cover on predator foraging efficiency (Li & Martin 1991, Segura *et al.* 2012). In consequence, birds in general have applied a plethora of behavioral techniques to avoid predation (Martin 1998, Clark & Shutler 1999, Rauter *et al.* 2002, Davis 2005). Therefore, predators are a powerful ecological force shaping many aspects of breeding biology and life histories of birds (Clark & Wilson 1981).

Another important environmental aspect for bird nesting is the precipitation, considered the main weather condition perceived by birds at tropical areas (Boag & Grant 1984, Lloyd 1999, Hau *et al.* 2008). The onset of rains is associated with greater food availability, either fruits or arthropods (Wolda 1978, Grant & Boag 1980, Leigh-Jr. *et al.* 1996, Ahumada 2001, Dantas *et al.* 2002). Presumably, this peak must also match with the greater breeding period energy demand for egg production (Lack 1968, Ewald & Rohwer 1982, Martin 1987), parental care (Lack 1954) or juveniles' dispersal (Morton 1971). Additionally, the breeding season may be adjusted by molting process that also occurs most often in the rainy season, when there is plenty of food supply (Poulin *et al.* 1992).

The Pale-breasted Thrush (*Turdus leucomelas*) is a common species with breeding biology poorly studied (Collar 2005, Davanço *et al.* 2013). Its large occurrence in South America makes it a good model species to investigate the variations of reproductive traits among regions, habitats and climate conditions. The present study contributes to this knowledge describing the nesting biology of the species in the extreme of its distribution. In addition, our objectives were to correlate some aspects of the reproduction of the species with habitat characteristics, precipitation and molt occurrence. We also discussed the effects of the frequency of occurrence of the migrant congener Creamy-bellied Thrush (*Turdus amaurochalinus*), a possible competitor in the area.

METHODS

Study area and species

We monitored *T. leucomelas* breeding biology in a plot of 550 × 550 m (30.25 ha) formed by an array of eleven rows and columns (50 m apart) located at *Centro de Lançamento Barreira do Inferno - CLBI* (Barreira do Inferno Launch Center, Brazilian Air Force) city of Parnamirim, Rio Grande do Norte state, Brazil (05°54'S; 35°10'W, 1800 ha). The area has tropical coastal vegetation of Atlantic Forest sandbank (Scarano 2002) and classified as semi deciduous forest of lowlands (Cestaro 2002). According to the Köppen (1936) classification system, the climate of the region is AS (tropical and humid) with dry summer and rainy winter (IBAMA 2003). The species *T. leucomelas* is widespread in central, east and north of South America (Sick 1997, Collar 2005), where it inhabits pristine and disturbed humid forests, drier deciduous woodland, savannas, gallery woodland, and anthropogenic environments (Collar & Garcia 2016). This common, non-threatened, species feeds mainly on fruits, arthropods, worms and small lizards (Collar & Garcia 2016).

Data collecting and analysis

From 2010–2012 we determined the breeding period of the species through records of the brood patches occurrence resulting from a monthly demographic monitoring captures at the same study area. In 2013–2014, we started the search for active nests one month before the breeding season and extended it to one month after to avoid loss of any reproduction attempt. During this time interval, we searched the whole study area for nests at least once a week in the early hours of the morning (05:00–10:00 h), using previous established parallel paths at 50 m each (1050 h-observer in total). We applied ordinary nest-searching methods through the area, looking for visual contacts and behavioral clues of adults in breeding activity (vocalizations, territory defense, carrying of nest materials or food for nestlings) (Lopes & Marini 2005). We photographed, georeferenced and described the active nests found according its stage (construction, incubation, nestling) and we monitored them and the parental behavior at intervals between 2 to 4 days until it became inactive. We manipulated the contents once in the incubation stage (to measure and to weigh the eggs with a 20 g scale and 0.05 mm caliper) and another time in the end of the nestling stage for ringing. The description of the egg shape was based on Baicich & Harrison (1997) and the colors on Smithe (1975). The nestlings were marked with aluminum bands provided by the *Centro Nacional de Pesquisa e Conservação*

de Aves Silvestres (CEMAVE/ICMBio), and with colored bands to follow them during the post-nestling period. We also monitored the nests after each breeding attempt (successfully or not) in order to check reuse.

We considered as incubation period the time between the laying and hatching of the last egg, and the nestling period between the hatching of the last egg and when the last nestling leaving the nest. When we could not register the exact day of an event, we assumed the day at half of the period from the last research visit to establish these periods. We considered successful nests those that produced at least one nestling, and failure when no eggs hatched (during incubation) or no offspring was produced (during nestling period). We estimated the breeding success as a simple ratio of successful nests to total nests found (apparent success, see Jehle *et al.* 2004) and by using Mayfield's method, which estimates the mortality rate as a ratio between failures and observation period (Mayfield 1961, 1975). Since the nests were not monitored daily, we assumed as the exact date of loss or success the middle day between the last two consecutive visits (following Mayfield 1975). Based on our results, we considered 12 days the incubation period and 14 days the nestling period to obtain the survival rates.

For each nest, we identified the plant species where it was built, the perpendicular distance of the superior ridge of the nest to the ground (height from the ground) and its position in the plant support (branches or main axis). We also measured the largest and smallest internal and external diameter, depth and height of the nest using a ruler and caliper. The description of the nests followed the proposal of standardization for Neotropical birds (Simon & Pacheco 2005). At the end of each reproductive period, we collected and dried each nest to identify the material composition of the base and the incubation chamber. The dried materials were weighed using a digital precision scale (0.01 g).

The frequency of occurrence of the migrant *T. amaurochalinus* was estimated monthly as the number of captures per 100 h-net (nets Ecotone® 18 × 3 m, mesh

size 19 mm and five shelves). These records and the molt occurrence were obtained from our monthly demographic monitoring program developed at the same study area.

RESULTS

During the monthly captures from demographic monitoring, we found brood patches mainly between January and April, with isolated records in November (1), December (2) and May (1). Thus, the nest searching and monitoring in the breeding seasons of 2012/2013 and 2013/2014 occurred from December through April. During the first breeding season monitored, we recorded 12 active nests, starting on 22 January and ending on 6 April 2013. In the second breeding season monitored, we recorded seven nests (from 12 January through 09 April 2014).

The apparent success of nests was 10.8% and 12.5% each year, respectively. The Mayfield success in 2013 was 33.6% during the incubation, and 21.7% during the nestling period, resulting in the annual success of 7.3%. In 2014 it was 49.7% during the incubation, and 9.0% during the nestling period, resulting in the annual success of 4.5% (Table 1, Fig. 1). The nest survival was lower during the nestling period than during the incubation for both years. The losses occurred on whole clutch, with none individual losses registered. Among the 16 nests preyed, 87.5% ($n = 14$) presented intact structure, and with no signs of destruction or displacement of the nest original position. After the use of the nest (with success or loss), there was no reuse or second attempt in all nest monitored.

All nests monitored ($n = 19$) were built above the ground on vegetation (average height from the ground of 1.43 ± 0.35 m, range between 0.86–2 m). Only once the nest was built away from the main trunk of the plant support (-95 cm), all others were built on forks of the main axis. The nests were mainly built on the arboreal cactus called locally as Facheiro (*Pilosocereus cattingicola*,

Table 1. Nesting survival rates of *Turdus leucomelas* obtained on 2013 and 2014 in the north of Atlantic Forest, Brazil.

Year	Breeding period	Exposure (days)	Nests lost (n)	Daily survival rate	Mayfield survival rate	Apparent survival rate
2013	Incubation	46	4 of 7	0.9130	0.3355	0.4286
	Nestling	58	6 of 8	0.8966	0.2170	0.2500
	Entire breeding period				0.0728	0.1071
2014	Incubation	53	3 of 6	0.9434	0.4970	0.500
	Nestling	19	3 of 4	0.8421	0.0902	0.250
	Entire breeding period			0.0448		0.1250

Assumed 12 days for incubation period and 14 days for nestling period.

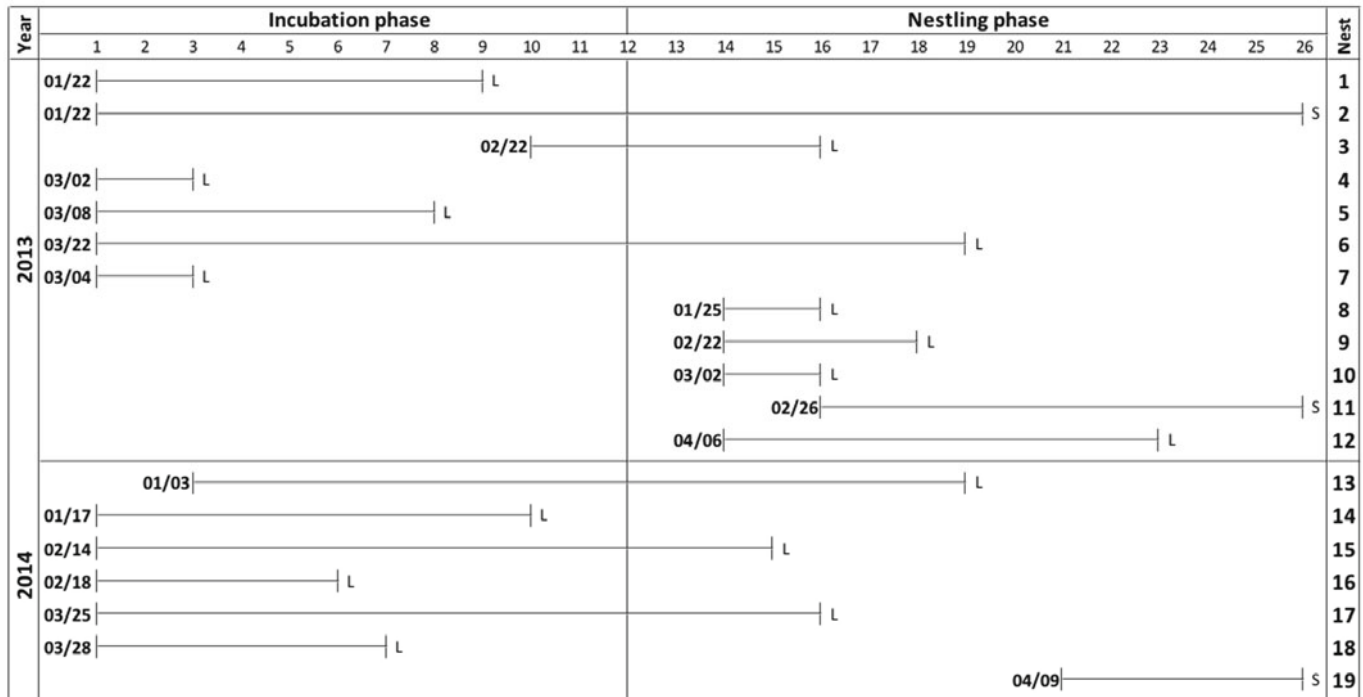


Figure 1. History of nests of Pale-breasted Thrush (*Turdus leucomelas*) monitored in 2013 and 2014 in the north of Atlantic Forest, Brazil (the numbers before each line means the date (day/month) when the nest was found; S = success and L = loss).

Cactaceae) (57.9%; $n = 11$) followed by the Mangabeira tree (*Hancornia speciosa*, Apocynaceae) (26.3%; $n = 5$), Myrtaceae (10.5%; $n = 2$) and *Coccoloba mollis* (Polygonaceae) (5.3%; $n = 1$). During the incubation period the apparent success of nests built on arboreal cactus was 73% (8 of 11), and during nestling period it was 25% (2 of 8).

The nest shape varied between circular and oval, with the diameter ranging from 94–155 mm (mean largest external diameter = 132.0 ± 12.8 mm; mean smallest external diameter = 113.3 ± 12.6 mm). The incubation chamber was oval with highest and lowest diameters ranging from 60–90 mm (mean largest internal diameter = 81.5 ± 6.8 mm; mean smallest internal diameter = 71.3 ± 4.9 mm) and its depth varied between 35–55 mm (mean depth = 44.9 ± 5.4 mm). The nest height ranged from 82–170 mm (mean height = 102.6 ± 22.6 mm). The general structure fits in the definition of “low cup/ base” following Simon & Pacheco (2005) (Fig. 2).

The nests were composed basically by roots, mosses, fungus mycelium, leaves, twigs, and a mix of fragmented vegetal material with soil and sand at the base (Table 2). It is worth mentioning that the mycelia were found in 83.3% of the nests, however this last mass may be biased by the aggregate material added to it (e.g. sand, mosses, leaves), which was not separated in order do not compromise the integrity and identification. Also, it is noteworthy the representativeness of the roots, most used material at the nest bottom and the incubation

chamber, composing 9.4% and 65.2%, respectively, and present on all the nests. Leaves and mosses had high representativeness in the bases and chambers of the nests; while the woody plant twigs had presented at high frequency on the bases. Instead, we recorded a few items in a single nest, but with a significant participation, as *Polycarpaea corymbosa* (Caryophyllaceae), Eriocaulaceae, Facheiro, bromeliad inflorescence and, in a lesser ratio, *Lycopodium* sp. (Lycopodiaceae).

During the incubation period, we found clutch sizes of three ($n = 9$), two ($n = 3$) and one ($n = 1$) eggs. The clutch with just one egg was preyed a day after the last visit, and probably it was not greater because the loss. The observed eggs ($n = 34$) had coloration ranging from 168D Light Sky Blue and 93 Robin's Egg Blue, with spots ranging from 121A Prout's Brown and 121B Brussels Brown. The spots concentration prevailed at rhombic pole, but we also recorded the fully spotted pattern, with intermediary stages (Fig. 3). The eggs shape were intermediate between “Oval” and “Short-Oval” and they measured ($n = 21$): length = 26.6 ± 1.3 mm (range 22.2–28.4 mm), width = 19.5 ± 0.5 mm (range 18.0–21.1 mm), and mass = 5.1 ± 0.9 g (range 4.2–6.1 g). At the nests in which we could follow the parental care during incubation ($n = 3$), we have always recorded the same parental (marked with colored bands) at incubation duties and territory defense. We observed in four nests the maximum incubation period of 12 days (Fig. 1).

During the nestling period, individuals of 0–3

Table 2. Nest materials of Pale-breasted Thrush (*Turdus leucomelas*) in the north of Atlantic Forest, Brazil (Σ Mass = sum of masses recorded for each item; % Relat = relative frequency of the item based on the mass; Freq = number of nests with the item).

Material	Whole nest			Base			Camera		
	Σ Mass (g)	% Relat	Freq	Σ Mass (g)	% Relat	Freq	Σ Mass (g)	% Relat	Freq
Roots	302.16	0.1468	19	177.21	0.0947	17	124.95	0.6661	13
Mosses	82.66	0.0402	15	74.23	0.0397	15	8.43	0.0449	8
Fungus mycelium	64.89	0.0315	15	64.89	0.0347	16	0.15	0.0008	2
Leaves	49.53	0.0241	19	46.73	0.0250	19	2.80	0.0149	11
Bryaceae	47.12	0.0229	9	46.84	0.0250	8	0.28	0.0015	4
Woody plant twigs	40.80	0.0198	17	39.86	0.0213	17	0.94	0.0050	5
Araceae- <i>Anthurium affini</i>	23.42	0.0114	13	22.25	0.0119	12	1.17	0.0062	4
Bromeliaceae	15.64	0.0076	10	18.65	0.0099	9			
<i>Cattleya granulosa</i> (root)	12.62	0.0061	3	12.62	0.0067	3			
Gramineae	11.73	0.0057	10	10.19	0.0054	10	1.54	0.0082	2
<i>Microgramma</i> sp.	9.53	0.0046	4	8.19	0.0044	4	1.34	0.0071	2
Lichens	4.87	0.0024	1	4.43	0.0024	1	0.44	0.0023	1
Bromeliad inflorescence	3.01	0.0015	1	3.01	0.0016	1			
<i>Polycarpha corymbosa</i>	2.06	0.0010	1	2.06	0.0011	1			
Eriocaulaceae	1.17	0.0006	1	1.17	0.0007	1			
<i>Pilosocereus cattingicola</i>	1.10	0.0005	1	1.51	0.0006	1			
Unknown Vegetable Fiber	0.99	0.0005	3	0.99	0.0005	3			
<i>Lycopodium</i>	0.77	0.0004	1	0.77	0.0004	1			
Residues not identified *	1383.66	0.6724	19	1338.11	0.7155	19	45.55	0.2428	6

(*) Fragmented vegetal material, including soil and sand.

**Figure 2.** Upper and lateral views of Pale-breasted Thrush (*Turdus leucomelas*) nest recorded in the north of Atlantic Forest, Brazil.

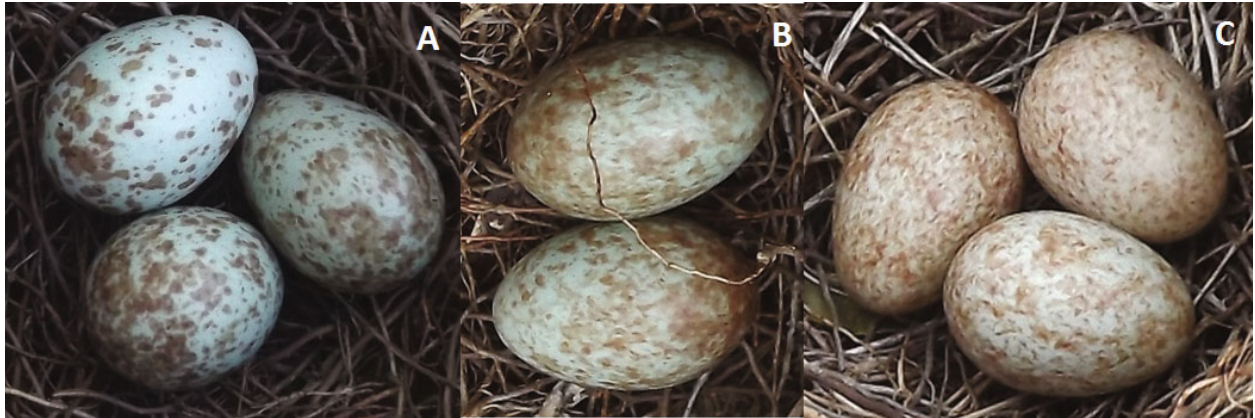


Figure 3. Pale-breasted Thrush (*Turdus leucomelas*) eggs spotted patterns (A-C) and shape (B) recorded in the north of Atlantic Forest, Brazil.



Figure 4. Nestlings development stages of Pale-breasted Thrush (*Turdus leucomelas*) in the north of Atlantic Forest, Brazil (A = 0–3 days; B = 4–5 days; C = 8–10 days; D = 11–12 days, age of ringing; E = 13–14 days).

days old ($n = 11$) were naked with yellow skin and a narrow spinal pterylya (dorsal tract) extending from nape to rump with thin beige pinfeathers. The beak and the tarsus were beige, the eyes closed, the abdomen skin was pale and wrinkled, and they begged for food (Fig. 4A). Between 4–5 days the nestlings ($n = 10$) began to open their eyes and being more active (begging behavior only with parents). The pinfeathers of the remiges were already visible as a narrow gray strip, but the tips had not yet erupted (Fig. 4B). Between 6–7 days ($n = 7$ nestlings) the rectrices were visible, but without external tips. The spinal pterylya had pinfeathers from head to rump, and the beak and tarsus were slightly dimmed. At age of 8–10 days ($n = 5$ nestlings) they always opened eyes during the visit, showing off dark brown iris, and they were curious with the surroundings, following movements. The pinfeathers of the spinal and ventral pterylya showed unsheathed tips (larger on back), and also the remiges began to show unsheathed tips (-2 – 5 mm, Fig. 4C). Between 11–12 days ($n = 5$ nestlings) they had the body $\sim 70\%$ covered with feathers, naked areas remained on central belly and flanks, and the rectrices began to show unsheathed tips. They have tried to hide themselves with the researcher approaching, and after touched they moved up and flapped the wings. We ringed the

nestlings at this age, and when they were being removed from the nest, they held fast to the nest material. On two occasions, two of them jumped out of the nest in this situation, and they were returned after handling (Fig. 4D). Between 13–14 living days the nestlings ($n = 3$) had plumage similar of juvenile pattern, with beige and gray spots at belly and upper cover feathers. The tarsus and beak were dark gray, with yellow gape flanges in the later. At this age the nestlings leaved the nest (Fig. 4E), and the maximum nestling period observed was of 14 days (Fig. 1, Nest 2). From all nestlings monitored ($n = 29$), we recovered two after leaving the nest (17 days and 108 days after ringing), both showed juvenile plumage pattern, and were captured close to their nests (< 40 m).

Finally, through the demographic analysis of ringing data from November 2010 until November 2014, we found in March a marked overlapping of brood patches and molt (remiges, rectrices and both of them) and the frequency on individuals captured with brood patch and the months considered as breeding period (Fig. 5). Also through this data, we have recorded the highest frequency of occurrence of the migrant *T. amaurochalinus* in June (2010 to 2014) in synchrony with the largest annual peak of rainfall (Fig. 5).

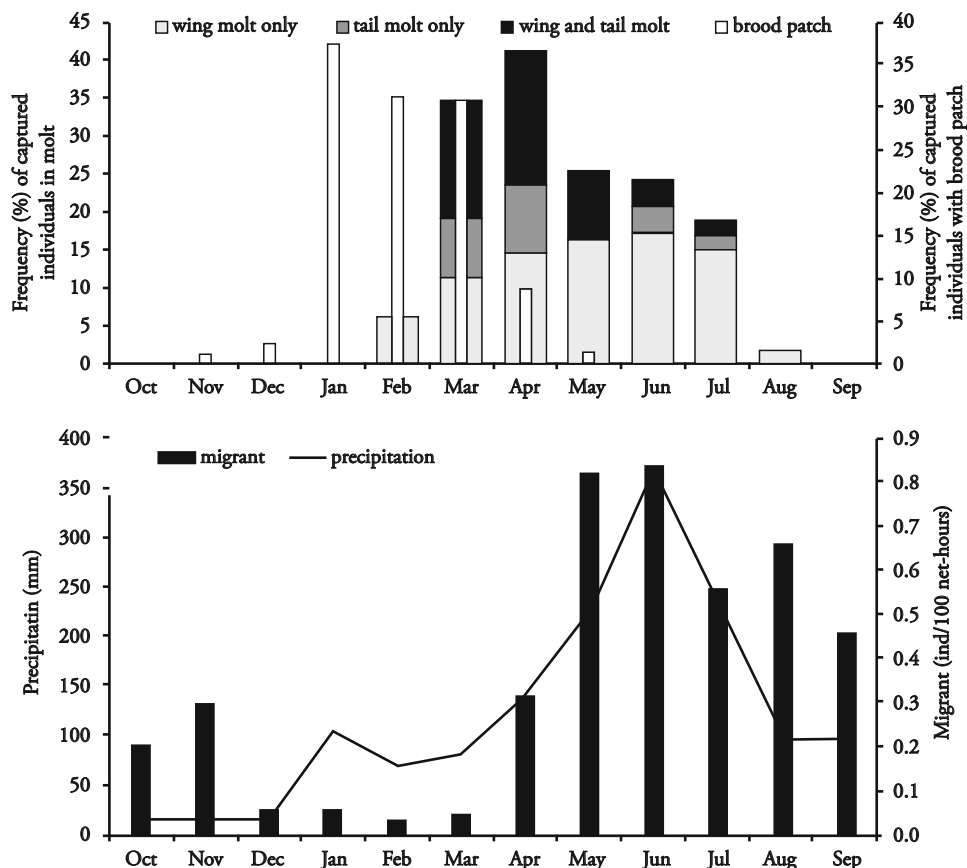


Figure 5. Annual conjugation between molt, brood patch, precipitation and migrant frequency of occurrence of Creamy-bellied Thrush *Turdus amaurochalinus* between 2010 and 2014 in the north of Atlantic Forest, Brazil.

DISCUSSION

We estimated a very low (< 10%) and unexpected nest success for a tropical passerine. Previous estimate for *T. leucomelas* was of 57% in the southeast of Brazil (Davanço *et al.* 2013), and for *Turdus rufiventris* 35–41% in Argentina (Ferreti *et al.* 2005). For temperate thrushes, like *Turdus migratorius* and *Turdus merula*, the nest survival is ~30–50% (Knupp *et al.* 1977, Cresswell 1997, Djemadi *et al.* 2015). One explanation for the low nest survival we found is the fact that the studied area is in the periphery of the species range. In the extreme northeast Brazil *T. leucomelas* occurs in a narrow strip of forest close to the coast, and it is rarely found in the drier countryside covered by Caatinga vegetation. In addition, the numbers of nests that we found was low, even with a great effort (1050 h in total). It seems that the studied area represents an extreme of distribution with few nest attempts and low nesting success. In many species, reproductive success is lower near the boundary of distribution, where limited resources can result in reduced fitness (Sexton *et al.* 2009). Usually, in the border of occurrence of a species there are “sink populations” because of the environmental and ecological restrictions. It is possible that our results represent an example of this demographic limitation, where the local productivity is perhaps not enough to maintain the population level, an hypothesis which needs to be tested.

There are basically two factors that can potentially affect breeding performance in birds: resources and predation (Paradis *et al.* 2000). We did not measure the resource availability in our area, but considering the occurrence of other thrushes, and many other frugivorous species, we suspect that food *per se* is not a limitation. Actually, food limitation is much less important to life-history in birds than suggested by traditional theory (Ferreti *et al.* 2005). However, predation seems to be the main factor accounting for low nest success in our study area. The majority of nest losses that we detected was caused by predation, probably by reptiles and birds, due the intact structure of the left nests. Birds and snakes normally do not destroy the nest when they are preying, while mammals do (Martin 1993, Woodworth 1997, Marini *et al.* 2007). At the study area, there is a record of a *T. leucomelas* nestling predation by the snake *Leptophis abietulla* (Colubridae) (Ribeiro *et al.* 2014). Some other known bird predators recorded in the area were *Oxyrhopus trigeminus* (Colubridae) (Alencar *et al.* 2012), *Caracara plancus* (Falconidae), *Rupornis magnirostris* (Accipitridae), and *Cyanocorax cyanopogon* (Corvidae) (Sick 1997). For possible mammal predators, we frequently observed in the area the opossums (Didelphidae) *Didelphis albiventris* (Cáceres 2000) and *Caluromys philander* (Eisenberg & Redford 1999), and also the marmoset *Callithrix jacchus*

(Cebidae). Marmosets have been recorded widely in the literature as a common predator of bird nests, including *T. leucomelas*, and they have skills to prey without nest destruction (Pontes & Soares 2005, Lyra-Neves *et al.* 2007, Alexandrino *et al.* 2012, Vinhas & Souza-Alves 2014). Therefore, the high level of predation in the studied area seems to constrain the nest productiveness of *T. leucomelas* in this extreme site of distribution of the species.

Another important aspect related to predation in the area was the preference for nest building on the Facheiro cacti. This plant support was the most common and provided greater nest success during incubation. Probably, the protection given by its thorny stems and branches is the main beneficial characteristic of this plant. It is interesting to highlight that those nests on cacti were more exposed and without concealment, even thus, this plant was the most frequent nest support.

The nest shape observed is consistent with what has been described by other authors for tropical thrushes (Euler 1900, von Ihering 1900, de la Peña 1987, Sick 1997). However, we identified the proportionality of the used items, where fragmented vegetal material, including soil and sand predominated at the base and roots in the incubator chamber. It is worth mentioning the plasticity of the species to adapt to the environment of its surroundings. In the study area, there is little availability of mud, because the soil is predominantly sandy. Hence, the base was composed of fragmented vegetal material, soil and sand mixed with fungal mycelium to promote the adhesion among these materials. In some cases, living roots of *Cattleya granulosa* and *Microgramma* sp., and mosses promoted the adhesion of the materials. Therefore, the nests were quite compact and adhered to the substrate, regardless of the absence of mud.

Our records about height of the nest, eggs measurements (mass, length and width) and predominance of clutch sizes of three eggs were similar to those reported previously for this species (Carvalho 1957, Haverschmidt 1959, Camargo & Höfling 1993, Collar 2005, Rodrigues 2005, Marini *et al.* 2007, Davanço *et al.* 2013). It seems that the clutch size in *T. leucomelas* does not vary much along its latitudinal gradient. The incubation period of 12 days that we observed was similar to other studies (Carvalho 1957, Haverschmidt 1959, Sick 1997, Collar 2005, Davanço *et al.* 2013). However, the nestling period has been reported as longer in the literature (16–17 days, Carvalho 1957, Haverschmidt 1959, Sick 1997, Collar 2005, Davanço *et al.* 2013). Maybe, the short nestling period that we recorded represents an adaptation against the high level of predation in the area. Sometimes young should grow faster to reduce predation risk (Bosque & Bosque 1995, Remeš & Martin 2002). Probably, the premature leaving from the nest is compensated by a longer period of parental care of the fledglings, behavior

already cited to other tropical birds (Russell *et al.* 2004, Schaefer *et al.* 2006, Tarwater & Brawn 2010). We could record at least one juvenile close to the nest site after ~3.5 months. Inversely to our observations, several multiple breeding attempts of *T. leucomelas* during the breeding period were related (Davanço *et al.* 2013), even four different attempts for the same nest have been cited (Collar 2005).

Previous records have indicated that *T. leucomelas* breeds throughout the year, but in different periods among regions. The northernmost nest records (Surinam) are between November and May, avoiding the long rainy season in the region (April–August, Haverschmidt 1959). In Colombia, breeding occurs between January and August (Hilty & Brown 1986). In Brazil there are nest records in the north between July and February (Oniki & Willis 1983a, b), in the central between August and October (Antas & Cavalcanti 1988), in the southeast between August and January (Marini *et al.* 2007, Davanço *et al.* 2013), and in the south in November (Belton 1994). In Argentina, there is a record of nest in October (de la Peña 1987). These records show that the reproduction of the species starts at the end of the dry season or at the beginning of the rainy season, and rarely coincides with the peak of precipitation in each region. Our observations in the northeastern of Brazil reinforce this idea, because the reproduction occurred from December through April, before the annual peak of rainfall in the area. Probably, the extension of the breeding season is more associated with the rain cycle in the region than other factors, like latitude. We could not confirm the idea that the breeding season is extended in lower latitudes, as suggested in previous studies (Hemborg *et al.* 2001, Davanço *et al.* 2013). For example, we observed a breeding season of five months in our area (~6°S), while Davanço *et al.* (2013) reported the same period in the southeast of Brazil (~23°S). However, in the central Brazil it seems to be shorter (five months, Antas & Cavalcanti 1988). We suggest, for this tropical thrush, that the length of the breeding season is more influenced by rain than latitude.

Actually, this pattern of integrating the rainy season with the breeding period has been observed for other tropical bird species (Lack 1968, Morton 1971, Wyndham 1986, Martin 1987, Wikelski *et al.* 2000, Aguilar *et al.* 2000, Marini & Durães 2001, Mezquida & Marone 2002, Rubolini *et al.* 2002, Duca & Marini 2011). The avoidance of the peak of precipitation can be an adaptation to prevent nest loss, as mentioned for other species (Medeiros & Marini 2007).

Another important factor in our region is that the rainfall peak is associated with the highest capture rates of the migrant *T. amaurochalinus*. Probably, this species competes for resources with *T. leucomelas*, and its massive presence in the area during the rainy season is another

variable possibly shaping the breeding period of resident birds in the studied area, avoiding the peak frequency of occurrence of this migrant. The breeding season can also be adjusted by the molting process. In general, for birds of temperate zones the feathers molt does not overlap with the breeding period (Miller 1961, Payne 1969, Foster 1975, Poulin *et al.* 1992, Ralph & Fancy 1994, Tallman & Tallman 1997, Stutchbury & Morton 2000, Newton & Rothery 2005). However, for tropical regions, these events may occur simultaneously (Foster 1975). We saw some individuals with brood patches and molt, but the peak of molting occurred at the middle of the rainy season. Thus, there was overlap only at the end of the breeding period.

Finally, our findings confirm some patterns of reproductive biology of tropical birds, as high nest predation and low clutch size. However, the nest survival was low, and the breeding season was not extended. These happened probably due to the studied area situated in the peripheral distribution of the species, coupled with a high frequency of competitors and the influence of the rainy season. These results show how poorly we understand the ecology and limiting factors of bird populations in the South America. Thus, we emphasize the necessity to expand geographical breeding analysis in tropical environments. This is essential for the comprehension of the factors that change the life history attributes across different ecosystems. Knowing the importance of limiting factors for a species, and when they operate, are essential for the understanding of life history traits and the evolutionary ecology in the tropics.

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