

RESEARCH ARTICLE

Breeding behavior of the Helmeted Manakin *Antilophia galeata* (Passeriformes: Pipridae) in a gallery forest from São Paulo state, Brazil

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ABSTRACT. Information on the breeding biology of most Neotropical birds, and interpopulation comparisons, are insufficient. The Helmeted Manakin, *Antilophia galeata* (Lichtenstein, 1823), is a forest understory passerine commonly found in the gallery forests of the tropical savanna-like Cerrado biome. We provide information about the nesting phenology, nesting cycle, nests, eggs, nestlings, and nest-site characteristics of a population of the Helmeted Manakin in the state of São Paulo, southeastern Brazil. During two breeding seasons we found 16 active, and 30 inactive nests. Breeding activities occurred from mid- August to mid- January, and nests were constructed in bushes and saplings in the forest's understory, 0.45–3.48 m above ground (1.56 ± 0.66 m). Clutch size was two eggs, which were laid in intervals of one to three days. Three remarkable patterns of interclutch egg color and marking variations were observed. The incubation period of two nests was 18 and 19 days, and nestling periods were 16.3 ± 0.6 days (16–17 days, $n = 3$ nests). The apparent nest survival of 11 thoroughly monitored nests was 36.4%. In addition to the first description of the interclutch egg pattern variations, the following information differs from previous literature data: egg laying interval and nestling periods. Our data contribute to the overall knowledge of the variations in breeding parameters of the Helmeted Manakin.

KEY WORDS. Breeding biology, Cerrado, Neotropics, nesting biology, reproductive behavior.

INTRODUCTION

Breeding biology parameters vary among avian populations due to their different adaptations to local environmental conditions (Lack 1947, Sanz 2008, Jahn et al. 2014). In the Nearctic region, studies on multiple populations and their associated patterns of variation have allowed the formulation of important life history hypotheses (Lack 1947, Martin 1987, 1995, 1996, 2002, Ricklefs 2000). In the Neotropics, by contrast, basic reproductive information on most taxa is lacking (Xiao et al. 2017), and comparative studies among populations are very scarce (Young 1994, Jahn et al. 2014).

Manakins (Pipridae) are commonly found in the understory of Neotropical forests (Loiselle et al. 2007, Kirwan and Green 2011, Winkler et al. 2020). These small frugivorous birds are characterized by intense sexual dimorphism, and complex pre-nuptial displays (Duval 2007, Francisco et al. 2009, Foster 1981, 1985, Loiselle et al. 2007, McDonald 1989, Ribeiro et al.

2019, Winkler et al. 2020). While males are bright colored, females are generally green. As far as known, the females are solely responsible for nest construction and parental care (Kirwan and Green 2011, Zima et al. 2017, Marçal and Lopes 2019). Although aspects of courtship display, nest and egg characteristics have been documented for most species of Manakins (Kirwan and Green 2011, Winkler et al. 2020), other reproductive parameters have been seldom addressed (for reviews see Kirwan and Green 2011, Zima et al. 2017).

The Helmeted Manakin, *Antilophia galeata* (Lichtenstein, 1823) occurs in Central and Southeastern Brazil, and western to northeast Bolivia and Paraguay (Silva 1997, Snow and de Juana 2020). It inhabits mainly the gallery forests, typical of the Cerrado biome, and also ecotonal areas between Atlantic Forest and Cerrado (Marini and Cavalcanti 1992, Silva 1997, Marçal and Lopes 2019). Their nests and eggs in Central Brazil and in the state of Minas Gerais (southeastern Brazil) were thoroughly described (Marini 1992a, Marini et al. 1997, Marçal and Lopes 2019), but

other reproductive aspects of these birds have been only recently studied in a population from an Atlantic Forest fragment in the state of Minas Gerais (Marçal and Lopes 2019). Here we provide information on the breeding biology of a population of the Helmeted Manakin monitored in an old-growth gallery forest in the state of São Paulo. Specifically, we give information on the nesting phenology, nesting cycle, eggs, nestlings, and nest-site characteristics. Some of these parameters differ from those obtained in previous studies. This information is important to gain knowledge on the ranges of variation of these parameters and to investigate the potential local adaptations of these birds.

MATERIAL AND METHODS

This study was carried out in an old-growth gallery forest, located at the campus of São Carlos Federal University, in the municipality of São Carlos, state of São Paulo, southeastern Brazil (21°58'37"S, 47°52'18"W). Gallery forests are narrow tropical forests that occur along streams within the savanna-like Cerrado Biome (Oliveira-Filho and Ratter 2002). The gallery forest where the present study was conducted varies from 44 to 120 m in width, is 2.6 km long, on both sides of a small stream that ranges from 0.5–1.0 m in width, and about 30–50 cm in depth. The local climate is Cwa according to Köppen's classification (warm climate with dry winter) (Alvares et al. 2013), with an annual average temperature of 21.5 °C and annual average rainfall of 1362 mm (Embrapa 2020). This study area is about 500 km far from the previously studied population of the Helmeted Manakin from the state of Minas Gerais (Marçal and Lopes 2019) and about 800 km from the studied population from Central Brazil (Marini 1992a, Marini et al. 1997).

We searched the entire area for nests, three to five times per week, on average every 20 days. The field work took place during two breeding seasons: from September to February in 2019/2020 and from August to January in 2020/2021. We located the nests by following the females that were carrying nesting material or food for nestlings, and by inspecting the vegetation (Martin and Geupel 1993). We checked active nests (from construction to nestling stages) every two to three days. We increased nest surveillance to daily when the females were about to lay eggs, when the eggs were about to hatch, and during the fledging stages. We measured nests and eggs using a metal caliper accurate to 0.1 mm, and the eggs were weighed using a spring scale accurate to 0.1 g (Pesola Inc.). Since birds were not banded, it is possible that some of the monitored nests belonged to a same female. The incubation period was determined from the first day of incubation until the day the first egg hatched. The nestling period started on the day the first egg hatched and ended with the first bird fledging (Ferreira and Lopes 2018). Clutch sizes were determined only from nests found during the incubation stage. The nests were filmed during the incubation and nestling stages using a handheld camera (GoPro Hero 5 black), attached to branches at 1.5–3.0 m from the nests to document parental care.

For nest-site characterization, we measured nest height above the ground; the diameter of the main trunk of the plant supporting the nest at its mean portion (i.e. plants that were 1.0 m in height had the diameter measured at 0.5 m above ground), and the diameter of the branch supporting the nest just before the bifurcation at which the nest was attached. The diameter of the main trunk of the supporting plant was measured at its mean portion because many plants used for nest construction were shorter than 1.3 m, where diameter at breast height, for instance, is often measured. A measuring tape and a metal caliper accurate to 0.1 mm were used to collect the data and the values were presented as means \pm standard deviations. We collected biometric data from the nests in their egg-laying, egg incubation, and nestling stages, and also from inactive nests that seemed ready and had no signs of deterioration. Inactive nests with loose or shattered materials were not considered. The Helmeted Manakin was the only Pipridae occurring in the study area, and in this site their nests were clearly distinguishable from those of other passerines based on size, shape, nest attachment mode and the use of dry leaves on the outer nest walls. Nest misidentification, therefore, is unlikely. Nest predation was considered when eggs or nestlings disappeared from nests before fledging age. Due to small sample size, nest survival was estimated by apparent survival, i.e. the simple percentage of nests with eggs or nestlings that survived to the fledging stage.

RESULTS

During the two reproductive seasons, we recorded 46 nests, 16 of which were active (those in construction, laying, incubation, or nestling stages), and were 30 inactive. The earliest active nest was found on August 31, 2020, with two eggs already in the incubation stage. The latest active nest was observed on January 10, 2021 and it contained two nestlings in the middle of their development. These nestlings were not monitored. If they succeeded, they would likely have fledged in mid- January. The breeding season lasted approximately from mid- August to mid- January.

As previously described, the nests were rim-supported, and were constructed on horizontal forks or on horizontal parallel branches of bushes and saplings at the gallery forest's understory. They were 0.45–3.48 m above ground (1.56 ± 0.66 m), on supporting plants with the main trunk varying from 8–26 mm (15.98 ± 5 mm) in diameter. In the case of nests built on forks (93.5% of the nests), the diameter of the supporting branch at the base of the fork varied from 4.10–17 mm (6.55 ± 2.38 mm) ($n = 43$ nests). Nests were 53.0 ± 7.0 mm in inner diameter (39.2 – 82.4); 68.4 ± 7.7 mm in outer diameter (55.7 – 88.2); 31.7 ± 6.4 mm in depth (23.0 – 50.0); and 48.9 ± 10.9 mm in height (27.6 – 72.6) ($n = 36$ nests).

The clutch size was always two eggs ($n = 7$ nests). Individual eggs were 23.4 ± 0.8 mm long (22.3 – 24.4 , $n = 7$) and 16.5 ± 0.2 mm wide (16.1 – 16.6 , $n = 7$), and they weighted 3.2 ± 0.2 g

(3.1–3.5, $n = 6$). We verified at least three clearly diagnosable egg color patterns: white background color with mostly longitudinal dark brown streaks and blotches, slightly concentrated at the larger end ($n = 3$ nests) (Fig. 1); eggs with pale beige background, densely marked with darker ochraceous pale spots and blotches almost homogeneously distributed across egg surface ($n = 2$ nests) (Fig. 2), and eggs with pinkish background color and pinkish-brown blotches and streaks forming a crown near the wide end ($n = 2$ nests) (Fig. 3). We also observed that eggs varied in shape, from short oval ($n = 2$ nests) to long oval ($n = 5$ nests). The second egg was laid 48 ($n = 1$ nest) and 72 hours after the first egg ($n = 1$ nest), and incubation started on the morning the second egg was laid ($n = 2$ nests). Incubation periods in two nests were 18 and 19 days.

Hatching was synchronous in three nests and in one nest the eggs hatched within one day interval. Hatchlings had dark-red skin and were covered by dark-gray down (Fig. 4). The lining of their mouths was bright-yellow and their rictal flanges were whitish (Fig. 5). All successful nests fledged two young ($n = 4$). In three nests fledging was synchronous, and in only one case fledging occurred during two consecutive days. Nestling periods lasted from 16 to 17 days (16.3 ± 0.6 days, $n = 3$ nests) (Figs 4–8).

Two filming sessions performed on two nests during the early and mid- incubation stages (103 and 64 min) confirmed that only females incubated the eggs, and they spent about

83.5% and 75% of the time on it, respectively. Three filming sessions at three nests at their mid- nestling stage (109, 49, and 60 min) also registered that only the females fed the nestlings, at an average rate of 5.2 times per hour (See also Martin et al. 2000).

Of the 16 active nests, three were abandoned in the late construction stage, and of the 13 nests containing eggs or young, 11 had their fate recorded: contents of one nest (eggs) fell down after a heavy storm; in one nest the nestlings were found dead without signs of depredation with a five-day interval between deaths; five nests were depredated, and four nests fledged young successively. The apparent nest survival of the 11 nests containing eggs or young was 36.4%.

DISCUSSION

This study adds information on the breeding biology of the Helmeted Manakin. A set of the reproductive parameters in our data differs from previous studies. Our main findings include a noticeable pattern of interclutch egg color variations; divergences in the time between laying the first and the second egg, and variations in the nestling periods.

Among the passerines, intraspecific variations in egg color and markings can occur both within and between clutches (Oien et al. 1995, Cassey et al. 2009, Poláček et al. 2017). The consistent interclutch variations, and the consequent intraclutch homogeni-



Figures 1–8. Egg color patterns, hatchlings and nestlings of the Helmeted Manakin, *Antilophia galeata*, in different developmental stages observed in a gallery forest from southeastern Brazil: (1) eggs with light background color and streaks distributed throughout their surfaces; (2) eggs with pale beige background and blotches; (3) eggs with reddish-brown blotches and scratches forming a crown; (4) hatchlings; (5) three days old nestlings evidencing the bright-yellow mouth lining; (6) seven days old nestlings; (7) 10 ten days old nestlings; (8) nestling in the day before fledging.

zation observed for the Helmeted Manakin is intriguing because the hypotheses previously proposed to account for this type of polymorphism in other birds does not seem to apply here. One hypothesis predicts that interclutch egg color variation signals female quality to males. This may be true when the male is involved in parental care (Moreno and Osorno 2003, Cassey et al. 2009). However, in Manakins, only females construct the nests and provide parental care, making this hypothesis unlikely. Alternatively, it has been hypothesized that traits that help egg identification may allow females to discriminate and to eject eggs laid by inter- or intraspecific brood parasites (Brown and Sherman 1989, Oien et al. 1995 Kilner 2006). Based on its geographic distribution, broods of the Helmeted Manakin could be potentially parasitized by the Pavonine Cuckoo *Dromococcyx pavoninus* Pelzeln, 1870, the Striped Cuckoo *Tapera naevia* (Linnaeus, 1766), and by the Shiny-cowbird *Molothrus bonariensis* (Gmelin, 1789). The Pavonine Cuckoo and the Striped Cuckoo can enter gallery forests, while the Shiny Cowbird is an open area species. Regardless, the eggs of these parasites are clearly distinguishable from those of the Helmeted Manakin (see for instance Salvador 1982, Gloag et al. 2014, Sanchez-Martínez et al. 2017), and cases of interspecific parasitism have not been observed in the current or previous studies (Marini 1992a, Marini et al. 1997, Lowther 2019 Marçal and Lopes 2019). The hypothesis that the observed variations could provide females with the capacity to recognize intraspecific parasitic eggs also seems implausible because direct evidence of intraspecific parasitism has not been observed for the Helmeted Manakin, i.e. the existence of clutches with an excessive number of eggs (three or more eggs), or laying of more than one egg on the same day (see for instance Davanço et al. 2013). Although the latter hypothesis could not be totally discarded without the use of DNA-based parentage analyses involving females and their broods, to our knowledge, clutches of three or more eggs were never reported for any Pipridae. In at least one nest photographed in Minas Gerais (see Marçal and Lopes 2019), slight variations in the densities of markings were observed between the two eggs of a clutch, although they were similar in their background colors and in the shapes and colors of their markings. We are unaware if constant interclutch egg color variations could occur across all Helmeted Manakin populations. It is possible that variations in the nutritional state of females or their ages (see also Siefferman et al. 2006) caused the interclutch differences in egg patterns we observed.

While in a previously studied population of the Helmeted Manakin from Minas Gerais, eggs in a clutch were laid on consecutive days ($n = 9$ nests) (Marçal and Lopes 2019), our observations differed in that eggs were laid in two- to three-day intervals ($n = 2$ nests). The eggs of the congener Araripe Manakin, *A. bockermanni* Coelho & Silva, 1998 are laid within two to four days intervals (Gaiotti et al. 2019), and in the closely-related Blue Manakin, *Chiroxiphia caudata* (Shaw & Nodder, 1793), intrapopulation variations could be observed, with eggs laid on consecutive days ($n = 2$ nests) or with a one-day gap ($n = 3$) (Zima et al. 2017). A hypothesis proposed to account

for egg-laying gaps before clutch completion is related to food limitation; i.e., individuals or populations with nutritional constraints would take longer to produce subsequent eggs (Wiebe and Martin 1995). The Helmeted Manakin is highly frugivorous (Marini 1992b). The nestlings eat fruits and arthropods (Marini 1992a, Marçal and Lopes 2019). Fruits consumed by piprids are scarcer during the dry season (here, the non-reproductive season) at least in a disturbed forest fragment from Colombia (Morales-Betancourt et al. 2012). It is possible that egg laying gaps observed in the above mentioned Manakin species is a response to food availability, and the female nutritional constraint hypothesis should be tested in future contributions. We also do not discard the possibility that the death of the nestlings from one nest without depredation marks could have been caused by food scarcity, especially because this nest was active in August, early in the breeding season.

The nestling period of 16–17 days in our data is similar to that of the Araripe Manakin (16 days) (Gaiotti et al. 2019); of the Blue Manakin (15–16 days) (Zima et al. 2017), and of the Pale-bellied Tyrant-manakin, *Neopelma pallescens* (Lafresnaye, 1853) (15 days) (Ferreira and Lopes 2018), while nestling periods of 17–19 days observed in another population of the Helmeted Manakin from Minas Gerais state (Marçal and Lopes 2019) were longer in relation to these, and to other eight Manakin species reviewed in Zima et al. (2017). Hypotheses trying to explain intraspecific differences in the nestling period involve food availability and predation risks, with nestling periods tending to be longer in areas where there is food shortage, due to slower growth rates of the nestlings (Martin 1987), or lower predation pressures (reviewed in Martin 2002).

Many other parameters matched the findings of previous studies, including the approximately five-month long breeding season, nest and nest site parameters, clutch sizes of two eggs, nest construction in bushes or saplings in forest understory, egg incubation and nestling provisioning provided only by the females, and nestling characteristics (Marini 1992a, Marini et al. 1997, Marçal and Lopes 2019). A number of the nests in this study were built near the ground (some nests as close as 0.45 m to the ground). Although one nest reported by Marini (1992a) for Central Brazil was 0.5 m above ground, in other studies nests were observed at least 1.15 m above ground (Marini et al. 1997, Marçal and Lopes 2019).

Our data improved the understanding about the ranges of variation of a few reproductive parameters of the Helmeted Manakin. It emphasizes the need for studies across multiple populations (see also Young 1994, Jahn et al. 2014), which in turn will guide the tests of current, and new hypotheses related to interpopulation breeding adaptations.

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