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Authors: Milene G. Gaiotti, João H. Oliveira, and Regina H. Macedo

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## Breeding biology of the critically endangered Araripe Manakin (*Antilophia bokermanni*) in Brazil

Milene G. Gaiotti,<sup>1\*</sup> João H. Oliveira,<sup>2</sup> and Regina H. Macedo<sup>3</sup>

**ABSTRACT**—Lack of information about basic life history traits of endangered species hinders conservation efforts, since such data have important implications for species' long-term survival. Little is known about the reproductive biology, ecology, and behavior of the Araripe Manakin (*Antilophia bokermanni*), despite its highly threatened status in Brazil. In this study, we provide detailed information about the Araripe Manakin's breeding biology and discuss ecological factors that affected nest survival rates across 3 breeding seasons. Females lay 1- or 2-egg clutches and may attempt re-nesting if the nest fails. The open-cup nests are built in the forking branches of 14 different identified plant species. The Araripe Manakin's nesting period corresponds to the rainy season of approximately 6 months, and its annual reproductive capacity is 2 fledglings. Nesting success of the species was high (72%) compared to other Neotropical species with similar nests, but varied across seasons and sampled areas. Fewer nests were associated with periods of less rainfall, more fragmented forest areas, and areas with higher rates of human activity. The shape of the nest also seemed relevant for nest success, where external diameter of the nest appeared to play an important role. Only females provided parental care in all nesting stages and no differences were found in parental investment between nests with 1 or 2 nestlings. We believe our findings are crucial for future population viability analyses and effective conservation strategies. We argue that although these results point toward this species' critical situation, they also suggest its intrinsic resilience. Received 13 November 2018. Accepted 6 April 2019.

**Key words:** *Antilophia bokermanni*, Araripe Manakin, natural history, nesting biology, Pipridae, reproduction, threatened species

### Biologia reprodutiva do criticamente ameaçado Soldadinho do Araripe (*Antilophia bokermanni*) no Brasil

**RESUMO** (Portuguese)—A falta de informações sobre traços básicos da história de vida de espécies ameaçadas dificulta os esforços de conservação, uma vez que geram informações importantes para a sobrevivência a longo prazo da espécie. Pouco se sabe sobre a biologia reprodutiva, ecologia e comportamento do soldadinho do Araripe (*Antilophia bokermanni*), apesar do seu alto grau de ameaça no Brasil. Neste estudo, nós fornecemos informações detalhadas sobre a biologia reprodutiva do soldadinho do Araripe e discutimos fatores ecológicos que afetam as taxas de sobrevivência de ninho durante 3 estações reprodutivas. Fêmeas põem 1 ou 2 ovos e podem fazer mais de uma tentativa de nidificação em caso de perda do primeiro ninho. Os ninhos de cesta são construídos em forquilha de galhos de 14 espécies diferentes de plantas. O período reprodutivo do soldadinho do Araripe coincide com o período chuvoso que dura aproximadamente 6 meses, e a sua capacidade reprodutiva anual é de 2 ninhos. O sucesso reprodutivo da espécie foi alto (72%) quando comparado com outras espécies de aves Neotropicais com ninhos similares, porém, variou em relação à estação reprodutiva e às áreas amostradas. A menor quantidade de ninhos em determinados anos e locais foi associada ao menor volume de chuva, à fragmentação de áreas e áreas com intensa atividade humana. As dimensões do ninho também são importantes na sobrevivência dos filhotes, onde o diâmetro externo aparenta ter um papel fundamental. Somente as fêmeas realizam o cuidado parental durante todos os estágios de desenvolvimento do filhote e não encontramos diferenças no investimento da fêmea para ninhos com 1 ou 2 filhotes. Nós acreditamos que nossos resultados são cruciais para futuras análises de viabilidade populacional da espécie, assim como para estratégias de conservação efetivas. Nós argumentamos ainda que apesar de nosso estudo apontar a situação crítica da espécie, ele também aponta para a sua resiliência intrínseca.

**Palavras-chave:** *Antilophia bokermanni*, biologia reprodutiva, espécie ameaçada, história natural, Pipridae, reprodução, soldadinho do Araripe

Data about a species' breeding parameters and predation rates provide basic knowledge that allows experts to answer complex questions about ecology, evolution, and behavior (Ricklefs 1969, Bartholomew 1986, Rotenberry and Wiens 1989, Martin et al. 2000, Bennett and Owens 2002, Valcu et al. 2014, Xiao et al. 2016). For

endangered species, such information is even more relevant since breeding parameters affect population rates of establishment and dispersion. Such data provide the rudimentary information necessary for population viability analyses to determine long-term chances of species survival. In fact, breeding parameters are necessary to allow an assessment of the degree of threat as classified by IUCN (IUCN 2001, Van Allen et al. 2012, Stirmemann et al. 2016). Such data, despite their importance, are lacking for a large number of threatened species, especially those in tropical forests (Martin 1996, Stutchbury and Morton 2001, Marini et al. 2012, Xiao et al. 2016).

<sup>1</sup> Programa de Pós-Graduação em Ecologia, Universidade de Brasília, Brasília, Distrito Federal- Brazil

<sup>2</sup> Programa de Graduação em Ciências Biológicas, Universidade Regional do Cariri, Crato, Ceará – Brazil

<sup>3</sup> Departamento de Zoologia, Universidade de Brasília, Brasília, Distrito Federal- Brazil

\* Corresponding author: enelim@gmail.com

The Araripe Manakin (*Antilophia bokermanni*) is an example of the knowledge gap characterizing an endangered species' breeding biology and life history. The species is the only endangered member of the Pipridae family and one of the most threatened birds in the world (IUCN 2015, BirdLife International 2017). This endemic species was described in 1998 (Coelho and Silva 1998) and its currently estimated surviving population is limited to ~800 individuals (IUCN 2015). The Araripe plateau where the species occurs is also an Important Bird and Biodiversity Area (IBA), given the small geographic range and endemism of the Araripe Manakin (Rêgo et al. 2010, IUCN 2015), which has a range of less than 31 km<sup>2</sup> and even more restricted available breeding sites (Rêgo et al. 2010). The plateau is constantly being degraded by human activities and is frequently subjected to lengthy dry seasons and fires (Novaes et al. 2013).

Despite the critically endangered status of the Araripe Manakin and the fragile state of its restricted habitat, there have been few research efforts focusing on its population dynamics (e.g., sex ratio), breeding biology, behavior, or mating system. Such data will contribute to future population viability analyses and allow formulation of effective conservation plans to deter the species' extinction. In view of this urgent need, in this study we investigated the breeding biology and natural history of the Araripe Manakin, which allowed us to determine the species' sex ratio and to estimate its nest survival rates for the first time.

## Methods

### Study area

We conducted the study in the Araripe Plateau located in northeastern Brazil (7°16'S, 39°26'W). The plateau borders 3 states (Ceará, Pernambuco, and Piauí), but the Araripe Manakin occurs only along the slope edging Ceará state, probably due to the unique humid forest found on that part of the plateau. The area is surrounded by the Caatinga ecoregion (Figueira 1989), composed of xeric shrubland and thorn forests. The plateau slope where the bird occurs is the only one with abundant spring waters and which is humid all year (INESP 2009), explaining the development of a humid forest. This slope is contained within an Environmental Protection Area, which despite the name is the most permissive protection category

according to Brazilian conservation legislation (SNUC 2000). Because the slope is not a continuous forest, we developed the study in 6 field sites close to 2 different towns: Barbalha (one site) and Crato (5 sites) (Fig. 1). The different-sized field sites exhibited varying degrees of human disturbance (HD), which was informally assessed based on daily encounters with people and number of tracks and paths. The 6 sites were Grangeiro (size = 0.35 km<sup>2</sup>, HD = low), Coqueiro (size = 0.14 km<sup>2</sup>, HD = low), Caianas (size = 0.16 km<sup>2</sup>, HD = low), Riacho do Meio (size = 0.21 km<sup>2</sup>, HD = high), Serrano (size = 0.16 km<sup>2</sup>, HD = intermediate), and Nascente (size = 0.25 km<sup>2</sup>, HD = intermediate).

### Data collection

We collected data across 3 breeding seasons: November–March (2013/2014), October–March (2014/2015), and December–March (2015/2016). We mist netted, color-banded, and took body measurements (mass and wing, tail, bill, and tarsus lengths) from all Araripe Manakins captured. Blood samples (~60 µl) were obtained from brachial venipuncture and stored in 99% ethanol at 4 °C. Blood samples were necessary for sexing analyses since young males exhibit the same plumage as adult females. Sexing was conducted according to Griffiths et al. (1998) using PCR (polymerase chain reaction) analyses with 2550/2718 primers (Fridolfsson and Ellegren 1999).

We determined the beginning of each breeding season at the first sign of any type of nesting activities. We classified the different stages of breeding in the following categories: nesting (nest construction), incubation (presence of eggs), nestling (presence of nestlings), and fledging (fledglings leaving the nest). When no breeding activity (i.e., no nesting activity or males singing) was registered for at least 2 weeks, we considered that the breeding season had ended.

As the plateau has very marked and short rainy seasons and the Araripe Manakin breeds only during this period, we used the monthly volume of rain across each season (mm/month) to assess whether there was an association between the amount or even presence of rain with the beginning of each breeding stage (Fig. 2). Climatological data were obtained from governmental meteorological stations located in the study



**Figure 1.** Location of the 6 field sites sampled in 2 areas in the Araripe Plateau, Ceará, Brazil, during 3 breeding seasons of the Araripe Manakin. Sites are close to disturbed urban regions. Field sites were A: Riacho do Meio, B: Coqueiro, C: Grangeiro, D: Caianas, E: Serrano, and F: Nascente.

area (Fundação Cearense de Meteorologia e Recursos Hídricos - FUNCEME).

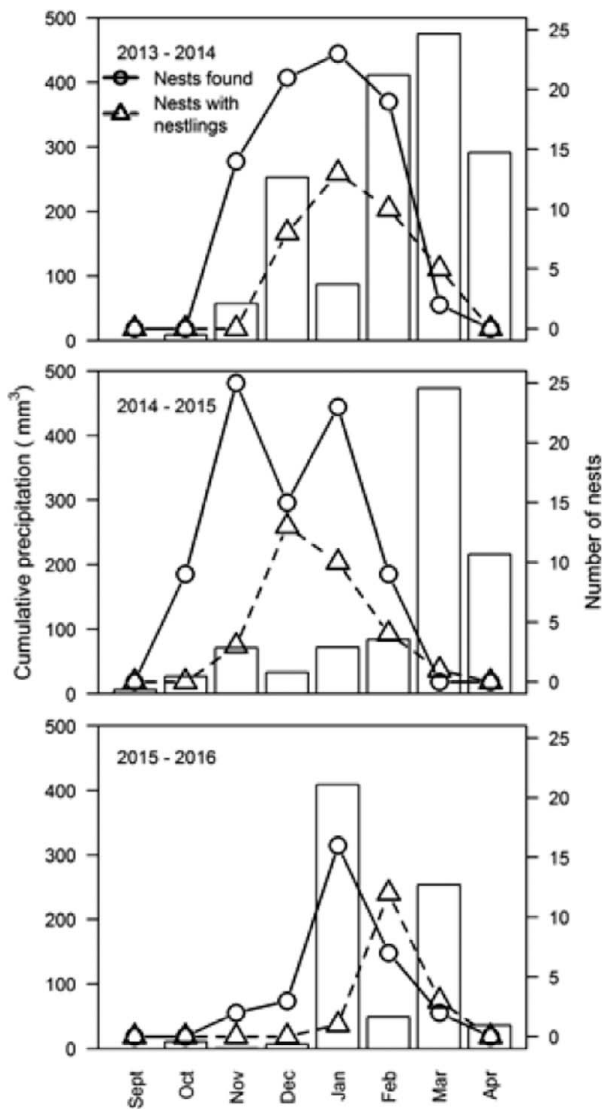
We found nests by searching vegetation that could potentially be used as nest support, and also by following adults carrying nest construction material or food for the nestlings (see Martin and Geupel 1992). We also directed our searching toward plants that are known to be used by Araripe Manakins for nesting (Linhares *et al.* 2010). Once found, nests were monitored every 2 d to register their status (under construction, ready but inactive, and active). Nests found during the incubation period were visited daily to ascertain hatch date. Descriptive nest measurements, taken after the nesting cycle was concluded, included nest height relative to the ground (m), internal nest basket depth (mm), external diameter (mm), and external nest basket height (mm). We used these measurements to check whether nest shape affected nest survival. Eggs had their length, width, and mass measured and we described egg shape and coloration according to Podulka *et al.* (2004). We considered a nest successful when at least one nestling survived to fledging. A nest was considered abandoned when its construction was incom-

plete, when it never became active, or when the adult ceased its activities during incubation or nestling stages. We registered predation when there were clues of such events, such as a destroyed nest, broken or missing eggs, or missing nestlings.

To determine patterns of parental care during different breeding stages we conducted focal observations and also filmed the nests. We used 2 camouflaged digital cameras (Kodak Zx1 and Multilaser DC115, zoom 10×) set 2 m from the nests. We made five 2 h videos of nests under construction, and subsequently, 130 videos of 1.5 h every 3 d during the nestling period starting when nestlings were 1–2 d old until they fledged. Additionally, multiple focal 1 h observation periods were conducted during incubation to confirm the sex of the parent responsible for such activity.

During the nestling period we determined the behaviors used by the parent and also the amount of time spent in each parental care behavior. We classified parental care behavior as brooding (sitting over nestlings), feeding nestlings, cleaning the nest, watching (when perched by the nest),





**Figure 2.** Seasonal variation in discovery rate of Araripe Manakin nests and in nests containing nestlings across 3 breeding seasons and relative to rainfall volume in the Araripe Plateau, Ceará, Brazil.

cleaning the nestlings, and time absent from the nest. In nests with 2 nestlings we determined whether parental investment deviated from equality by recording which nestling received food. To keep track of the nestlings in these nests, we marked one of them on the tarsus with a waterproof pen and determined its position within the nest prior to beginning each video session. Pen marks were refreshed every 2 d, when we monitored chick growth.

### Statistical analyses

We determined breeding success rates using the program MARK (White and Burnham 1999,

Dinsmore and Dinsmore 2007), which provides nest daily survival rate (DSR) and generates models that can include co-variables that may influence DSR. The program also allowed us to verify whether DSR varied as a quadratic, linear, or constant function over the breeding season. We selected the models using Akaike's information criterion (AIC; Burnham and Anderson 2002), where the values were corrected for small samples (AIC<sub>c</sub>). A model was considered a good fit for the data when  $\Delta AIC_c < 2$  (Burnham and Anderson 2002). The relative importance of each variable (sum of AIC weight for all models that use a given variable) was also considered to verify the value of a given model to predict the DSR.

We used nest height relative to the ground, external diameter, year sampled, and area (field site) as co-variables. We excluded internal diameter, nest basket internal depth, and nest basket height from the model because they were correlated. We were able to fulfill all the premises that MARK requires, including that all nests were under the same ecological conditions, as area was used as a co-variable. We ran the model and DSR analysis separately for the incubation and nestling periods, since survival rates usually differ between these stages (Duca and Marini 2005, Lopes and Marini 2005, Carvalho et al. 2007).

We analyzed the parental care videos using the program JWatcher Video (Blumstein and Daniel 2007). We used the PAST 3.13 software (Hammer et al. 2001) to conduct Student *t*-tests to determine whether feeding rate differed between nestlings for nests with 2 chicks and also to verify whether there was a difference in parental effort between nests with 1 and 2 nestlings.

## Results

### Breeding season

We captured and banded 350 Araripe Manakins (molecular sexing: 181 males and 169 females), 231 of which were adults and 119 of which were nestlings. Of the latter, 113 were sexed molecularly (55 females and 58 males). Adult males ( $n = 122$ ) and females ( $n = 109$ ) did not differ in mass (males:  $20.65 \pm 0.10$  g and females  $20.69 \pm 0.16$  g; Mann-Whitney  $U = 4118.5$ ,  $P = 0.86$ ). We found 190 nests (79, 81, and 30 in the 3 breeding seasons, respectively), of which 124 (65.26%) became active and 75 (39.47%) reached the

nestling stage. Among the active nests, 53 (27.89%) were unsuccessful: 10 were abandoned during the incubation period, 32 were depredated during incubation and nestling stages, 5 were lost for other reasons (rainfall, tree fall), and in 6 nests a total of 9 nestlings died in the nest, possibly from starvation.

Based on the dates of nesting activities in all 3 breeding seasons, we determined that the breeding period started on 30 October (when we found 9 nests) and ended on 4 April. The start and end dates of the incubation periods varied across seasons but they all started in November and ended in February, except for the last season, when we found a nest with eggs on 1 April, which eventually failed due to predation. We found an analogous pattern for the nestling period but the variation of the initial date was more pronounced between seasons: season 1 started on 5 December, season 2 on 24 November, and season 3 only on 29 January. However, in all 3 seasons the nestling period ended in March. The fledging period started on 5 December and ended on 27 March.

Rainfall appears to trigger the start of nest construction and also egg hatching (nestling period; Fig. 2). This was especially clear in the third season (2015/2016), when rainfall was delayed and in lower volume compared with the other 2 seasons, which resulted in a smaller number of nests being built. In the first 2 seasons, with abundant rainfall starting in October–November, the peak of the nestling period preceded the peak of rainfall (Fig. 2). This typical pattern suggests that the increase in food availability that occurs with more rain can provide nourishment for the nestlings. In the third season, however, the delay in rainfall led to nestlings hatching much later than in the preceding seasons. Based on these patterns, the species' dependence upon rainfall is very clear.

### Nests, eggs, and nestling parameters

Over the 3 seasons, we found a total of 190 nests at various stages of breeding. We monitored 54 nests discovered during the construction phase (direct observation and filming) and found that only females were involved in nest construction. The nests, built over 4 d, were open baskets placed in forked branches (Fig. 3), made of spider webs, dry leaves, and twigs. Nest average measurements



**Figure 3.** Araripe Manakin nest built in forking branches, using leaves and twigs.

( $n = 63$ ) were as follows: nest basket height =  $55.87 \pm 1.38$  mm, external diameter =  $72.62 \pm 1.10$  mm, nest basket internal depth =  $27.18 \pm 0.73$  mm, and height relative to the ground =  $1.89 \pm 0.7$  m.

For 87 different nests we were able to identify 14 support plant species belonging to 10 families. Three species had not been described previously by Linhares et al. (2010) as support plants for Araripe Manakin nests: *Cyathea microdonta*, *Inga* spp., and *Mangifera indica*. The 2 most commonly used nest support plants were *Psychotria colorata* ( $n = 13$ ) and *Hirtella glandulosa* ( $n = 10$ ). Among nests found on the plants we identified, those built on ferns (*Cyathea pungens* and *Cyathea microdonta*) had the highest loss rate due to falling, probably because of lack of structural support (10 of 16 nests).

We monitored 117 nests during the incubation period. The eggs are pear-shaped with a beige background and dark brown spots that are larger at the base of the egg (Fig. 4). Average egg measurements ( $n = 147$ ) were as follows: length =  $23.91 \pm 0.07$  mm, width =  $16.49 \pm 0.05$  mm, and mass =  $3.19 \pm 0.03$  g. Clutch size varied between 1 and 2 eggs but the majority of nests had 2 eggs ( $n = 97$ ). The period between laying of the first and second eggs was as long as 4 d, but on average the difference was 2 d ( $n = 39$ ). Only females performed egg incubation, which started only after the second egg was laid; average incubation took 19 d ( $n = 125$  nests). Sixteen females laid more than one clutch in the same breeding season in cases of predation or nest loss. The maximum number of nesting attempts in a



**Figure 4.** Araripe Manakin pear-shaped egg with a beige background and dark brown spots.

single breeding season observed for a single female was 6, but only 5 (31%) females that attempted renesting were successful.

Of the 124 nests that became active, 75 (60%) reached the nestling stage ( $n = 119$  nestlings). Of these nests where chicks hatched, 56 (74.6%) succeeded in reaching the fledging stage. The average duration of the nestling period was 16 d and nestling average measurements (at 10 d;  $n = 51$ ) were as follows: wing length =  $20.81 \pm 0.29$  mm, tarsus length =  $18.79 \pm 0.19$  mm, and mass =  $15.01 \pm 0.19$  g.

### Nest survival

With the Mayfield method (Mayfield 1975) we found that the probability of egg hatching was

56% with a predation rate of 30% across the egg-laying and incubation periods, while for the nestling period the probability of success was 72% with a predation rate of 20%. We calculated the DSR with MARK, for pooled eggs and nestlings in incubation and nestling periods, and our models show that the DSR varied between areas and across breeding seasons (Table 1). In terms of differences between areas, we found that the area “Coqueiro” presented the highest pooled daily survival rate (98%) but because the area “Grangeiro” had the highest number of nests ( $n = 62$ ) and a similar DSR for the pooled data (97% survival), we can consider “Grangeiro” as having the relatively higher nest survival. In terms of differences across seasons, we found that the first breeding season had the lowest daily survival rate (96%) but the highest number of nests ( $n = 54$ ).

For these pooled data (incubation and nestling periods), the model that included constant time ( $T_c$ ), external nest diameter (externdiam), and area (area) was the one that presented the best adjustment to the DSR and lowest  $\Delta AIC_c$ , with 26% evidence of being the best model (Table 2). Other models also presented some relevance with  $\Delta AIC_c$  values lower than 2.0, but the evidence for being good models was much lower (<14%; Table 2).

We also analyzed the incubation and nestling periods separately. We found that the model that better adjusted the DSR for the incubation period was linear time (T linear), with the lowest  $\Delta AIC_c$

**Table 1.** Pooled (eggs and nestlings) daily survival rate (DSR) for Araripe Manakin nests by field site and breeding season using constant time across 3 breeding seasons in the Araripe Plateau, Ceará, Brazil. We estimated the level of human disturbance (HD) at each field site.  $DSR^{35}$  is the daily survival rate corrected to the appropriate power from initiation to completion (19 days incubation + 16 days nestling period = 35), to determine the corrected probability of estimated survival for nests not found on the day the first egg was laid.

Variable	Size (km <sup>2</sup> )	HD	DSR	DSR <sup>35</sup>	Survival %	N nests
<b>Area</b>						
Grangeiro	0.35	Low	0.97	0.386	38.6	62
Nascente	0.25	Intermediate	0.97	0.404	40.5	17
Caiana	0.16	Low	0.96	0.314	31.5	16
Riacho do Meio	0.21	High	0.97	0.438	43.8	14
Coqueiro	0.14	Low	0.98	0.632	63.3	12
Serrano	0.16	Intermediate	0.88	0.013	1.3	3
<b>Season</b>						
2013/2014			0.96	0.33	33.2	54
2014/2015			0.97	0.47	47	39
2015/2016			0.97	0.37	37	31
Total						124

**Table 2.** Results from models selection using Akaike information criteria for small samples ( $AIC_c$ ) for daily survival rate DSR (incubation and nestlings;  $N = 47$  nests) for Araripe Manakin nests across 3 breeding seasons, in the Araripe Plateau, Ceará, Brazil. Scenarios ran with constant time (Tc), linear time (Tl), and quadratic time (Tq). Models included nest external diameter (externdiam), area sampled (area), nest height (height), and breeding season (year). Num. par. is the number of parameters used in each scenario.

Model	$AIC_c$	$\Delta AIC_c$	$AIC_c$ weight	Model likelihood	Num. par.	Deviation
{Tc + externdiam + area}	182.557	0	0.264	1	4	174.51
{Tc + externdiam}	183.871	1.314	0.136	0.51	2	179.85
{Tc + area}	184.115	1.558	0.121	0.45	3	178.09
{Tc + externdiam + height + area}	184.440	1.883	0.103	0.39	5	174.38
{T constant}	184.953	2.396	0.079	0.30	1	182.94
{Tl + externdiam}	185.784	3.226	0.052	0.19	3	179.76
{Tl + area}	185.824	3.267	0.051	0.19	4	177.78
{Tc + externdiam + height}	185.875	3.318	0.050	0.19	3	179.85
{Tc + height + area}	185.983	3.426	0.047	0.18	4	177.94
{T linear}	186.928	4.371	0.029	0.11	2	182.91
{Tc + height}	186.940	4.383	0.029	0.11	2	182.92
{Tc + year}	188.758	6.201	0.011	0.04	3	182.73
{Tl + height}	188.924	6.366	0.010	0.04	3	182.90
{Tq}	188.940	6.382	0.010	0.04	3	182.91

and strong evidence of being a good model (Table 3). The model including the co-variable external nest diameter with linear time also seems to be important for the incubation period DSR (Table 3). As for the nestling period, we found that the model including quadratic time (Tq) and area was the one with the best adjustment to the DSR, and the model including Tq, area, and external diameter was also relevant (Table 4).

We also ran scenarios for the nestling period where the co-variable area was excluded because of the differences in number of nests found in each area (see Table 1). In this scenario, the model including constant time and year was the strongest one and external nest diameter still appeared as an important co-variable when included with linear time (Tl) and year (Table 5).

**Table 3.** Results from models selection using Akaike information criteria for small samples ( $AIC_c$ ) for the incubation period daily survival rate DSR ( $N = 74$  nests) for the Araripe Manakin nests across 3 breeding seasons in the Araripe Plateau, Ceará, Brazil. Scenarios ran with linear time (Tl), Constant time (Tc), and Quadratic time (Tq). Models included nest external diameter (externdiam), area sampled (area), and breeding season (year). Num. par. is the number of parameters used in each scenario.

Model	$AIC_c$	$\Delta AIC_c$	$AIC_c$ weight	Model likelihood	Num. par.	Deviation
{T linear}	190.062	0	0.260	1	2	186.05
{T constant}	191.002	0.94	0.162	0.625	1	188.99
{T quadratic}	191.866	1.804	0.105	0.405	3	185.84
{Tl + externdiam}	191.919	1.857	0.103	0.395	3	185.89
{Tl + area}	192.350	2.288	0.083	0.318	6	180.27
{Tc + externdiam}	192.975	2.913	0.060	0.232	2	188.96
{Tq + externdiam}	193.781	3.719	0.040	0.155	4	185.74
{Tl + year}	193.997	3.935	0.036	0.139	4	185.96
{Tq + area}	194.033	3.971	0.035	0.137	7	179.93
{Tc + year}	194.047	3.985	0.035	0.136	3	188.02
{Tc + area}	194.187	4.125	0.033	0.127	5	184.13
{Tq + year}	195.719	5.657	0.015	0.059	5	185.66
{Tc + externdiam + area}	195.963	5.901	0.013	0.052	6	183.88
{Tc + externdiam + year}	195.991	5.929	0.013	0.051	4	187.95



**Table 4.** Results from models selection using Akaike information criteria for small samples ( $AIC_c$ ) for the nestling period daily survival rate DSR ( $N = 50$  nests) for the Araripe Manakin nests across 3 breeding seasons in the Araripe Plateau, Ceará, Brazil. Scenarios ran with quadratic (Tq), constant time (Tc), and linear time (Tl). Models included area sampled (area), nest external diameter (externdiam), and breeding season (year). Num. par. is the number of parameters used in each scenario.

Model	$AIC_c$	$\Delta AIC_c$	$AIC_c$ weight	Model likelihood	Num. par.	Deviation
{Tq + area}	86.990	0	0.204	1	5	76.88
{Tc + area}	88.339	1.348	0.104	0.509	3	82.29
{T quadratic}	88.422	1.432	0.100	0.488	3	82.38
{Tq + area + externdiam}	88.904	1.913	0.078	0.384	6	76.75
{Tq + area + year}	89.024	2.034	0.074	0.361	7	74.82
{Tc + area +externdiam}	89.114	2.124	0.070	0.345	4	81.04
{Tl + area}	89.151	2.160	0.069	0.339	4	81.08
{T constant}	89.724	2.733	0.052	0.254	1	87.71
{Tc + area + year}	89.981	2.991	0.045	0.224	5	79.87
{Tc + externdiam}	90.377	3.387	0.037	0.183	2	86.35
{Tq + externdiam}	90.391	3.401	0.037	0.182	4	82.32
{Tq + ano1}	90.767	3.777	0.030	0.151	5	80.66
{T linear}	90.802	3.812	0.030	0.148	2	86.78
{Tl + externdiam}	91.855	4.864	0.017	0.087	3	85.81
{Tc + externdiam + ano}	92.394	5.404	0.013	0.067	4	84.32
{Tq + year + externdiam-}	92.582	5.592	0.012	0.061	6	80.43
{Tc + year}	92.590	5.600	0.012	0.060	3	86.54
{Tl + year}	93.900	6.909	0.006	0.031	4	85.82

## Parental care

We analyzed 195 h of videos from 20 nests (12 with 2 nestlings and 8 with 1 nestling). In all nests, only females performed parental care. While on the nest, the behavior “brooding” had the longest average duration (33.87 h), although females spent 92.21 h away from the nest. We also filmed one agonistic encounter in which a brooding Araripe Manakin female was attacked by a Black-tailed Flycatcher (*Myiobius atricaudus*). We believe this resulted from resource competition since the 2 species nest at the same time and in the same areas, and their nests are frequently close to each other (MGG, pers. observ.).

We found no differences in total time invested by females for any parental care behavior for nests containing 1 ( $n = 8$ ) and 2 ( $n = 12$ ) nestlings (cleaning the nest  $t = -0.69$ ,  $P = 0.49$ ; cleaning the nestlings:  $t = -0.21$ ,  $P = 0.82$ ; watching:  $t = -0.63$ ,  $P = 0.53$ ; brooding:  $t = 0.17$ ,  $P = 0.86$ ; absent from nest:  $t = -1.5$ ,  $P = 0.13$ ). For the nests with 2 chicks ( $n = 12$ ) we also found no evidence of female preference for differential allocation of food ( $t = 0.43$ ,  $P = 0.66$ ).

## Discussion

This study provides the first breeding biology data for the critically endangered Araripe Manakin. Contrary to our expectations based on small and isolated populations (Steiffetten and Dale 2006), we found a well-balanced sex ratio for the Araripe Manakin (51.72% males and 48.28% females). Determining sex ratio for endangered species is central to future population viability analyses and conservation plans, since sex-biased populations tend to show a faster decline and require different conservation strategies (Steiffetten and Dale 2006). Nevertheless, because the species diverged recently from its sister species (Helmeted Manakin [*A. galeata*]; Luna et al. 2017) and is under great anthropic pressure, it is important to monitor sex ratio continuously, since the scenario for this bird could quickly change.

Our results show that the species has a long nesting period and low annual fecundity. We consider that this species' breeding period of at least 6 months is relatively long when compared to other manakins and Neotropical species, which on average, have breeding periods of ~3.5 months (Foster 1976, McDonald 1989, Marini 1992, Prum

**Table 5.** Results from models selection using Akaike information criteria for small samples ( $AIC_c$ ) for the nestling period daily survival rate DSR ( $N=28$  nests) for the Araripe Manakin nests across 3 breeding seasons in the Araripe Plateau, Ceará, Brazil. Scenarios ran with constant time (Tc), linear time (Tl), and quadratic time (Tq). Models included breeding season (year), nest external diameter (externdiam), and nest height (height), but excluding co-variable Area. Num. par. is the number of parameters used in each scenario.

Model	$AIC_c$	$\Delta AIC_c$	$AIC_c$ weight	Model likelihood	Num. par.	Deviation
{Tc + year}	39.461	0	0.263	1	2	35.42
{Tl + year+ externdiam + height}	40.154	0.693	0.186	0.706	5	29.95
{Tl + year+ externdiam}	40.656	1.195	0.145	0.55	4	32.52
{Tl + year}	40.867	1.406	0.130	0.495	3	34.78
{Tl + year+ height}	40.977	1.516	0.123	0.468	4	32.84
{Tc + externdiam}	43.887	4.426	0.028	0.109	2	39.84
{T linear}	43.987	4.526	0.027	0.104	2	39.94
{T constant}	44.342	4.881	0.022	0.087	1	42.32
{Tl + externdiam}	44.712	5.251	0.019	0.072	3	38.63
{Tc + externdiam + height}	45.919	6.458	0.010	0.039	3	39.83
{Tl + height}	46.006	6.545	0.01	0.037	3	39.92
{Tc + height}	46.355	6.894	0.008	0.031	2	42.31
{Tq + externdiam}	46.563	7.102	0.007	0.028	4	38.43
{Tl + height + externdiam}	46.76	7.299	0.006	0.026	4	38.62
{Tq + height}	47.028	7.567	0.006	0.022	4	38.89
{Tq + height + externdiam}	48.570	9.109	0.002	0.010	5	38.37

et al. 1996, Aleixo and Galetti 1997, Diniz et al. 2013). The nesting period (comprising incubation and nestling stages) is also longer than that of other species with open-cup nests (Ricklefs and Brawn 2013, Marques-Santos et al. 2015, Repening and Fontana 2016). Typically, prolonged nest periods have increased nest predation rates (Martin 2002, Tieleman et al. 2004, Ricklefs and Brawn 2013), which is believed to be one of the key factors that determine breeding season length (Ricklefs 1969, Skutch 1985). In the case of the Araripe Manakin, however, the relatively long nesting period is associated with a predation rate of only 25.8%, which is low compared to other Neotropical species that exhibit predation rates varying from 65% to 70% (Aguilar et al. 2000, Noske et al. 2008, Nóbrega and Pinho 2010).

Among the 14 plant species identified as nest support, 4 are known to be food sources for the Araripe Manakin (Linhares et al. 2010). We also highlight our observation that the Araripe Manakin may use the mango tree (*Magnifica indica*), an introduced species common in urban areas, as nest support. The area where nesting on a mango tree took place is one that is highly disturbed and where illegal water extraction causes enormous natural vegetation damage. Also, the nests built on fern plants had extremely high failure rates (68%),

with nest loss caused by rainfall and wind. Fern plants are very abundant within forested areas, but with fragmentation of the area (Brito et al. 2013), internal sites may be suffering from an edge effect with heavier rain and wind during the rainy season. Araripe Manakins may frequently use ferns as a nest substrate because of their proximity to watercourses, but also because the fragility of the ferns may present an obstacle for predators, even small ones such as rodents, attempting to reach the nest. Increased failure of nests built on fern species may have a relevant negative consequence for the species' success.

The field sites had different levels of fragmentation; “Grangeiro” was the largest and best conserved area, despite the presence of invasive palm trees. This possibly explains the high number of nests and captured manakins in this area. Some sites exhibited a high nest survival rate, but the number of nests found in these areas needs to be taken into account. For example, “Coqueiros” had the highest nest survival rate, but this was based upon a sample of only 12 nests. In the second semester of 2015 this field site was almost entirely destroyed by fire, resulting in a low sample size. The fire also affected “Grangeiro” and we estimate that at least 10 breeding territories were lost.

The variability in DSR between areas and seasons is a common pattern for many bird species (Moynahan et al. 2006, Manica 2008, Newmark and Stanley 2011). The main reasons for this variation are usually rainfall volume, food availability, competition, temperature changes, and natural catastrophes (Rotenberry and Wiens 1989, Donovan et al. 1997, Stutchbury and Morton 2001, Moynahan et al. 2006). We also found that nest external diameter was an important variable determining reproductive success, being positively correlated with it. Few studies have investigated the effect of avian nest size on nesting success (Caccamise 1977, Alabrudzinska et al. 2003, Hudson and Bollinger 2013), but in some cases nest size, shape, and height from the ground are important factors that influence nest survival (Møller 1989, Martin 1993, Söderström and Rydén 1998, Hansell 2000, Aguilar et al. 2008, Newmark and Stanley 2011). We believe that nest diameter is important for Araripe Manakin reproductive success because the nestlings appear to be large compared to the offspring of other manakins, such as those of the Yungas Manakin (*Chiroxiphia boliviana*; Hazlehurst and Londoño 2012). The greater diameter of the Araripe Manakin nests may protect the larger offspring during their long tenure as nestlings.

Despite previous assumptions relative to an apparent dependency of the Araripe Manakin upon watercourses for breeding (ICMBIO 2011), we found a large number of nests and breeding territories relatively far from creeks or springs and many were found at high altitudes along the slope of the Araripe Plateau. These are notable results considering possible conservation plans for the species. If nesting sites are not strictly associated with creeks, breeding areas may be larger than initially imagined. This may affect plans for defining conservation areas for the species. It is also worthwhile to point out that the presence of some specific plants most frequently used as nest support and identified in this study appear to be necessary for nest establishment.

Our study of Araripe Manakin natural history and breeding biology provides some of the basic knowledge needed for the development of more complex studies of the species' evolutionary ecology, behavior, and genetics, and positively

paves the way for conservation actions. The fact that we found many nests in areas with high anthropic influence does not mean that the species is successful in these areas, since the important point to keep in mind is the percentage of successful nests. We can conclude that human interference is one of the main survival threats for the Araripe Manakin. On the other hand, the species' persistence and its relatively high reproductive success suggest that it is resilient, which generates some optimism about its survival if the correct conservation decisions are implemented. In this regard, appropriate actions would include increased enforcement of protection in the bird's nesting areas, especially during the breeding season, as well as employing more trained firefighters to quickly and efficiently control the frequent forest fires. But most important, it is essential that the current protection status of the area along the plateau slopes (APA), which is the least protected type according to Brazilian environmental legislation, be changed to the status of National Forest, similarly to the status established for the areas at the top of the Araripe Plateau, but where the Araripe Manakin does not occur.

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