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Nest design and parental care of Striped Woodhaunter *Automolus subulatus*

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Summary.—The western and trans-Andean populations of Striped Woodhaunter *Automolus subulatus* are sometimes considered separate species. We discuss previously published data on the nesting of Striped Woodhaunter and present novel information concerning the nest, eggs, nestlings and parental care of western *A. s virgatus* and trans-Andean *A. s. subulatus*. Nest placement and architecture of the two populations are similar to each other and to other *Automolus* species. However, Striped Woodhaunter build shorter nest tunnels than other related species and genera. All similarities in nest design, nestbuilding behaviour and parental care presented herein support the genetic clade including *Automolus*, *Thripadectes* and *Clibanornis*, but do not differentiate between the subspecies of Striped Woodhaunter. More studies are required about adult attendance and nest design within this clade, taking into account more samples across the species' range.

The systematics of the non-monophyletic genus *Automolus* (Furnariidae: Philydorini) are still under scrutiny (Claramunt *et al*. 2013, Schultz *et al*. 2017). The most recent changes that have gained acceptance are the subsuming of *Hyloctistes* within *Automolus* (Claramunt *et al*. 2013) and the splits of Pará Foliage-gleaner *A. paraensis* from Olive-blacked Foliage-gleaner *A. infuscatus* (Claramunt *et al*. 2013, Clements *et al*. 2019) and Chiriquí Foliage-gleaner *A. exsertus* from Buff-throated Foliage-gleaner *A ochrolaemus* (Freeman & Montgomery 2017, Chesser *et al*. 2018). Like other furnariids (Irestedt *et al*. 2006), nesting behaviour and nest architecture of *Automolus* spp. may prove useful for testing DNA-based taxonomic arrangements. However, the nesting biology of *Automolus* species is well known only for Chiriquí Foliage-gleaner (Skutch 1952, 1969) and White-eyed Foliage-gleaner *A. leucophthalmus* (Euler 1900, J. C. R. Magalhães *in* Remsen 2003a, Marini *et al*. 2007, Cockle & Bodrati 2017) but poorly known or unpublished for the other seven species (Remsen 2003a).

Striped Woodhaunter *A. subulatus* is distributed from eastern Nicaragua south to western Ecuador and, east of the Andes, from southern Venezuela and south-east Colombia to northern Bolivia and western Amazonian Brazil (Stiles & Skutch 1995, Remsen 2003a). Some authors treat western and trans-Andean populations as separate species, Western Woodhaunter *A. virgatus* and Amazonian Woodhaunter *A. subulatus* (Ridgely & Greenfield 2001, Hilty 2003, del Hoyo & Collar 2016) based largely on vocal differences (Ridgely & Tudor 1994, Freeman & Montgomery 2017). This split is considered premature by other authorities (see Remsen 2003b) and herein we follow Clements *et al*. (2019). Here we discuss and clarify published data on the nesting of Striped Woodhaunter and present novel information concerning the nests, eggs, nestlings and parental care for two subspecies, *A. s. virgatus* and *A. s. subulatus*.

Historical data for A. s. subulatus and A. s. assimilis.—The first published nest description attributed to Striped Woodhaunter was presented by Sclater & Salvin (1873). They quoted the notes of E. Bartlett, which accompanied a specimen of *A. subulatus* collected at Chamicuros, Loreto, eastern Peru (05°30'S, 75°30'W, *sensu* Stephens & Traylor

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TABLE 1

Monitoring dates, localities, nest contents and main observations of Striped Woodhaunter *Automolus subulatus* nests found in western Colombia (nest 1; Zyskowski & Prum 1999, Hilty 2003; K. J. Zyskowski *in litt*. 2018), in central-west Costa Rica (nest 2) and in eastern Ecuador (nests 3–7).

Nest	Date found	Days monitored	Location/elevation	Coordinates	Nest contents	Observations
1	15 Feb 1976		San Isidro, Buenaventura, dpto. Valle del Cauca, Colombia	03°27′0″N 77°10′0″W	2 nestlings	Nestlings more than half-grown
2	19 Dec 2002		Finca Rafiki Safari Lounge, Santo Domingo, Perez Zeledón, prov. San José, Costa Rica; 130 m	09°27′41″N 83°59′39″W	1 egg	Egg: 28.1 × 21.0 mm
3	15 May 2004	15–20 May 2004 and 25 Jun 2004	Near La Selva Jungle Lodge, *c*.75 km north-east of Coca, adjacent to Lake Garzacocha, prov. Sucumbíos, Ecuador; 250 m	00°29′53″S 76°22′23″W	2 fresh eggs	Eggs: 24.2 × 17.2 and 22.8 × 17.1 mm. Adult behaviour documented on video.
4	17 Feb 2012	17, 20, 25 Feb 2012	Cabañas Yankuam, south of río Pastaza, south (right) bank of río Nangaritza, prov. Zamora-Chinchipe, Ecuador; 1,100 m	04°15′0″S 78°39′30″W	empty	Burrow excavation.
5	26 Sep 2012	26 Sep 2012	Boanamo, near the prov. Pastaza/Orellana border, Ecuador; 230 m	01°15′45″S 76°22′54″W	2 eggs (1 inviable*)	Eggs: 24.2 × 17.8 and 23.7 × 17.9* mm; mass: 3.8 and 3.5 g.
6	5 Mar 2013	5, 7, 8, 10 Mar 2013	Gareno Lodge, south of río Napo, prov. Napo, Ecuador; 400 m	01°01′59″S 77°23′42″W	empty	Nest cup construction. Adult behaviour documented on video.
7	6 Mar 2013	7, 10 Mar 2013	Gareno Lodge, south of río Napo, prov. Napo, Ecuador; 400 m	01°02′01″S 77°23′15″W	2 eggs, 1 hatched	Eggs: 25.4 × 18.5 and 25.4 × 18.5 mm; mass: 4.2 and 4.3 g. Nestling mass: 4.7 g. Adult behaviour documented on video.

1983). However, the description, of a cup nest built 2–3 m above ground among dead palm fronds and holding two spotted eggs, is clearly in error, as first noted by Zyskowski & Prum (1999). The last-named authors provided the only other published information on the nest architecture of Striped Woodhaunter, including a photograph, based on a nest collected by N. Wheelwright in western Colombia (nest 1; Table 1). This nest was described as a platform-like cup of loosely interlaced leaf petioles placed at the end of an earth tunnel, and the photograph revealed two nestlings probably less than half-grown at the time of discovery (Zyskowski & Prum 1999). K. Zyskowski (*in litt*. 2018) kindly provided additional details (Table 1) on this nest which, based on its locality, is attributable to *A. s. assimilis*.

Nest and egg of A. s. virgatus.—We examined a nest of *A. s. virgatus* collected by J. E. Sánchez & E. M. Carman at Finca Rafiki Safari Lounge, Costa Rica (nest 2; Table 1), and deposited at the Museo Nacional de Costa Rica, San José (MNCR-ONH772). Sánchez *et al*. (2004) provided a habitat description for the locality. Nest 2 was collected from a burrow excavated in a dirt bank adjacent to a forest trail (cavity with tunnel, *sensu* Simon & Pacheco 2005), with an expanded inner chamber at the end of a tunnel. The nest itself was a shallow, platform-like cup composed entirely of loosely interwoven leaf rachises (Fig. 1A). We detected both leaflet scars and extra-floral nectaries on most of the rachises, suggesting that they were probably from a plant in the family Fabaceae. No additional details concerning the burrow are provided on the specimen label, but we were able to measure the nest platform (Table 2; on Fig. 2, see measurements 10–15). A single, unmarked white egg

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Figure 1. (A) Nest of Striped Woodhaunter *Automolus subulatus virgatus*, collected at Finca Rafiki, Santo Domingo, Perez Zeledón, San José Province, Costa Rica (nest 2) (© Alberto Pérez). (B) Immaculate white egg found in the nest (Karla Conejo-Barboza)

accompanied the nest (MZUCR-H205; Table 1; Fig. 1B) but the specimen label provides no details regarding clutch size or egg development. The size of the hole opened in the egg, however, suggested that it may have contained a well-developed embryo when collected.

Nests of A. s. subulatus.—HFG studied five nests of *A. s. subulatus* found between 2004 and 2013 at four localities in eastern Ecuador (Table 1): near La Selva Jungle Lodge (nest 3; Fig. 3A), Cabañas Yankuam (nest 4), Boanamo (nest 5; Fig. 3B–C) and Gareno Lodge (nests 6–7; Fig. 3D). Habitat was similar at all four localities, all representing mosaics typical of relatively undisturbed western Amazonian forest (see Greeney 2017, Greeney *et al*. 2018 for detailed descriptions). HFG visited the nests periodically to ascertain their status and contents. He checked nest contents either directly or using a small lighted mirror, and made direct observations of adult behaviours. When possible to document nest attendance by adults, he filmed nest activity at nests 3, 6 and 7 (Table 1) by placing a video camera on a tripod 1.5 m tall, 3 m from the nest entrance. Due to its position the video camera could not film activity within the inner chamber. Behaviour of the adults appeared to be unaffected by the presence of the camera.

All Ecuadorian nests were sited in earth burrows (cavity with tunnel, *sensu* Simon & Pacheco 2005) as described for *assimilis* and *virgatus* with entrances at a mean height of 124 cm (range = 60–230 cm; SD = 63.5 cm; Table 2) above ground (Fig. 2, measure 1). Nest 3 was in the root mass of an overturned *Cecropia* tree (Urticaceae), nest 4 was in a 1.5 m-tall bank with a 60 cm overhang along a road-cut, nest 5 was in streamside bank below an overhang of dirt and roots, and the other two nests were in the large (*c*.3 m tall) root masses of trees felled by wind action. The burrows' entrances led to tunnels that varied in slope from downward at a *c*.30º angle (nest 3) to sloping slightly upward, and opened into enlarged chambers containing the nest (nests 6 and 7). Nest cups of *A. s. subulatus* were platform-like structures of loosely arranged, stiff, unbranched leaf rachises that were barely sufficiently cohesive to remain intact when removed from the burrow. In the case of nest 5 (Fig. 3B), all rachises appeared to be from the same species of plant, but the taxonomic affinities of the nest materials were not examined closely at the other nests.

Measurements of *A. s. subulatus* burrows (Table 2; Fig. 2, measurements 2–9) were: entrance height = 7.1 cm (6.0–8.5 cm; SD = 1.1 cm; *n* = 4) and entrance max. diameter = 9.1 cm (8–11 cm; SD = 1.3 cm; *n* = 4); min. tunnel height = 5 cm (*n* = 1); tunnel width = 8.5 cm (7–10 cm; SD = 2.1 cm; *n* = 2); tunnel length (from entrance lip to start of inner chamber) =

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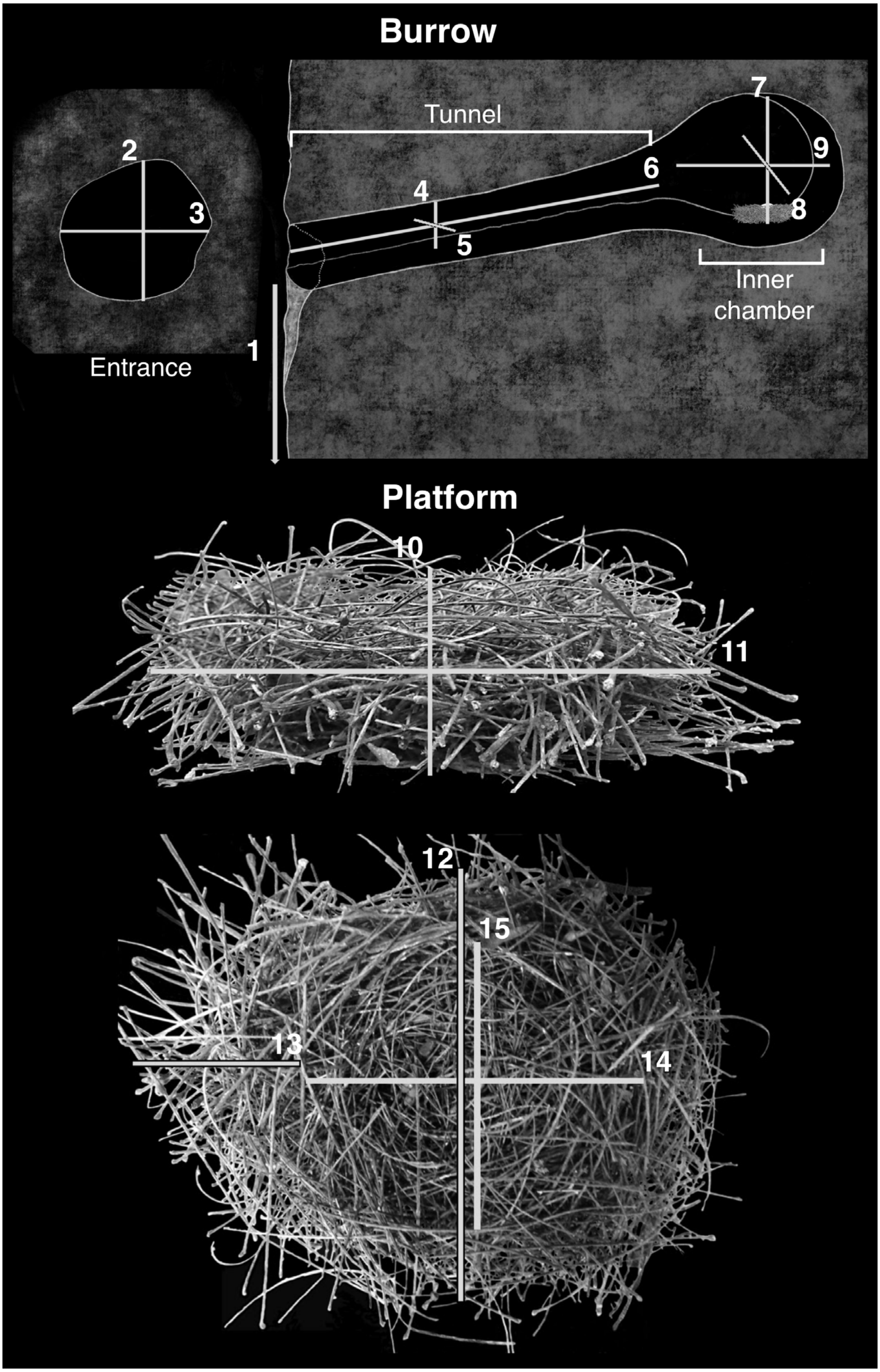

Figure 2. From top to bottom: schematic internal view of the burrow of a nest of Striped Woodhaunter *Automolus s. subulatus*, based on those found in eastern Ecuador (nests 3 and 5) and, a lateral and superior view of the platform nest of *A. s. virgatus* collected in central-west Costa Rica (nest 2). As in Table 2, numbers correspond to burrow height (1), entrance height (2), entrance max. diameter (3), tunnel height (4), tunnel max. diameter (5), tunnel length (6), inner chamber height (7), inner chamber max. diameter (8), inner chamber min. diameter (9), platform height (10), external max. diameter (11), external min. diameter (12), wall thickness (13), internal max. diameter (14), internal min. diameter (15) (Karla Conejo-Barboza)

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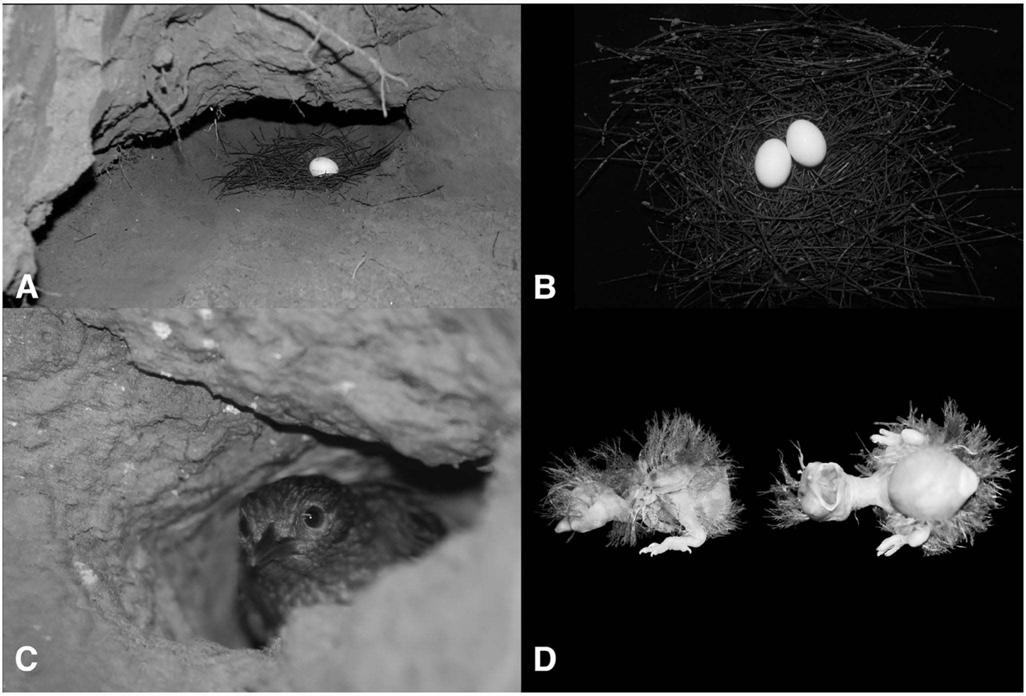

Figure 3. (A) Inner chamber and nest platform of Striped Woodhaunter *Automolus s. subulatus*, found near La Selva Jungle Lodge, *c.*75 km north-east of Coca, adjacent to Lake Garzacocha, Sucumbíos province, Ecuador (nest 3). (B) Nest platform, eggs and (C) an adult Striped Woodhaunter *A. s. subulatus*, found at Boanamo, near the Pastaza and Orellana province border, Ecuador (nest 5). (D) Chicks of Striped Woodhaunter *A. s. subulatus*, found in a nest at Gareno Lodge, south of the río Napo, Napo province, Ecuador (nest 7) (Harold F. Greeney)

26.3 cm (20–31 cm; SD = 5.2 cm; *n* = 4). Inner chamber height = 11 cm (10–12 cm; SD = 1.4 cm; *n* = 2); inner chamber max. diameter = 18 cm (13–23 cm; SD = 7.1 cm; *n* = 2); inner chamber min. diameter = 14 cm (12–16 cm; SD = 2.8 cm; *n* = 2). The inner chamber max. and min. diameter were measured perpendicular to each other on the horizontal plane (Fig. 2). HFG measured only the platform of nest 5 (Fig. 2).

Eggs and nestlings of A. s. subulatus.—The complete clutch at three of the five *A. s. subulatus* nests comprised two immaculate white eggs, although some were slightly stained pale brown, probably from the surrounding earth of the inner chamber (Fig. 3A–B).When the adults were not at the nests, HFG measured and photographed the eggs (nests 3, 5 and 7; Table 1; Fig. 3A–B) and one newly hatched nestling (nest 7; Table 1; Fig. 3D). Mean measurements of six eggs were 24.3 mm (22.8–25.4 mm, SD = 1.0 mm; Table 1) × 17.8 mm (17.1–18.5 mm, SD = 0.6 cm; Table 1). The masses of three eggs with advanced embryonic development were 4.1 g (3.8–4.3 g; SD = 0.3 g; Table 1). An undeveloped and slightly damaged egg weighed during the latter half of incubation had a mass of 3.5 g (nest 5). On HFG's final visit to nest 7 (Table 1), at 16.30 h, it contained a single nestling that probably hatched on the morning of the same day based on its physical appearance and mass. The second egg was lightly pipped, suggesting that the eggs' hatching would occur *c.*24 hours apart. The nestling weighed 4.7 g. It had long, densely plumose, grey natal down on its capital, spinal dorsal, spinal pelvic, alar, ventral sternal, femoral and crural regions (*sensu* Proctor & Lynch 1993). The skin was pinkish, including the tarsi and toes, with the cloaca and surrounding skin noticeably more whitish. Its nails were dusky white, as was the bill,

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TABLE 2

Measurements (cm) of all Striped Woodhaunter *Automolus subulatus* nests that we found, in central-west Costa Rica (nest 2) and eastern Ecuador (nests 3–7). Ent. = entrance, max. = maximum, diam. = diameter, I. cham. = Inner chamber, min. = minimum, Ext. = external, Int. = internal. Numbers in parentheses correspond to the measurement's numbers in Fig. 2.

Measurements	Nest 2 (cm)	Nest 3 (cm)	Nest 4 (cm)	Nest 5 (cm)	Nest 6 (cm)	Nest 7 (cm)
Burrow height (1)		110	120	230	60	100
Ent. height (2)		7.5		8.5	6	6.5
Ent. max. diam. (3)		11		9	8	8.5
Tunnel height (4)		5				
Tunnel max. diam. (5)		10		7		
Tunnel length (6)		31		20	24	30
I. cham. height (7)		12		10		
I. cham. max. diam. (8)		23		13		
I. cham. min. diam. (9)		16		12		
Platform height (10)	4.2					
Ext. max. diam. (11)	14.9			14		
Ext. min. diam. (12)	12.4					
Wall thickness (13)	3.4					
Int. max. diam. (14)	6.2			5.5		
Int. min. diam. (15)	6.0					
Depth (16)	1.9			1.5		

except the dusky-grey tip. The prominent egg tooth, tomia and inflated rictal flanges were bright white and the mouth lining was pale pink, similar to the skin colour (Fig. 3D).

Behaviour of A. s. subulatus adults.—At two nests (4 and 6) HFG observed nest construction over the course of 3–4 days. Nest 4 was visited three times during burrow excavation and, when first found, was *c*.10 cm deep. Three days later the tunnel was *c*.1.5 cm deeper, and eight days after discovery it was *c*.15 cm deep. A single adult was flushed from the nest on both the first (09.30 h) and final (14.30 h) visits. On both occasions the adult emerged with soil on its bill, flew directly into dense vegetation 3–5 m from the nest, and vocalised continually for the 4–5 minutes that HFG remained at the nest. The vocalisation, presumably an alarm call, was nearly identical to that recorded at a nearby locality by B. M. Whitney, given by an adult in response to playback of the same vocalisation (www.xeno-canto.org/86344). HFG was unable to determine if both sexes participated in excavation. The burrow of nest 6, when discovered, contained an empty but apparently fully formed nest. HFG visited the nest six times over the course of five days, between 06.15 h and 17.00 h, without observing an adult. Three days after discovery, during one hour of video observation (08.30–09.30 h), HFG recorded a single adult visit. The adult, of unknown sex, arrived with a single leaf petiole in its bill and remained in the burrow for *c*.3 minutes before flying away.

When first encountered, nest 3 contained a single egg showing no signs of development and a second with a tiny (>1 mm) embryo. Based on the experience of HFG with the embryonic development of numerous tropical suboscine passerines, we estimate that the clutch was completed 2–4 days prior and suspect that the undeveloped egg was inviable. HFG recorded adult incubation rhythms (on/off-bouts), between 06.00 h and 18.00 h (sunrise to sunset) on the five consecutive days following discovery of nest 3. As he was able to record only entrances and exits at the nest burrow, he inferred that the eggs were

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covered during the entire period an adult was inside. Both adults incubated the eggs, as evidenced by the observation of adults replacing each other at the nest, but HFG could not distinguish the sexes. During the entire observation period, adults spent 63.5% of daylight hours warming the eggs. Daily percentage attendance for the five days was 64.5, 43.4, 37.2, 79.2 and 80.0%, respectively. On HFG's final visit to nest 7 (Table 1), direct observations of adults at the nest revealed that both brooded the nestling and delivered single, very small (1–3 mm) prey items.

Discussion

The nest placement and architecture of the three Striped Woodhaunter subspecies reported here are similar to those reported for other *Automolus* (*A. leucophthalmus*: Euler 1900, J. C. R. Magalhães *in* Remsen 2003a, Marini *et al*. 2007, Cockle & Bodrati 2017; *A. ochrolaemus*: Van Tyne 1926; *A. paraensis*: Snethlage 1935, Pinto 1953; *A. exsertus*: Skutch 1952, 1969). In particular, the exclusive use of leaf rachises in nest construction appears to be ubiquitous in *Automolus*, but their nests are otherwise similar in form and placement to the nests of related genera (*Thripadectes*, *Clibanornis* and Buff-fronted Foliage-gleaner *Philydor rufum*: Derryberry *et al*. 2011) being platforms of loosely woven material placed at the end of upward-angled earth burrows (Skutch 1969, Kiff *et al*. 1989, Strewe 2001, Remsen 2003a, Maillard *et al*. 2006, Faria *et al*. 2008, Botero-Delgadillo & Guayara 2009, Zyskowski & Greeney 2010, Miller *et al*. 2012, Smith & Londoño 2013, Cockle & Bodrati 2017). The nest descriptions reported here demonstrate that general nest placement and design support the strong relationship within genera of the *Automolus*-*Thripadectes*-*Clibanornis* clade (see Cockle & Bodrati 2017), and do not appear to vary between currently recognised subspecies or populations of Striped Woodhaunter (Remsen 2003a, Clements *et al*. 2019).

Perhaps of significance, we found that tunnel length of Striped Woodhaunter burrows is generally shorter (26.3 cm; 20–31 cm; SD = 5.2 cm) than reported for related genera (81.4 cm; 38–200 cm; SD = 47.5 cm; Van Tyne 1926, Remsen 2003a, Marini *et al*. 2007, Faria *et al*. 2008, Botero-Delgadillo & Guayara 2009, Zyskowski & Greeney 2010, Miller *et al*. 2012, Cockle & Bodrati 2017). We know from other burrow nesters that habitat and nest design (e. g., entrance size and orientation, and tunnel length) may be important for the regulation of appropriate nest microclimates (Ellis 1982, Haggerty 1995, Ke & Lu 2009). The single nest of *A. s subulatus* that we observed with a downward-sloping entrance tunnel (nest 3), may reflect regional variation in architecture based on local microclimate or, alternatively, may have been an error by the adults or one forced by roots, rocks, or other obstructions within the substrate.

At present, we are unable to confirm that both sexes of Striped Woodhaunter participate in burrow excavation and nest construction, as is known for some species in the *Automolus*-*Thripadectes*-*Clibanornis* clade (see Cockle & Bodrati 2017). We can confirm, however, that both parents participate in incubation and chick provisioning. This behaviour is shared among most furnariids including all members of the *Automolus*-*Thripadectes*-*Clibanornis* clade studied to date (Remsen 2003a, Cockle & Bodrati 2017) but differs vs. other relatives in the Philydorini (*sensu* Derryberry *et al*. 2011), e.g., Ochre-breasted Foliage-gleaner *Anabacerthia lichtensteini* and Sharp-billed Treehunter *Heliobletus contaminatus*, which have uniparental care (Cockle & Bodrati 2017). Although based on relatively small sample sizes, it appears that parental attendance during incubation may be higher in Striped Woodhaunter (63.5%) than has been reported for Chiriquí Foliage-gleaner (58.0%: Skutch 1952). A preliminary interpretation of these data might be that the shorter entrance tunnels of Striped Woodhaunter burrows, which may promote more rapid loss of heat within the nest (Ke & Lu 2009), may promote improved attendance. We suggest that further

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information on adult attendance and nest design within this group may uncover interesting correlations. Furthermore, the seemingly rare occurrence of downward-inclined burrows in Striped Woodhaunter merits further investigation.

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