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NESTING BIOLOGY OF THE GOLDEN-WINGED MANAKIN (*MASIUS CHRYSOPTERUS*), WITH A REVIEW OF NESTING TRAITS FOR LOWLAND AND HIGHLAND SPECIES OF PIPRIDAE

Jhan C. Salazar[1, 2] · Gustavo A. Londoño[2]

[1] Department of Biology and Biomedical Sciences, Washington University, St. Louis, MO 63110, USA

[2] Departamento de Ciencias Biológicas, Facultad de Ciencias Naturales, Universidad Icesi, Cali, Valle del Cauca 76000, Colombia

E-mail: Jhan C. Salazar · jhancsalazar@wustl.edu

Abstract · Complete nesting information is available for only 4 out of 52 species of manakins (Pipridae), and most nesting information regards lowland species. Much less is known about the nesting of highland manakin species. Our study presents nesting information on a highland cloud forest manakin species, the Golden-winged Manakin (*Masius chrysopterus*), which is distributed from western Colombia to northern Peru between 1,000 and 2,300 m a.s.l. We monitored 10 nests from February through July in 2014 and 2015 at Parque Nacional Natural Tatamá, Colombia. We describe the nest, eggs, and nestlings of *M. chrysopterus*, and provide information on adult behavior by means of thermal sensors and a GoPro camera. The cup nest was similar to those of most manakins. Eggs were cream-colored with brown spots and measured 18.7 ± 0.89 mm x 13.3 ± 0.39 mm (mean ± SD; N = 16 eggs). The nestling growth rate (*K*) was 0.34 (N = 6 nestlings). The incubation and nestling periods were 22 and 16 days, respectively. Females alone were responsible for incubation, with on-bouts of 19.9 ± 16.0 min (N = 774 on-bouts) and nest attentiveness of 69.8 to 73.5% during daytime hours (N = 3). They conducted 69.7 ± 16.8 off-bout trips per day that lasted, on average, 8.3 ± 5.4 min (N = 805 off-bouts without nighttime incubation). During 63 min of video taken at one nest during the nestling period, the female delivered red, green, and black fruits into the bill of the nestling, and swallowed three fecal sacs. Overall, *M. chrysopterus* incubation and nestling period are longer when compared to other manakin species, but the nest structure and composition, as well as egg coloration, are similar to other species that inhabit lowlands and highlands.

Resumen · Biología de la anidación en el saltarín alidorado (*Masius chrysopterus*), con una revisión de los rasgos de anidación de las especies de pípridos de alta y baja montaña
Hay información completa de anidación está disponible para 4 de las 52 especies de la familia Pipridae. Sin embargo, la mayor parte de esta información se refiere a especies de tierras bajas, y sabemos mucho menos sobre anidación de las especies de pípridos de las tierras altas. Nuestro estudio presenta información de anidación en una especie de píprido de bosque nublado, el saltarín alidorado (*Masius chrysopterus*), que se distribuye desde el oeste de Colombia hasta el norte de Perú entre los 1.000 y 2.300 m s.n.m. Monitoreamos 10 nidos, de febrero a julio de 2014 y 2015, en el Parque Nacional Natural Tatamá, Colombia. Describimos el nido, los huevos y los pichones de *M. chrysopterus*, y proporcionamos información sobre el comportamiento del adulto con el uso de sensores térmico y una cámara GoPro. El nido en copa fue similar a los encontrados en la mayoría de las especies de esta familia. Los huevos fueron de color crema, con manchas marrones concentradas en la base del huevo, y midieron 18,70 ± 0,89 mm x 13,30 ± 0,39 mm (media ± DE; N = 16 huevos). La tasa de crecimiento de los pichones (*K*) fue de 0,34 (N = 6 polluelos). Los períodos de incubación y anidación fueron de 22 y 16 días, respectivamente. Solo las hembras fueron encargadas del cuidado parental; con una duración promedio de viaje de 19.9 ± 16.0 min (N = 774 viajes), y con una atención al nido que variable entre 69.8 y 73.5% durante las horas del día (N = 3 nidos). Las hembras realizaron en promedio 69,7 ± 16,8 viajes fuera del nido por día, los cuales duraban 8,3 ± 5,4 min (N = 805 estadías en el nido sin incluir la anidación nocturna). Durante 63 minutos de grabación de video del nido durante el periodo de polluelos, se vio que la hembra alimentaba a los polluelos con frutos rojos, verdes y negros y se tragó tres sacos fecales. En general, los períodos de incubación y cría de *M. chrysopterus* son más largos en comparación con otras especies de pípridos. Pero la estructura y composición del nido, y la coloración de los huevos son muy similares a los de otras especiesde esta familia que habitan en las tierras bajas y altas.

Key words: Egg · Fledging · Incubation · Nest · Nestling · Pipridae

INTRODUCTION

The Neotropical manakin family Pipridae includes 17 genera and 52 species that inhabit humid tropical and subtropical forests, with approximately 43 species in lowlands (<1,500 m a.s.l.) and nine species occurring on mountains above 1,500 m a.s.l. (Kirwan & Green 2011; Supplementary Table 1). Manakins are mainly frugivorous, occasionally eating small arthropods. A remarkable characteristic of this family is the strong sexual dimorphism: males are flashy and colorful, while females are rather cryptic (Snow 2004). Most prior research effort has focused on lowland species' mating strategies associated with the "lek"

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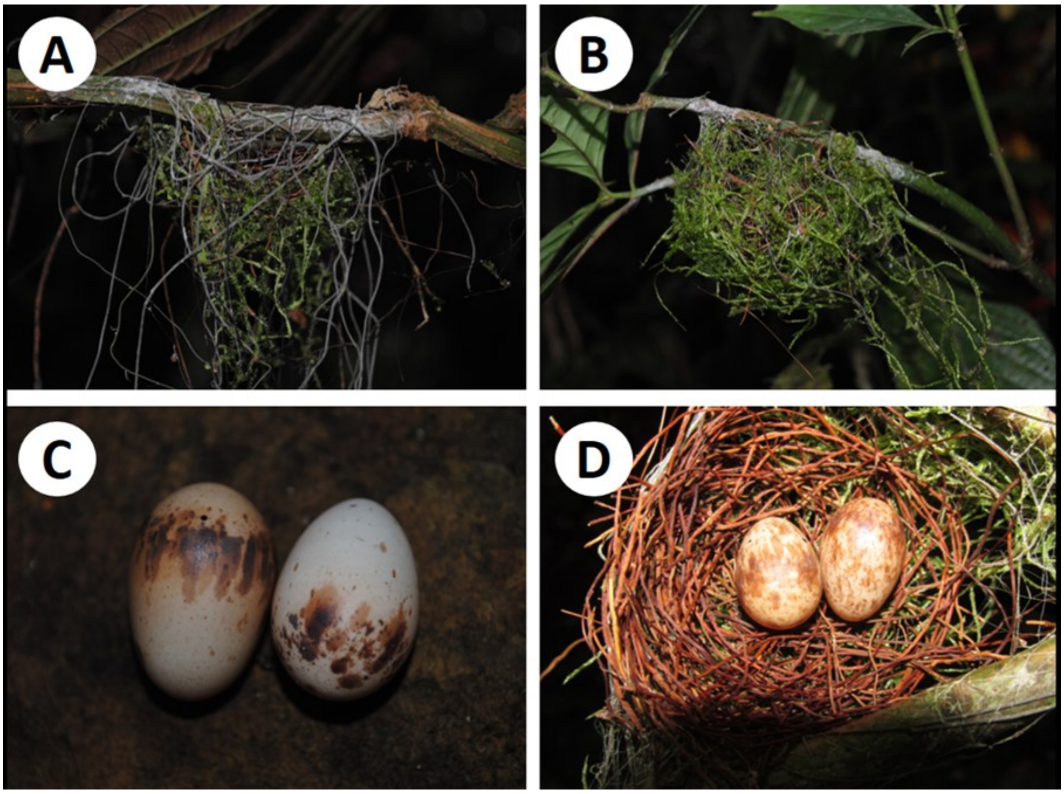

Figure 1. Nest and eggs of the Golden-winged Manakin (*Masius chrysopterus*). Side view of two nests with A) abundant rootlets on the exterior, and B) abundant moss on the exterior. C) Creamy eggs with brown spots concentrated at the broader end. D) Upper view of the nest with two eggs.

system (e.g., Durães et al. 2009, DuVal 2007, Kirwan & Green 2011); however, little is known about female behavior during the nesting period, when she has all reproductive responsibilities. Limited information on nesting is available for some species of Pipridae (Supplementary Tables 1, 2, 3 and 4 and references therein). Nevertheless, length of the incubation and nestling periods, as well as nest attentiveness, remain unknown for seven of the nine highland species of Pipridae (Supplementary Tables 3 and 4). Clearly, there is a substantial gap in our knowledge of the basic life history details of highland manakin species, which is important because patterns of natural history change with elevation (Johnson et al. 2006, Boyle et al. 2016) and can inform how rising temperatures will affect the distribution and life history of highland birds (Chamberlain et al. 2012, Boyle et al. 2016, Rocchia et al. 2018).

Our study aims to report a detailed account of the nesting biology and behavior of a highland manakin, the Golden–winged Manakin (*Masius chrysopterus*). *Masius* is a monospecific genus that dwells from western Colombia to northern Perú (Hilty & Brown 1986). The overall distribution of this species ranges from 400 to 2300 m a.s.l. (Stotz et al. 1996, Ridgely & Greenfield 2001, Restall et al. 2006, Kirwan & Green 2011). In Colombia, *M. chrysopterus* is found on the Pacific slope of the western Andes from 600 to 2,300 m a.s.l., usually inhabiting wet mountain forests and forest borders in the subtropical zone and foothills (Hilty & Brown 1986).

To date, limited nesting information is available for *M. chrysopterus*; Hilty and Brown (1986) described a single, thin-walled rootlet moss cup nest suspended from a horizontal fork 2.3 m above a stream on 22 June (year not reported) at Anchicayá, Valle del Cauca, Colombia. Information about the eggs is likewise sparse; Greeney & Gelis (2007) and Solano-Ugalde et al. (2007) reported that *M. Chrysopterus* has a clutch size of two eggs, which can be pale to dark olive-tan, with heavy brown blotching forming a ring around the larger end, or pale salmon with red-brown blotches thickest around the larger end. Hilty & Brown (1986) reported that the eggs they found in late June in Anchicayá Valley, Colombia, were cream-colored with brown markings concentrated at the larger end. Greeney & Gelis (2007) reported egg and nest measurements of four nests in the Mushullacta reserve in northeast Ecuador between 31 March and 11 April 2005. Solano-Ugalde et al. (2007) found a single active nest in Mindo, Pichinchá province, in the northwest of the same country on 28 January 2003. Beyond these brief accounts –nest material and egg measurements–, no further information has been available. Greeney & Gelis (2007) described four nests located within 40 m of streams as "shallow, sparse rootlet cups, bound together to the substrate with spider webs, and lightly decorated on the exterior and rim with pale green moss that dangled below the cup rim forming a 'tail' which helped obscure the nests' outline". Solano-Ugalde et al. (2007) described the nest as a "sparse, dark fiber cup sparsely decorated with moss which trailed 6.5 cm below the nest, with some thin strands hanging as far as 10.5 cm below." They did not report the nest location.

Based on 10 nests monitored at Parque Nacional Natural (PNN) Tatamá, Risaralda, Colombia, we provide detailed information on incubation period and incubation behaviors (eight nests), nestling period and nestling measurements (two nests), and feeding of nestlings (one nest).

METHODS

Study area. This study was conducted at the Montezuma peak, located in Parque Nacional Natural Tatamá, Pueblo Rico, Risaralda, Colombia (5°13'47.96"N, 76°5'1.51"W), at

Figure 2. Golden-winged Manakin (*Masius chrysopterus*) nestling development. A) One-day old nestling. B) Three-day old nestling; pin feathers emerging. C) Six-day old nestling; eyes opening. D) Twelve-day old nestling (age estimated); open eyes and feathers emerged.

the intersection of the Chocó, Risaralda, and Valle del Cauca departments in Western Colombia. The Park has 519 km^2 of protected land, from lowland rainforest up to *páramo*. Our study area covered an elevation gradient between 1,200 – 2,300 m a.s.l., with a mean daily temperature of 17 °C (min – max = 11.1 – 24.6 °C; Ballesteros et al. 2005). The mean annual rainfall in the park is 1,963 mm. The driest months are January and July, and the rainiest months are May and November (Ballesteros et al. 2005, Coca et al. 2012).

Nest searching and measurements. We collected data from February through July 2014 and 2015. Seven to 12 volunteers conducted daily nest searches from 07:00 h to 16:00 h six days a week in fixed plots, located at different elevations on the Montezuma peak. The plot sizes varied between 10 and 30 hectares.

We followed the method developed by Fierro-Calderón et al. (2021) for collecting data for Neotropical species. When eggs were found, the volunteers recorded their length, width, and mass. The incubation period was determined only from nests found with an incomplete clutch. Hence, we calculated the incubation period from the day the last egg was laid until the day the last egg hatched (Fierro-Calderón et al. 2021). Similarly, the nestling period began when the last egg hatched and continued until the last nestling left the nest (Fierro-Calderón et al. 2021). To monitor incubation behavior, the volunteers placed in three nest two thermal sensors attached to a U12 4-channel Hobo data logger, programmed to collect data every minute (Onset Computer Corporation, http://www.onsetcomp.com, Cape Cod, Massachusetts, USA). One sensor was installed inside the nest, under the eggs, to record nest temperature, and the other was located approximately 10 cm from the nest to record ambient temperature. The sensor in the nest was used to follow incubation behavior and the external sensor was used as a reference temperature to evaluate environmental temperature fluctuations. We analyzed these data following Cooper & Mills' (2005) protocol, considering an increase or decrease in nest temperature of at least 1.5°C as indicative of the beginning of an on- or off-bout, respectively. From day 13 to 15 of incubation, only one nest was monitored, as the other two were depredated. Volunteers visited the nest every five to six days during the incubation period, and on a daily basis when hatching was expecting to occur (Fierro-Calderón et al. 2021).

Nestling mass, tarsus, wing, and bill length were measured every other day by the volunteers that found the nest (Fierro-Calderón et al. 2021). Nestling morphological appearance was recorded every other day (Fierro-Calderón et al. 2021). We recorded feeding behavior of one nestling at a single nest with a GoPro camera on 22 May 2014, between 06:50 h and 07:53 h. We measured nests, eggs, and nestlings using a caliper with an accuracy of 0.01 mm, and a digital FlipScale (F2, Phoenix, AZ, USA) with an accuracy of 0.05 g. We compared the size of a nestling that was near fledging with that of adult males measured in Dr. Gustavo Londoño's project between 2015 and 2016.

Data analysis. To examine variation in the number of trips (off-bouts) and attentiveness across the incubation period, we used linear regressions in R v.3.2.2 (R Development Core Team, 2015). We used mass, wing chord, beak, and tarsus measurements to calculate nestling growth rates using the logistic equation (Ricklefs 1967):

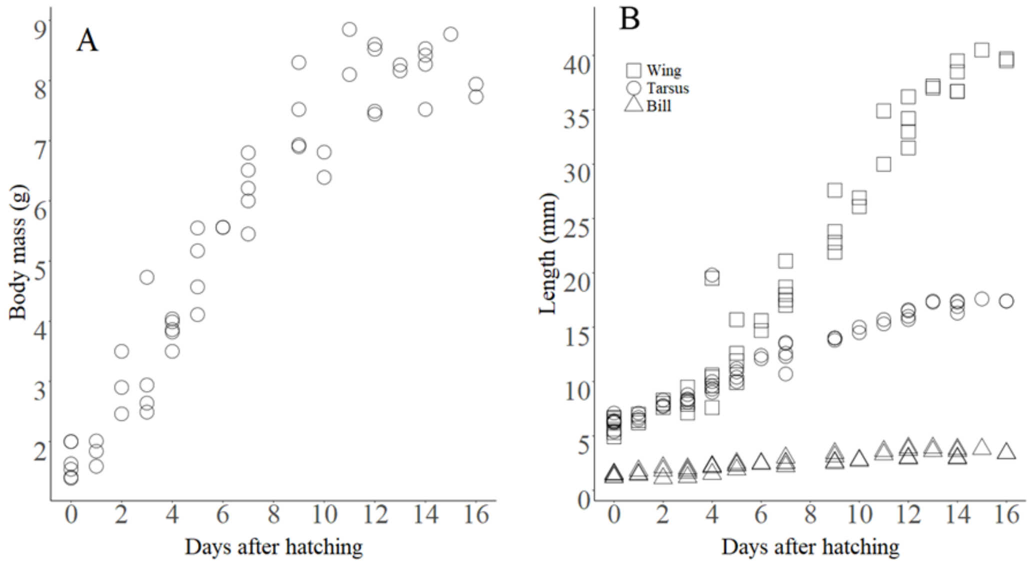

Figure 3. Nestling measurements from day 1 to 16, based on six nestlings from five nests of the Golden–winged Manakin (*Masius chrysopterus*) monitored at PNN Tatamá between 2014 and 2015. A) Mass. B) Wing, tarsus, and bill length.

$$W(t) = A / \{1 + e^{([-K(t - t_i)])}\}$$

Where W (t) is mass, wing chord, beak, or tarsus length at age t, A is the asymptote of the growth curve, K is a constant scaling rate of growth, t_i is the inflection point of the logistic, and e is the base natural logarithm. We applied the code proposed by Sofaer et al. (2013) using R v.3.2.2 (R Development Core Team, 2015), which included the used of the R package *nlme* (Pinheiro et al. 2021) to fit and compare different models of growth rate. We used nest ID as a random effect because nests were monitored by different people and there might have been small differences in the way the nestlings were measured. The figures were made with the package *ggplot2*, version 2.1.0 (Wickham 2009). All temperature, mass, and length measurements are reported as mean ± SD.

RESULTS

We found and monitored 10 nests of *M. chrysopterus* from March to June in 2014 and 2015, but most of them were found in March (N = 3, all of them found with eggs) and April (N = 3, two with eggs and one with nestlings). Of the 10 nests found, six were predated (one with eggs and five with nestlings), two were abandoned (both with eggs), and two were successful. Nests were placed between 1,367 and 1,629 m a.s.l. Measurements were based on all 10 nests unless otherwise noted. Eight nests were placed between two horizontal branches in shrubs, but the location varied widely: three were located at road edges, two near streams and three in primary forest. The other two nests were found in the forest, but we do not have notes on exact nest placement or location.

The incubation period lasted from 22 to 23 days (N = 2) and the nestling period lasted from 16 to 17 days (N = 2). At one nest, incubation period was calculated from the onset of incubation (25 March) until the hatching of the first egg (17 April, i.e., 23 days). The nest was predated afterwards. At another nest, the incubation period started on 25 March and finished on 16 April; thus, the incubation period lasted approximately 22 days. The nestling period of *M. chrysopterus*, obtained from two successful nests, was 16 to 17 days. In the first nest, the nestling period was calculated from the date the nest was found with newly hatched chicks (17 April) until they fledged (3 May, i.e., 16 days). In the second nest, the chicks hatched on 16 May, and fledged on 2 June (i.e., 17 days). The nests were small cups located 2.17 ± 0.49 m above ground. Overall, nest wet mass averaged 1.67 ± 0.90 g (range = 0.59 – 3.09, N = 10). The inner layer of the nest was made of dark brown plant fibers, roots, and moss, and its mass averaged 0.74 ± 0.62 g (range = 0.31 – 2.12, N = 7. For three of the bigger nests, we do not have inner layer weight). The outer layer weighed 0.67 ± 0.58 g (range = 0.19 – 1.86, N = 7. For three of the bigger nests, we do not have outer layer weight) and was made of dark brown rootlets, with spider webs that were used to attach the nests to the supporting branches. Two of the nests had long rootlets that gave the impression of material hanging from the outer surface. Internally, the nests averaged 55.0 ± 4.0 mm x 53.9 ± 5.0 and wall thickness averaged 7.2 ± 4.4 mm, while the inner cup depth was 18.4 ± 3.3 mm. Externally, the nest measured 62.1 ± 7.8 x 58.0 ± 8.3 x 26.4 ± 13.5 mm (length, width, and height; Figure 1).

The eggs of *M. chrysopterus* were cream-colored, with brown spots concentrated near the air-cell end, forming a "ring" at the larger end (Figure 1). Clutch size was consistently two eggs in all nests. The eggs measured 18.70 ± 0.89 mm x 13.30 ± 0.39 mm and weighed 1.73 ± 0.20 g (N = 16). Upon hatching (day zero), the nestling skin was pink, the belly orange, the mandible orange, and the maxilla dark gray. The eyes were closed. On day two, the pinfeathers began to emerge on the wings. On day six, pinfeathers were present on the belly, back, and wings, and the eyes began to open. On day seven, the pinfeathers on the back started to unsheathe. On day 13, the eyes were open, and the nestlings were halfway to being fully feathered on the wings and back (Figure 2). On day 16, the nestlings were almost fully feathered, and the eyes were completely open. On day 16, the last day the nestlings were in the nest, the nestlings' measure-

Figure 4. Incubating female of *Masius chrysopterus*. In the background, the red and black thermal sensors used to measure the temperature of the nest and the environment can be seen. Picture by Jhan C. Salazar.

ments (N = 1) were: mass 7.84 g (vs. adult mass: 11.53 ± 4.69 g, N = 29), wing length 39.6 mm (adult wing length: 58.02 ± 1.46 mm, N = 36), and tarsus 17.4 mm (adult tarsus length: 17.22 ± 1.77 mm, N = 32).

The growth rates were: K_{mass} = 0.34 (95% confidence interval = 0.30 - 0.38), asymptote = 8.37 ± 0.33 g (Figure 3A); $K_{wing\ length}$ = 0.21 (0.16 - 0.27), asymptote = 48.81 ± 1.40 mm (Figure 3B); and $K_{tarsus\ length}$ = 0.18 (0.16 - 0.20), asymptote = 18.07 ± 1.52 mm (Figure 3B). In one of the nests, a nestling of unknown age was parasitized by *Philornis* sp. flies (Figure 2D).

We monitored the incubation rhythm at three nests for 15 days (360 hours). Only the female incubated and provided nestling care (Figure 4). We present data only for the daytime period. The earliest off-bouts in the morning started between 05:31 h and 06:19 h, and the female returned to nonstop nocturnal incubation between 15:24 h and 18:37 h. Nocturnal incubation lasted from 10 hours and 21 minutes to 12 hours 25 minutes (N = 3). At one nest, for 11 days, the female incubated the eggs during 73.5 ± 2.3 % of the daytime, with on-bouts of 14.6 ± 11.0 min (range = 1 – 62 min) and 35.8 ± 8.1 off-bout trips/day. When the female returned to the nest, the temperature increased from 22.9 ± 3.0 °C to 28.2 ± 3.0 °C (range = 16.4 – 37.1 °C). At a second nest, during eight days, the female incubated the eggs during 68.3 ± 5.7 % of the daytime, with on-bouts of 22.5 ± 13.3 min (range = 2 – 76 min) and 22.9 ± 4.2 off-bout trips/day. When the female returned to the nest, the temperature increased from 25.5 ± 4.3 °C to 36.1 ± 1.7 °C (range = 16.8 – 42.3 °C). At a third and last nest, for 14 days the female incubated the eggs during 69.8 ± 4.5 % of the daytime, with on-bouts 28.3 ± 20.1 min (range = 1 – 135 min) and 17.7 ± 3.2 off-bout trips/day. The nest temperature increased from 26.0 ± 2.0 °C to 32.4 ± 1.7 °C (range = 18.9 – 35.3 °C) when that female returned to the nest. We found no evident pattern in the number of trips the female made during the day as the incubation period progressed. Similarly, no consistent change in nest attentiveness occurred throughout the incubation period. Based on a single video-monitored nest during the nestling period, we observed four feeding trips in 63 minutes on 22 May 2014 (between 6:50 h and 07:53 h). The female delivered red, green, and black fruits into the bill of the 7-day old nestling and swallowed three fecal sacs.

DISCUSSION

We provide the first detailed nesting biology account for a cloud forest (highland) manakin species, *M. chrysopterus*. Below we compare our findings with related lowland and highland species based on the phylogenetic tree proposed by McKay et al. (2010) and Ohlson et al. (2013).

Our breeding season observations of *M. chrysopterus* are in agreement with prior research indicating that the species initiates breeding at the beginning of, or during the wet season (Hilty & Brown 1986, Stiles & Skutch 1989, Snow 2004, Kirwan & Green 2011). Overall, manakins that breed south of the equator lay eggs between August and February (Velho 1932, de la Peña 1989), and those north of the equator between March and August (Hellebrekers 1945, Skutch 1969, Wetmore 1972, Foster 1976, Hilty & Brown 1986, Snow 2004, Kirwan & Green 2011). These differences in breeding seasons are associated with latitudinal differences that coincide with the beginning of the rainy season north and south of the Equator.

The 10 nests of *M. chrysopterus* were 18.2 % larger in internal diameter than the three nests reported by Greeney

& Gelis (2007; Mushullacta, Ecuador, 1,150 m a.s.l.) for the same species. The nests found by Greeney & Gelis (2007) were 26.4% deeper and 4.5% wider than the nests we found, while the nests we found were 16.7% higher above ground. The nests described by Hilty & Brown (1986), Greeney & Gelis (2007) and Solano-Ugalde et al. (2007) are similar to the ones we described; they were also found in horizontal forks frequently near streams, with spiderwebs present on the tree branches where the nest was attached. The *M. chrysopterus* nests we found were located 6 m lower than a nest of the White-throated Manakin (*Corapipo gutturalis*; 8.30 m, Kirwan & Green 2011), the most closely related species to *M. chrysopterus* with nest information. The nest materials were similar for both species: mosses on the outside with a thin layer of black fungal rhizomorphs in the inner cup (Kirwan & Green 2011).

In our study, *M. chrysopterus* laid two cream-colored eggs with brown spots, similar to the egg coloration described by Hilty & Brown (1986), Greeney & Gelis (2007) and Solano-Ugalde et al. (2007) for the same species (cream-colored eggs with dark spots forming a ring around the larger end) and also similar to other lowland and highland manakin species (Hilty & Brown 1986, Stiles & Skutch 1989, Snow 2004, Kirwan & Green 2011). The egg size of *M. chrysopterus* in our study (18.7 ± 0.89 mm x 13.3 ± 0.39 mm, N = 16) was smaller than the egg size reported by Greeney & Gelis (2007) (20.8 ± 0.8 mm x 14.5 ± 0.4 mm, N = 5) for the same species in Mushullacta, Ecuador. We observed that eggs of lowland species were 12% and 13% larger in length and width, respectively, compared to the eggs of *M. chrysopterus* (see *Chiroxiphia lanceolata*, *Ceratopipra erythrocephala*, *Manacus manacus, Chiroxiphia linearis, Lepidothrix coronata* and *Machaeropterus regulus* in Supplementary Table 3).

The 22-day incubation period of *M. chrysopterus* is 18% (four days) longer than the average 18 days (range = 15 – 21 days) reported for lowland manakin species (see *Manacus vitellinus*, *M. aurantiacus*, *M. manacus, Pipra erythrocephala, Lepidothrix coronata, M. aurantiacus*, *Chiroxiphia pareola*, *Ceratopipra mentalis* and *Chiroxiphia lanceolata* in Supplementary Table 3). Similarly, the 16-day nestling period of *M. chrysopterus* was 12.5% (2 days) longer than the average 14 day nestling periods found in lowland species (range = 12 – 16 days; *Manacus vitellinus, M. aurantiacus*, *M. manacus*, *Pipra erythrocephala*, *P. rubrocapilla, Lepidothrix coronata, Chiroxiphia pareola*, *Ceratopipra mentalis* and *Chiroxiphia lanceolata* in Supplementary Table 3). Lower ambient temperatures at higher elevation in tropical mountains may slow growth and development (compared to tropical lowlands) (Williams 2012, Nord & Williams 2015).

Our research goal was to provide novel nesting information for a highland manakin, improving our understanding of avian neotropical nesting ecology and behavior of piprids. Although we show that there is important variation in nesting traits among manakin species, this is just a glimpse of the variation in manakins' nesting strategies, as there are several species for which nesting information remains unknown.

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