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ORIGINAL ARTICLE



A NEST OF CLUB-WINGED MANAKIN *MACHAEROPTERUS DELICIOSUS* IN NORTHWEST ECUADOR

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Abstract • The Club-winged Manakin *Machaeropterus deliciosus* is an iconic Pipridae species due to its display behavior that includes unique mechanical sounds produced by vibrating modified wing feathers of one wing against the other wing's feathers. However, its nesting biology remains poorly known. In this note, we present a detailed description of one nest studied in northwest Ecuador in June–July 2021. We also provide new information on incubation behavior and maternal care. The nest was a low cup/fork sited on three forks, covered extensively with moss, built 90 cm above the ground and 50 m in linear distance from a lekking site. The female had a high percentage of nest attentiveness during the incubation period. Still, brood attentiveness decreased markedly in the first nine days after hatching, when female visits to the nest were short provisioning bouts from the nest rim. The nest produced two juveniles that fledged 16 days after hatching. Several aspects of the breeding biology of this species remain poorly studied, so we recommend further research, including more protracted monitoring of additional nests to understand better important aspects of *M. deliciosus* breeding biology, including incubation period, attendance rates, and nesting success.

Resumen · Un nido del Saltarín Alitorcido Machaeropterus deliciosus en el noroeste de Ecuador

El Saltarín Alitorcido *Machaeropterus deliciosus* es una especie emblemática de Pipridae por su comportamiento de despliegue, que incluye sonidos mecánicos únicos entre las aves producidos por la vibración de plumas alares modificadas de un ala contra las plumas del ala contraria. Sin embargo, el conocimiento sobre su nidificación es escaso. En este trabajo presentamos una descripción detallada de un nido estudiado en el noroeste de Ecuador, entre junio y julio 2021. Además, presentamos nueva información sobre el comportamiento de incubación y cuidado maternal. El nido era una taza baja apoyada en la bifurcación de tres ramitas, recubierto extensamente con musgos, colocado a 90 cm del suelo, y a 50 m en línea recta de un área de lek. La hembra presentó un alto porcentaje de atención al nido durante la incubación, pero la atención durante el empollamiento disminuyó marcadamente los nueve primeros días después de la eclosión, cuando las visitas de la hembra consistieron solo de breves turnos de provisión desde el borde del nido. La nidada fue de dos volantones que salieron del nido 16 días después de la eclosión. Varios aspectos de la biología reproductiva permanecen poco documentados en esta especie, por lo que sugerimos mayor investigación, incluyendo el seguimiento de más nidos para comprender mejor aspectos importantes de la biología reproductiva de *M. deliciosus* incluyendo el periodo de incubación, atención al nido y éxito de nidada.

Key words: Andes · breeding · materials · nest attentiveness · nesting · Pipridae · reproduction.

INTRODUCTION

Manakins are an extraordinary group of birds and ideal study systems for understanding the evolution of sexual selection (Prum 2019). Complex courtship displays are present in nearly two-thirds of the currently recognized taxa (Kirwan & Green 2011), which also show marked sexual dimorphism (i.e., males exhibiting bright colors, females clad in dull green tones). Males of several species are remarkably adapted to produce mechanical sounds by vibrating and slapping wing feathers (Prum 1998, Bostwick et al. 2010), whereas females alone build nests, incubate and raise their offspring.

In the Club-winged Manakin *Machaeropterus deliciosus*, a species confined to wet foothill and subtropical forests in western Colombia and western Ecuador (Kirwan & Green 2011), males produce an electronic, ringing 'whistle' while quivering the clubbed feathers of one wing against those in the other wing (Bostwick 2000). Its courtship display was first studied by Bostwick (2000), who described it as unique in a family full of peculiar display behaviors. Yet, several aspects of *M. deliciosus* breeding biol-



ogy remain poorly studied, including nesting biology, mechanisms of mate choice by females, mating success by displaying males, and the environmental factors that influence courtship and breeding activity (i.e., weather, resource availability, habitat structure).

Despite the species 'popularity' in courtship research, only a few nests have been described, most from anecdotic observations (Willis 1966, Ramírez-González & Arias-García 1995, Greeney et al. 2020). Nest placement, materials used, and shape generally resemble those of congeners, being small compact cups built in small treelets (Kirwan & Green 2011). However, further research might reveal specific features of *M. deliciosus* nesting ecology (Salazar & Londoño 2022). In this note, we provide details of a nest studied in northwest Ecuador, including information on incubation behavior and nestling period not previously available for the species (Salazar & Londoño 2022), aiming to contribute to knowledge about *M. deliciosus* breeding biology.

METHODS

One nest was monitored from 18 June through 18 July 2021. It was discovered when HB accidentally flushed an incubating female from the nest while patrolling forest trails at Reserva Mindo Lindo (0°01'25''S, 78°46'7''W; 1660 m a.s.l.), Pichincha prov., northwest Ecuador. Mindo Lindo is a 7-ha reserve dominated by old secondary cloud forest, at 1500–1660 m a.s.l., characterized by dense understory, heavy epiphyte, and moss

load, and a regular daily presence of fog. Afterwards, the nest was briefly visited once a day for 20 days to monitor female activity and nest contents by direct and brief (less than 2 min) observations. A camera trap (Plotwatcher Pro) was set up on 22 June 2021 and removed on 18 July 2021, when the nest was found empty. The camera took one photo every 1 min for 12 h/day, with a 1.5 h break at midday. Images were examined using Deep Meerkat (Weinstein 2018) and VLC software. For each photo, we determined whether the female was present at the nest. We calculated the length of each incubation bout (in minutes) by adding the number of consecutive photos with a female in the nest (during the incubation period). Nest attentiveness (covering the incubation and nestling periods) was estimated each day as the percentage of photos in which the female was at the nest.

The nest was collected 12 days after it was found empty and was later disassembled to classify material. Measurements of the nest, nest substrate, and nesting place were taken with a plastic ruler and a measuring tape. Since the nest was already partially destroyed and detached when collected, materials were not weighed or measured individually.

RESULTS

Nest. The nest was placed 90 cm above the ground in a 121 cm tall treelet in the Rubiaceae family, next to a seldom-used trail (Figure 1A, D). It was supported by three thin branches that formed a fork off the main stem of the treelet (i.e., sited



Figure 1. Nest of Club-winged Manakin *Machaeropterus deliciosus* in northwest Ecuador, June-July 2021. A) Nest placement in a Rubiaceae treelet (18 June 2021; Heike Brieschke); B) Female incubating two eggs (18 June 2021; Heike Brieschke); C) Eggs, 3 days after nest discovery (Heike Brieschke) and D) 8 days after discovery (J. Freile); E) Two nestlings 14 days after hatching (16 July 2021; Heike Brieschke).

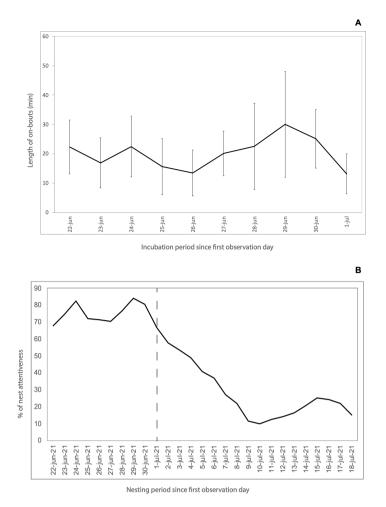


Figure 2. Mean length of on-bouts during incubation (A) and percentage of nest and brood attentiveness (B) during a 12-h diurnal monitoring period each day by a nesting female Club-winged Manakin *Machaeropterus deliciosus* in northwest Ecuador, June–July 2021. 2A, the bars indicate standard deviation and 2B, the dashed vertical line indicates hatching day.

on the branches), but also supported from the rim by at least one horizontal branch (i.e., suspended), had little foliage cover from the frontal and upper sides, but was partially covered by the treelet's leaves from the rear sides (as seen from the trail) (Figure 1B, D). It was a small, nearly rounded, and fairly deep cup (low cup/fork *fide* Simon & Pacheco 2005) that measured 7.5 cm (external cup diameter), 3 cm (cup depth), and 8.5 cm (external height, excluding tail of hanging vegetation).

The nest base was built with at least seven different types of thin, dry vegetal fibers. Shorter pieces formed the central portion of the nest base, from where longer strips of the same fibers were intertwined to form the lower inner portion of the cup. These fibers included dry brownish moss, very thin, strong, black rhizomorphs, brownish grass-like fibers, smaller vegetal pieces, and shorter fibers. The cup walls and base were internally constructed with long moss strips tightly interwoven, with small and thin brownish sticks and thin pieces of dark bark supporting the mossy structure from the inside. Externally, the cup base and walls had long pale brownish fibers. Long moss strips were used to attach the nest to branches. Externally, the nest was covered mainly in fresh green moss that provided camouflage; moss fibers were shorter than those in the inner structure, but were also tightly interwoven, and some longer moss fibers hung from the nest giving it a mossclump appearance. Scarce spiderweb was found inside the nest structure.

Incubation. When first found on 18 June 2021, the nest contained two whitish eggs heavily blotched and speckled dull brown, mostly forming a ring near the larger end (Figure 1C). They measured c. 2 x 1.5 cm. The female alone incubated the eggs for 14 days since nest discovery. Incubation bouts varied during the study period (Figure 2A). On 22 June, incubation bouts ranged from 8–42 min (mean = 22, SD = 9 min, N = 12), whereas on 29 June, incubation bouts ranged from 6–64 min (mean = 30, SD = 18 min, N = 12). Given that our estimates are based on photographs taken every 60 seconds, not continuous video footage, these figures must be taken cautiously. Daily nest attentiveness during incubation ranged from 67.6–84.1% (mean = 75.5%, SD = 5.7, N = 9) (Fig. 2B).

While incubating, the female remained seated but actively peered from side to side (Figure 1B). Most of the time, she faced the more open side of the nest (nest 'entrance'), switching position on only ten occasions during the entire incubation period. She occasionally raised her body to inspect the eggs or clean the nest. From 26–27 June onwards, the female more actively inspected the nest from the rim or while incubating the eggs by briefly raising her body. During two c. 150-min rainy periods, she remained on the nest 140 and 142 min.

On 1 July, at about 16:30 h–17:30 h, one egg hatched and at 8:00 h on 2 July a second nestling was noticed. Incubation lasted c. 14–15 days.

Maternal care and fledging. The female brooded and provisioned two nestlings, which fledged at 16 days. Brood attentiveness decreased notably for the first nine days and experienced a slight increase for the next five days (Fig. 2B). It ranged from 10–66.6% (mean = 29.1%, SD = 17.4, N = 18). We did not calculate brooding rhythms because 1-min photos failed to detect shorter provisioning visits that might have occurred (see Discussion).

The first 5–6 days since hatching, the female provisioned her nestlings from the nest rim in brief turns, after which she entered the nest to brood on most visits. Feeding was likely done only by regurgitation given that no prey or fruit item was observed in the female's bill. The number of short (less than 1 min) visits in which she did not enter the nest increased from days 3–4 since hatching. By day 7, nestlings more actively begged for food when the female arrived at the nest rim, and visits were shorter, with fewer and shorter brooding bouts and repeated short provisioning visits. By day 10, nestlings were very active and vigorous; female visits were primarily to provision food from the nest rim, and by day 15 nestlings even received food at the nest rim itself. We failed to observe if the female removed fecal sacs or swallowed them.

Nestlings had closed eyes, dark mouse grey down, and no feather sheaths by day four since hatching. On day seven, they still had closed eyes but were large enough to prevent the female from accommodating her body over them. On day eight since hatching, eyes remained closed, but the first feathers were emerging from sheaths in the dorsal tract. On day 11, both nestlings occupied the entire nest cup and had olive green feathers covering their dorsal parts; wing feather sheaths were emerging, but the head was still covered in down; eyes were open. By day 15, nestlings were largely covered in olive green feathers in the dorsal parts and pale yellowish in the belly, but downy feathers were still present on the head and back; wings had almost fully-grown feathers.

Nestlings raised their bodies and moved at the nest cup by days 12–13; on day 14 they both stood up at the rim, and on day 15 they even leaped to the nest rim, where they remained for several minutes (Figure 1E). On the morning of day 16, since hatching, nestlings were very active from 6:20 h. By 7:04 h, one nestling perched on the nest rim leaped around for 5 min and abandoned the nest from its frontal side. The second nestling abandoned the nest cup in the opposite direction one minute later.

DISCUSSION

Previous descriptions of nests of *M. deliciosus* generally match with the nest we studied in terms of habitat (fairly open understory of humid to very humid forest), substrate plants (small treelets), and measurements, but Willis (1966) and Kirwan & Green (2011) report that nests were located very close or within a lekking area. During our visits to the nest, we did not observe or hear displaying males near the nest, but a lekking area is located c. 50-m in straight line from the nest (HB, pers. observ.).

Nest building materials have not been previously described in detail, but dark-brown rhizomorphs are reported in the inner structure and copious green moss on the outside (Ramírez-González & Arias-García 1995, Kirwan & Green 2011). We provide the first detailed description of materials used in the inner structure and those used to intertwine the nest, whose shape was similar to previous descriptions. As reported by Kirwan & Green (2011), our nest was rather bulky, and contra Willis (1966), it was not a pensile cup, but was supported from below by three horizontal branches, and at the nest rim level by attachment to another branch, similar to 13 nests described by Ramírez-González & Arias-García (1995).

Clutch size and egg color are similar to the only available descriptions (Willis 1966; Ramírez-González & Arias-García 1995), whereas the nestling period, described for the first time for *M. deliciosus*, is longer than in most lowland species, as occurs in another wet montane forest species, *Masius chrysopterus* (Salazar & Londoño 2022), and might be explained by lower temperatures that may slow nestlings' growth (Williams 2012). We could not determine the incubation period because the nest already contained two eggs when found. The 14 days of incubation we observed is certainly incomplete, given that all manakin species for which incubation periods are known have longer periods, especially those occurring in montane habitats (Salazar & Londoño 2022).

General nest structure, shape, materials, placement, habitat, egg coloration, and clutch size resemble those of other Pipridae species (Kirwan & Green 2011, Salazar & Londoño 2022). Despite these general similarities in nesting characteristics, some peculiarities might deserve further discussion. For example, nests of the phylogenetically closest genera Dixiphia, Ceratopipra, and Pipra are shallower cups constructed of dead leaves or other brownish to yellow vegetal fibers, with less abundant moss on the outside (Hidalgo et al. 2008). These authors found one out of 76 nests studied of P. filicauda with heavy moss cover, whereas nests of the less related genus Lepidothrix resemble our M. deliciosus nest in being fairly deep, with green moss covering the outer rim and often hanging below the nest (Kirwan & Green 2011). The prevalence of moss in our nest could be a consequence of moss abundance in the cloud forest occupied by M. deliciosus. Likewise, moss is reported as regular or infrequent nest material in unrelated genera including Masius, Neopelma, Manacus, and Chiroxiphia (Salazar & Londoño 2022). Nest material choice in manakins could be related to material availability.

Nests of *Dixiphia* and *Ceratopipra* often incorporate a 'tail' of vegetal material under the nest, resembling the hanging material found in our *M. deliciosus* nest. Further, *Ceratopipra* species place their nests at higher heights than those reported for *M. deliciosus*, including the nest we studied, whereas *Dixiphia* nests are placed in areas with denser understory and at higher heights (Hidalgo et al. 2008). Whether nest construction and placement vary according to habitat or phylogenetic relatedness deserves further investigation.

Our nest had a slightly larger external diameter than *M. striolatus* nests, but resembled those in cup depth and in the 'tail' of hanging material under the nest (Durães et al. 2008). Further, the nest we studied was placed at a higher height than the mean height for eight *M. striolatus* nests (Durães et al. 2008), but in similar habitat: fairly open understory. Al-

though we did not measure the distance to the substrate plant stem, it also qualitatively resembled the mean distance reported for *M. striolatus*. A succinct description of female behavior in the nest provided by these authors is also similar to our observations. Breeding information on other *Machaeropterus* species is very scarce, precluding a more thorough comparison within the genus, but similarities in nest materials and placements between *M. striolatus* and *M. pyrocephalus* (Salazar & Londoño 2022) might indicate their closer relationship within the genus *Machaeropterus*.

There is apparently intrageneric variation in manakin nests' placement, with descriptions that include sited on, slung between, placed in, hanging in, or attached to branches (Salazar & Londoño 2022). For example, nests of Heterocercus are described as attached to a supporting branch (Álvarez Alonso 2001) or hanging in a descending fork (Prum et al. 1996). Nests of Machaeropterus are described as suspended in a fork for M. striolatus and M. pyrocephalus (Durães et al. 2008, Salazar & Londoño 2022), but as sited on a fork for M. deliciosus (Ramírez-González & Arias-García 1995; this study). Although these differences might have ecological or evolutionary implications, there is an apparent lack of rigor to describe manakin nest placement that halts any further analysis until more systematic information is gathered (Fierro-Calderón et al. 2021). The pensile cup described by Willis (1966) might be explained by conceptual differences in defining a pensile cup.

Although based on a single nest, the incubation rhythm we monitored generally recalled that of the montane *Masius chrysopterus* (Salazar & Londoño 2022). Nest attentiveness was within the range of other small tropical birds, including *Ceratopipra mentalis* (Tieleman et al. 2004), and brood attentiveness decreased as nestlings aged. The apparent increase in attentiveness during the provisioning period might reflect more frequent feeding bouts, not necessarily more time in the nest. We suggest video monitoring or radio-frequency identification (see Fierro-Calderón et al. 2021) to monitor brooding attentiveness more accurately.

Data scarcity precludes further comparisons of incubation and nestling attendance, but the female M. deliciosus we studied resembled other manakin females in her confidence at the nest (Kirwan & Green 2011). The fact that female manakins are reluctant to leave their nests even when approached by a potential predator or nest destroyer is likely a defense strategy to prevent revealing their fairly exposed and 'easy to reach' nests, given that nest depredation rates are reportedly high to very high (Hidalgo et al. 2008; Ryder et al. 2008, Ferreira & Lopes 2018, Salazar & Londoño 2022). Greeney (2006) even reports successful defense of Lepidothrix coronata against a potential nest predator. Manakin nests are apparently seldom abandoned, but nest and fledgling success is still low (Salazar & Londoño 2022). The female we studied produced two successful fledglings, but high depredation rates in M. deliciosus cannot be discarded.

Further nest descriptions and thorough monitoring of nesting will provide crucial information to fully understand the breeding biology of one of the most fascinating manakin species (Prum 2019). The relative abundance of *M. deliciosus* in suitable habitats (Stevens et al. 2021) offers promising opportunities for future study.

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