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REVIEW OF NEST ARCHITECTURE IN *THRIPADECTES* TREEHUNTERS (FURNARIIDAE) WITH DESCRIPTIONS OF NEW NESTS FROM ECUADOR

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Abstract. *Thripadectes* treehunters are among the most poorly known cavity-nesting furnariids. In this paper we review the existing information on their nests, present new field observations from Ecuador, and add unpublished museum data. We describe for the first time the nests of two species, *T. flammulatus* and *T. holostictus*. Nests of *Thripadectes* are all shallow cups of vegetative material, lacking any lining of animal origin such as feathers or hair. Most species have consistent preferences for particular plant materials. *Thripadectes rufobrunneus*, *T. virgaticeps*, and *T. holostictus* use mainly rootlets, *T. melanorhynchus* uses stems of compound leaves exclusively, and *T. flammulatus* incorporates plant materials derived from grass, bamboo, and

treeferns. Larger samples of nests from across these species' ranges are needed to determine the generality of this pattern and whether the availability of material plays a role. Several features of *Thripadectes* nest architecture are shared by putative sister genera *Automolus*, *Hylocryptus*, and *Hyloctistes*.

Key words: bamboo, Chusquea, Ecuador, Furnariidae, nest, ramenta, rootlets, *Thripadectes*, treehunter, tree-fern scales.

Revisión de la Arquitectura de Nidos en el Género *Thripadectes* con Descripciones de Nuevos Nidos de Ecuador

Resumen. Entre los furnáridos que anidan en cavidades, las especies del género *Thripadectes* son las menos conocidas. En este artículo revisamos la información existente sobre los nidos,

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presentamos nuevas observaciones de campo colectadas en Ecuador, y añadimos datos inéditos de museos. Describimos por primera vez los nidos de dos especies (*T. flammulatus* y *T. holostictus*). Los nidos de todos los *Thripadectes* son tazas poco profundas de material vegetativo que carecen de cualquier revestimiento de origen animal tal como plumas o pelos. La mayoría de las especies exhiben preferencias consistentes por materiales vegetales particulares. *Thripadectes rufobrunneus*, *T. virgaticeps* y *T. holostictus* usan principalmente raicillas, *T. melanorhynchus* utiliza exclusivamente hojas compuestas, y *T. flammulatus* incorpora materiales derivados de pasto, bambú y helechos arborescentes. Para determinar la generalidad de estos patrones y si la disponibilidad de materiales juega un papel importante, se requieren mayores muestras de nidos provenientes de toda la distribución de estas especies. Varias características de la arquitectura de los nidos de *Thripadectes* son compartidas con las de los nidos de las especies de sus géneros hermanos, *Automolus*, *Hylocryptus* y *Hyloctistes*.

Neotropical ovenbirds of the family Furnariidae have long been recognized for their architecturally diverse nests (e.g., Ihering 1914, Vaurie 1980), and more recently this extraordinary diversity has been analyzed in a phylogenetic context (Zyskowski and Prum 1999, Irestedt et al. 2006). Unfortunately, our ability to fully understand the evolution of nest-building behavior in this family is limited by the lack of critical details in many nest descriptions, limited data on intraspecific variation, and complete lack of information on nests of over 50 species. These deficiencies are most apparent among furnariids known or inferred to nest in subterranean or tree cavities (Zyskowski and Prum 1999, Remsen 2003). Treehunters of the genus *Thripadectes*, the subject of this article, are among the most poorly known.

Thripadectes treehunters are robust thrushlike furnariids with chestnut-brown plumage and variable amounts of buff streaking. Most species are Andean in distribution, but one reaches the Coastal Cordillera of Venezuela and another is confined to the highlands of Costa Rica and western Panama. The highest species diversity is reached in Colombia and Ecuador, where five of the seven species are found (Hilty and Brown 1986, Ridgely and Greenfield 2001). All species occupy the undergrowth of montane evergreen forests, often favoring dense bamboo thickets, from the foothills to 3500 m above sea level. The birds' dense, poorly illuminated habitat, combined with their skulking, furtive behavior, makes them difficult to find and study. For this reason, few nests have been found, and little is known about any aspect of the treehunters' breeding biology.

At the time of the first major review of furnariid nest architecture (Vaurie 1980), the nest of only one species, the Streak-breasted Treehunter (*T. rufobrunneus*), was known to science. Not surprisingly, this Central American species remains the only *Thripadectes* for which more than one nest has been described (Zyskowski and Prum 1999, Remsen 2003). Although we can now say with confidence that all studied species of *Thripadectes* construct their nests in self-excavated subterranean cavities, the structure and composition of the nest is known for only three of the seven species (Remsen 2003). Here we review the existing information on the nests and present new field observations of nesting behavior of four species from Ecuador along with some unpublished museum data.

MATERIALS AND METHODS

During field work in Ecuador from 2004 to 2006, we studied six nests of four species of *Thripadectes*. We found the nests at the

following localities: Bellavista Cloudforest Reserve, above the town of Tandayapa, Pichincha Province (0° 15' N, 78° 38' W); Tandayapa Bird Lodge, Tandayapa Valley, Pichincha Province (0° 00' N, 78° 41' W); Yanayacu Biological Station, Napo Province (0° 36' S, 77° 53.4' W); western slope of the Sumaco Volcano, along the access road to the town of Pacto Sumaco, Napo Province (0° 34' S, 77° 38' W); private reserve of the Mushullacta community, Napo Province (0° 50' S, 77° 34' W); and Tapichalaca Biological Reserve, near the town of Valladolid, Zamora-Chinchipe Province (4° 30' S, 79° 10' W). We identified adult birds attending nests by carefully examining plumage and body proportions through 10 × 42 binoculars and sometimes also by using species-specific song playback. In two instances, the birds arriving at their burrows were videotaped (*T. virgaticeps*) or photographed (*T. flammulatus*).

We also studied nests housed at the Western Foundation of Vertebrate Zoology in Camarillo, California (WVZ), and received unpublished descriptions and photographs of *Thripadectes* nests from colleagues working in Costa Rica, Colombia, and Ecuador (see Acknowledgments).

SPECIES ACCOUNTS

Uniform Treehunter (*Thripadectes ignobilis*). Three nest sites, all burrows in banks, have been described from southwestern Colombia, but the nests themselves have not been examined (Strewe 2001). In 1878, T. K. Salmon (in Sclater and Salvin 1879) collected the only known egg at the type locality of the species in Colombia. The description of the egg immediately follows that of the type specimen without a comment on their potential association (Sclater and Salvin 1879). Neither the egg voucher [British Museum (Natural History) (BMNH) SG 2844] nor the holotype (BMNH 1889.5.20.324) is accompanied by any mention of the nest (D. Russell, pers. comm., 2007).

Streak-breasted Treehunter (*Thripadectes rufobrunneus*). Three nests of this species have been reported previously (Worth 1939, Hartman 1957, Skutch 1969). Their architecture was summarized thoroughly by Wetmore (1972). Hartman's nest was well illustrated with photographs, and Worth's nest is now housed at WVZ (154898). Therefore, here we present only previously unpublished observations of nests subsequently found in Costa Rica. All nests found to date were built in burrows and were constructed of rootlets. To our knowledge, the use of leaf stems has never been reported (contra Remsen 2003).

F. G. Stiles (pers. comm., 2006) has seen active burrows of *T. rufobrunneus* several times in Costa Rica. A nest discovered at Muñeco (Cartago Province) on 25 March 1973 was at the end of a self-excavated burrow, 40 cm long, and was built of rootlets with a few treefern scales in the lining. It resembled the Colombian nest of *T. flammulatus* described above but was thinner and had fewer treefern scales. The nest contained two week-old nestlings on 4 June.

M. Marín and J. Schmitt found a nest of this species on 28 March 1986 on Volcán Barba, 2000 m, Heredia Province, Costa Rica, in a burrow 2 m high in a road embankment. The burrow was about 1.6 m long, ending in a chamber 10–15 cm high and 20 cm wide. The chamber contained a platform constructed entirely of rootlets. The adult bird was seen going in and out of the burrow, but the nest was empty. The nest is housed at WVZ (154831).

M. Marín collected another Costa Rican nest near Rancho Redondo on Río Tiribí, 2000 m, San José Province. The nest (WVZ 165491) was in a burrow 50–60 cm long in a high embankment along the river and was a thick platform of rootlets. On 4 June 1997 it contained one fresh egg.

Also noteworthy is a recent record of burrow excavation from Monteverde, Puntarenas Province, Costa Rica. We have seen a photograph, taken by L. P. J. Catchick on 23 April 2005, of a Streak-breasted Treehunter exiting a burrow with its bill filled and coated with soil.

Black-billed Treehunter (*Thripadectes melanorhynchus*). Only one nest of this species, representing the nominate subspecies, has been described previously (Kiff et al. 1989). The nest, discovered in Napo Province of Ecuador, was placed at the end of a 1-m-long burrow and constructed entirely of leaf rachises. We found two additional nests in Ecuador.

The first nest was discovered on 19 February 2005 on the western slope of the Sumaco Volcano at ca. 1300 m. The nest burrow was in the claylike soil of a roadside bank, 5 m above the road, and 1.5 m below the top of the bank. Surrounding vegetation was mostly second growth, with the nearest intact (but selectively logged) forest over 100 m away. Two adults were entering the burrow with food, and the loud begging of at least two nestlings was easily heard from the road below. One prey item was a butterfly (*Catoblepia* sp., Brassolinae, Nymphalidae). We were unable to access the nest.

We found the second nest on 3 April 2005 in the private forest reserve of the Mushullacta community at 1150 m. It contained two nestlings that fledged the following day. The nestlings were similar in appearance to adults, with only a few sparse tufts of gray down remaining on their heads. Rictal flanges were barely noticeable and were bright yellow. Two adults fed the nestlings, one arriving at the nest with a beetle grub (*Scarabaeidae*) 3–4 cm long.

The nest burrow was in the claylike soil of the side of a nearly circular (diameter ca. 3 × 4 m) collapsed depression (2.5 m deep) caused by subterranean flow of water inside a mature subtropical forest in the foothills. The entrance was 1 m above the depression's floor, 1.5 m below the surrounding ground, and well hidden by 0.5 m of overhanging soil. The tunnel entrance was round, 9 cm in diameter, and opened to a gently upsloping tunnel of roughly the same diameter. The tunnel continued straight for 34 cm, then turned at a 45° angle for 15 cm before opening into a chamber estimated to be 16 cm in diameter and 12 cm tall. The circular nest was built almost entirely of loosely interwoven bare leaf rachises mixed with only a few thin sticks (Fig. 1D). Outside dimensions were 14 cm wide by 4 cm high. The inner depression was 7 cm in diameter and 1.5 cm deep. We suspect that these vertical dimensions are significantly smaller than the original construction, having been flattened by the weight and movement of the nestlings.

Striped Treehunter (*Thripadectes holostictus*). Greeney and Nunnery (2006) reported two active nests in northwestern Ecuador, but here we describe the nest of this species for the first time. The nest was discovered on 26 November 2004 in the Tapichalaca Biological Reserve along the tunnel-like Quebrada Honda trail, 2000 m, about 200 m above the Quebrada Honda stream. The burrow was excavated in the south-facing bank of the trail, 1.45 m above the ground, and about 0.25 m below the lip of an overhang caused by tree roots. The tunnel was 8 cm in diameter and 82 cm long, first sloping upward for some 25 cm, then leveling off. It ended with an expanded chamber 13 cm wide and 9 cm tall. The entrance hole was vertically oval with lateral furrows on the lower lip corresponding to the feet of landing birds. This wear of the lower lip was responsible for the increased height (12.5 cm) of the entrance hole and was due mostly to the soil's being relatively dry and poorly compacted.

The nest extracted from the burrow was a circular cup with an external diameter of 13 cm and a height of 4 cm. The internal depression was 7 cm in diameter and 3 cm in depth, and the walls were on average 1.3 cm thick. The nest was constructed entirely of loosely

interwoven dark brown rootlets, coarse on the outside but finer and arranged circularly in the weakly differentiated lining (Fig. 1C).

The two nestlings, with eyes partially open and wings with pin feathers just breaking their sheaths, weighed 33.5 and 29.8 g. Their rictal flanges were pale yellow, and the mouth linings were yellow fading to pinkish internally. Contour pin feathers were protruding 1–2 mm from sheaths on the dorsum and breast but were still unbroken on the crown. Exposed skin was pinkish to bluish gray, obscured dorsally by sparse gray down. The soft begging calls of the nestlings, in the absence of an adult, revealed the nest as we were passing by. During our presence the adults remained silent, staying hidden in dense foliage except for one brief approach by a parent carrying a large (ca. 3 cm long) black caterpillar in its bill. In addition, we found shell fragments of a terrestrial snail on the front rim of the nest.

We found a second nest of this species on 4 August 2006 at the Tandayapa Bird Lodge, 1300 m. The nest burrow was in the sandy soil of a bank adjacent to the lodge's parking lot, 2.5 m above the ground, and 0.7 m below the top of the bank. The entrance was sheltered by a slight (ca. 10 cm) overhang. The round entrance was 9 cm in diameter and led to a straight, level tunnel, 45 cm long, of similar diameter, which opened into a larger chamber. We did not remove the nest cup to measure it, but by feel it was roughly 8 cm wide by 3 cm deep internally. We removed small portions of the nest from several locations in the cup and found only thin dark rootlets. The nest contained two white nonglossy eggs, slightly stained with dirt, cloacal secretions, and blood. The eggs measured 32.3 × 23.9 and 32.8 × 23.9 mm. The incubating adult was reluctant to flush, remaining in the burrow even when we tapped the bank near the entrance and blocked light at the opening. It flushed only when we inserted a stick into the tunnel.

The only previously known set of eggs of *T. holostictus* was collected by T. K. Salmon in Colombia (Sclater and Salvin 1879) and is housed at the Natural History Museum in Tring, England (BMNH). Unfortunately, the eggs are not accompanied by any mention of the nest (D. Russell, pers. comm., 2007).

Streak-capped Treehunter (*Thripadectes virgaticeps*). To date, the description of only one nest has been published (Marín and Carrión 1994), and it pertains to the nominate subspecies of the west slope of the Andes. The nest contained recently hatched nestlings on 13 June 1989 and was described as a nearly flat platform made entirely of rootlets. Its shape and size were not reported in the original publication, but the voucher specimen, which Zyskowski examined at WFWZ (159222) is oval with outside diameters of 23 and 15.5 cm; for a photograph, see Zyskowski and Prum (1999). Other published information on nesting of *T. virgaticeps* includes a report of five active burrows found in banks along forest roads in Colombia (Hilty and Brown 1986) and a nest with nestlings in October in northwest Ecuador (Greeney and Nunnery 2006). None of these nests, however, were examined closely.

On 2 December 2004 we found the first known nest of the east Andean subspecies *T. v. sumaco* near the Yanayacu Biological Station at ca. 2000 m. The area is adjacent to the Sumaco Volcano, the subspecies' type locality (Chapman 1925). The habitat was a steep slope covered with dense second-growth forest near the arc-shaped lip of a recent landslide. The vertical wall of exposed soil at the origin of the landslide had several avian excavations, at least one of these belonging to a Highland Motmot (*Momotus aequatorialis*). The burrow of the Streak-capped Treehunter was ca. 1.5 m below the top, 163 cm above the foot of the vertical wall, and was well hidden under a 2-m-long overhang created by the roots of a large tree. The tunnel was 100 cm long,

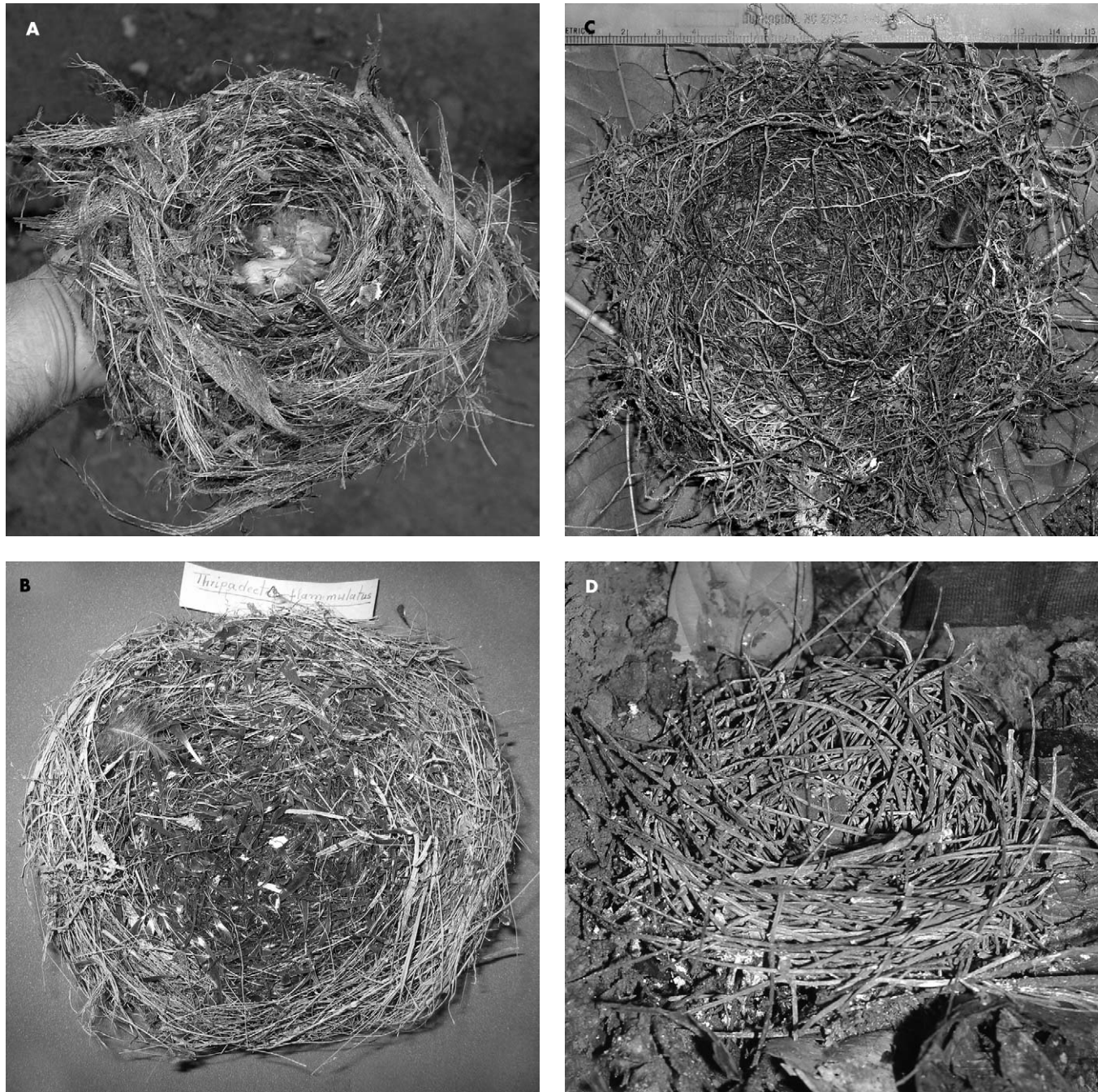


FIGURE 1. Nests of the Andean *Thripadectes* treehunters reported in this study: (A) Tandayapa (Ecuador) nest of *T. flammulatus* built of ribbonlike strips of decayed tree-fern petioles; (B) Colombian nest of *T. flammulatus* built of grasslike materials and lined with treefern scales (photo courtesy of F. G. Stiles); (C) Tapichalaca (Ecuador) nest of *T. holostictus* built of rootlets; (D) Mushullacta (Ecuador) nest of *T. melanorhynchus* built of rachises of compound leaves.

slightly inclined, and ended in an expanded nest chamber. Although we did not measure the chamber, from the nest's size we estimated it was about 19 cm in diameter. The burrow originated in a layer of wet clay, but the walls of the terminal chamber were relatively dry, and the soil was less compacted. The entrance hole was horizontally oval, 10×8.5 cm in diameter, and was worn smooth, presumably by the movement of adults. The entrance

was in the middle of a small clay protrusion and had a prominent lip below on which the adults perched.

The nest extracted from the terminal chamber was a bulky oval cup with external diameter of 18.5×16 cm and height of 7 cm. The internal depression was 10×8.5 cm in diameter and 3.5 cm in depth, and the walls were 2.5–4 cm thick. The nest was constructed mainly of dark brown rootlets and lined with

a mixture of fine rootlets and pale ochraceous palm fibers. The lining layer was weakly differentiated from the surrounding cup. Material on the outside was coarse and loosely interwoven, whereas that of the lining was much finer and tighter. The top surface of the nest was thinly coated with nestlings' white fecal material, and the nest smelled strongly of ammonia.

The nest contained two mid-aged nestlings with eyes already open and body masses of 41.5 and 40 g. Their rectal flanges were white, their mouth linings whitish pink. Their bare pink to bluish gray skin, paler white around the cloaca, was partially obscured dorsally with sparse gray down. Contour feathers protruded 1–2 mm from their sheaths ventrally and dorsally but not on the crown. On the wing, pin feathers were just breaking sheaths. Begging calls of the nestlings were loud and reminiscent of those of young *Scytalopus tapaculos* (Rhinocryptidae; Greeney, pers. obs.).

During 2 hr of videotaping (13:56–16:02), adults brought food to the nestlings five times. The intervals between feedings were 34, 2, 26, and 38 min, with the longest interval coinciding with 20 min of light rain and the shortest suggesting that two birds arrived with food in quick succession. The adults perched at the entrance before entering for 1–4 sec and remained inside the burrow for 15–46 sec. Because of dim light, we could not identify food items brought to nestlings on the video. Through binoculars, however, we observed three instances of adults bringing cicadas (Cicadidae, Homoptera) with the wings at least partially removed. While we were at the nest, the adults did not approach.

Flammulated Treehunter (*Thripadectes flammulatus*). The three nests described here represent the first reported for this species and represent the nominate subspecies. On 14 September 2005 Greeney discovered a nest burrow at the Bellavista Cloudforest Reserve, 2500 m, along the road above the town of Tandayapa. The forest around the nest was mostly old growth, with large patches of *Chusquea* bamboo and a few scattered regrowing pastures. The burrow was excavated in the loose sandy soil of a roadside bank, 2.2 m above the ground, and 0.8 m below the top. The entrance hole was 8 cm wide by 9 cm tall and was concealed under a half meter overhang of vegetation and dirt. The tunnel was straight, angling only slightly upward and opening into a chamber 46 cm from the entrance. Although the chamber was not measured, from the nest's size it was about 21 cm in diameter.

The nest was a bulky circular cup with an external diameter of 21 cm and height of 12 cm. The internal depression was 8 cm in diameter and 6 cm deep. The nest was constructed of treefern scales and ribbon-like strips of fibers torn from partially decayed (but dry) treefern petioles (Fig. 1A). The nest contained two recently hatched nestlings with closed eyes, pink skin (paler white around the cloaca), and long tufts of gray to whitish down on the crown and dorsum. Their rectal flanges were white and mouth linings were pinkish white. Both adults were seen entering the nest, and at one point one stayed to brood for over 15 min. One adult brought a 1.5-cm spider to the nestlings.

The second nest of *T. flammulatus* was discovered by P. A. Hosner (pers. comm.) on 11 October 2005 in the Tapichalaca Biological Reserve, ca. 2400 m. The habitat was temperate forest with an understory of *Chusquea* bamboo. The burrow was in a vertical wall of the eroded section of an old mule trail descending from Cerro Tapichalaca into Quebrada Honda. The nest entrance was about 1.2 m above the ground and about 0.2 m below the top of the bank, just below the level where the roots of plants growing on the bank could penetrate. The reddish clay-rich soil of the road bank included embedded rocks. Two meters to the right of the active nest, an additional burrow appeared to be constructed in the same manner but was only 15 cm deep.

The entrance to the nest burrow was horizontally oval, 9.5 wide and 6.5 cm tall. The tunnel was 38 cm long and angled about 10° up and slightly to the left. The passageway gradually shifted from being oval at the entrance to circular at the beginning of the nest chamber, constricting slightly at this point. The chamber was 18.5 × 14.5 × 11 cm (length × width × height) after the nest cup was removed. With a light, it was possible to see just a bit of nesting material from the entrance, before the nest was excavated for observation.

The nest was an oval cup with an external diameter of 16 × 13.5 cm and a height of 8 cm. The circular internal depression was 5.5 cm in diameter. The nest was woven of fibers of *Chusquea* bamboo and treeferns. The bottom and sides of the cup contained mostly slender black fibers and small pieces of fresh green moss. The interior of the cup was lined entirely with thin inflorescences from seeding *Chusquea* bamboo. The nest contained two white nonglossy eggs. The incubating bird flushed and skulked away in the undergrowth, uttering alarm calls.

The third nest of *T. flammulatus* was identified in the collection of the Instituto de Ciencias Naturales (ICN), Universidad Nacional de Colombia, Bogotá (F. G. Stiles, pers. comm., 2005). The nest and the two associated eggs were apparently collected by Pablo E. Bernal, a collector at ICN from 1950 to 1980 (Moraes et al. 2007). Unfortunately, the specimens are not accompanied by collection data beyond the handwritten scientific name of the species (in Bernal's hand). Although there is at ICN a skin of *T. flammulatus* taken by Bernal from Rondón, Departamento Boyacá, on 17 January 1972, there is no way of telling if the nest and eggs were collected with it (F. G. Stiles, pers. comm.).

The Colombian nest is a shallow cup 17 × 15 cm in outside diameter, 5 cm thick on the periphery, and 4 cm in the center. The circular central depression is 9 cm in diameter. The nest is constructed mainly of slender pale stalks, possibly derived from seed panicles of *Chusquea* bamboo, and some pale rootlets; it is profusely lined with loose treefern scales (Fig. 1B). Two poorly prepared eggs are white. One measures ca. 32.3 × 22.4 mm (length is approximate because of the hole at the small end); the other has a diameter of ca. 21.6 mm (only half of the egg is present). These measurements are close to the 33.6 × 22.6 mm reported for *T. flammulatus* by Schönwetter (1967).

Peruvian Treehunter (*Thripadectes scrutator*). Two active burrows excavated in dirt banks have been found by B. M. Whitney (pers. comm.), but the structure and composition of actual nests were not observed.

DISCUSSION

Our review confirms that *Thripadectes* treehunters nest exclusively in subterranean burrows. The birds are capable of excavating their own burrows, as evidenced by the piles of fresh earth often present below the entrance and by observations of birds emerging from burrows with their bills coated with fresh dirt. All nests described to date have been shallow cups of vegetative material, lacking any lining of animal origin such as feathers or hair. In the four species known from more than one nest, the intraspecific variation in nest composition is minimal (*T. rufobrunneus*, *T. melanorhynchus*, and *T. virgaticeps*) to moderate (*T. flammulatus*; see below). In contrast, differences among species in nest composition are pronounced (Table 1).

Plant materials used in nest construction fall into three general categories with rather different physical properties: rootlets (sinuous, wiry, branched), stems of compound leaves (nearly straight, elastic, unbranched), and grass and other plant debris (pliable, soft, often ribbonlike and decayed). The exclusive or nearly exclusive

TABLE 1. Summary of nest composition in *Thripadectes* treehunters. Sample sizes (*n*) are limited to nests extracted from burrows and examined for composition.

Species	<i>n</i>	Principal nest materials	Source
<i>T. ignobilis</i>	0	Unknown	
<i>T. rufobrunneus</i>	6	Rootlets (1 also ramenta)	References in Wetmore (1972), this study
<i>T. melanorhynchus</i>	2	Compound-leaf rachises	Kiff et al. (1989), this study
<i>T. holostictus</i>	1	Rootlets	Greeney and Nunnery (2006), this study
<i>T. virgaticeps</i>	2	Rootlets (1 also palm fibers)	Marín and Carrión (1994), Greeney and Nunnery (2006), this study
<i>T. flammulatus</i>	3	Grass, bamboo stalks, and ramenta	This study
<i>T. scrutator</i>	0	Unknown	

use of rootlets is now known in three species: *T. rufobrunneus*, *T. holostictus*, and *T. virgaticeps*. The use of compound-leaf stems is still unique to *T. melanorhynchus*. Somewhat heterogeneous, soft, ribbonlike materials, including grass, *Chusquea* bamboo stalks, and decayed strips of treefern petioles, are used by *T. flammulatus*. In addition, treefern scales (ramenta) appear to be typical of *T. flammulatus* (all three nests known) and apparently are used on occasion by *T. rufobrunneus* (one of six nests).

The availability of certain plant materials used by *Thripadectes* is likely limited spatially or temporally. Ramenta, for example, are only available around treeferns, which are distributed patchily. Even more limited is the availability of inflorescences and seed panicles of *Chusquea* bamboo, given that these plants produce synchronous seed crops once every several years (Judziewicz et al. 1999). The pair of *T. flammulatus* with the nest of bamboo panicles at Tapichalaca may have been taking advantage of the massive bamboo seeding at that time (P. A. Hosner, pers. comm.).

On the basis of morphology and behavior, *Thripadectes* treehunters are part of a large group of furnariids including genera *Anabacerthia*, *Anabazenops*, *Ancistrops*, *Automolus*, *Cichlocolaptes*, *Hylocryptus*, *Philydor*, *Simoxenops*, and *Syndactyla* (Remsen 2003). Besides *Ancistrops*, *Cichlocolaptes*, and *Simoxenops*, whose nesting biology is unknown, all these genera are cavity nesters that occupy not only subterranean tunnels but also cavities in trees, bamboo internodes, termite mounds, etc. (Zyskowski and Prum 1999). Recent molecular studies have further narrowed the list of putative sister taxa and hypothesized *Automolus*, *Hylocryptus*, and *Hyloctistes* as sister genera of *Thripadectes* (Irestedt et al. 2006, Moyle et al. 2009).

All three sister genera include species that nest in burrows and are capable of excavating them. Most species of *Automolus* construct nests entirely of compound-leaf stems; only the Ruddy Foliage-gleaner (*A. rubiginosus*) uses rootlets or structurally similar fungal rhizomorphs (Zyskowski and Prum 1999). Of the two species of *Hylocryptus* foliage-gleaners, the Henna-hooded (*H. erythrocephalus*) constructs nests mainly of fungal rhizomorphs and rootlets (E. T. Miller, M. B. Robbins, Zyskowski, unpubl. data), and the Chestnut-capped (*H. rectirostris*) reportedly uses fine sticks of uniform size (Faria et al. 2008). Finally, nest materials reported for the Striped Woodhaunter (*Hyloctistes subulatus*) are compound-leaf rachises (N. T. Wheelwright in Zyskowski and Prum 1999; Greeney, unpubl. data) or dry twigs and grass (J. A. Chaves, pers. comm.). In our experience, partially decomposed rachises of pinnately compound tree leaves found on the forest floor are structurally similar and often mistaken for fine sticks or twigs. Thus, plant materials reported in nests of the sister genera match closely those used by *Thripadectes*.

The monophyly of the genus *Thripadectes* has not yet been tested with molecular data. One possible exception to the

monophyly of the genus is the Uniform Treehunter (*T. ignobilis*), often described as aberrant because of its relatively small size, short bill, and apparently more arboreal foraging habits (Remsen 2003). Cory and Hellmayr (1925) and Ridgely and Tudor (1994) suggested that it should perhaps be separated generically from the other *Thripadectes* and perhaps placed in a monotypic genus. Unfortunately, the composition of this unique species' nest remains unknown.

The variation in nest composition in the genus *Thripadectes* is only partially congruent with the phylogenetic relationships among species inferable from the similarities in morphology and vocalizations. The hypothesized sister relationship of *T. rufobrunneus* and *T. virgaticeps* (see Remsen 2003) is supported by both species' nearly exclusive use of rootlets. However, on the basis of its plumage pattern, the third species that shares this apparent synapomorphy, *T. holostictus*, is considered part of the *T. flammulatus* group by Ridgely and Tudor (1994). Similarly, the occasional use of ramenta by *T. rufobrunneus* is an unlikely indicator of its phylogenetic affinity to the only other congener known to use this material, *T. flammulatus*. Among the species whose nests remain undescribed, *T. scrutator* of the Peruvian and Bolivian Andes is likely to have a nest similar to that of *T. flammulatus*, with which it forms a superspecies or may even be conspecific (Fjeldså and Krabbe 1990, Ridgely and Tudor 1994, Remsen 2003).

Despite the fact that this contribution nearly doubles the number of known nests of *Thripadectes*, our understanding of the intraspecific variation in nest architecture and its phylogenetic significance in this group remains inadequate. Many more nests from different parts of each species' range need to be studied before it can be determined if the pattern of material specificity we describe reflects real species-specific preferences and if the use of a material is influenced by its availability. Future discoverers of nest burrows of *Thripadectes* are encouraged to extract and analyze the composition of nest cup when the nest is no longer active. Given the relatively large diameter and only moderate length of the burrow, most nests can be extracted by hand for examination and replaced without the burrow being excavated.

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LITERATURE CITED

- CHAPMAN, F. M. 1925. Descriptions of new birds from Ecuador and Peru. *American Museum Novitates* 187:1–9.
- CORY, C. B., AND C. E. HELLMAYR. 1925. Catalogue of birds of the Americas. Field Museum of Natural History Publications, Zoological Series 13, part 4.
- FARIA, L. C. P., L. A. CARRARA, AND M. RODRIGUES. 2008. Biología reproductiva do fura-barreira *Hylocryptus rectirostris* (Aves: Furnariidae). *Revista Brasileira de Zoologia* 25:172–181.
- FJELDSÅ, J., AND N. KRABBE. 1990. Birds of the high Andes. University of Copenhagen Zoological Museum, Copenhagen.
- GREENEY, H. F., AND T. NUNNERY. 2006. Notes on the breeding of northwest Ecuadorian birds. *Bulletin of the British Ornithologists' Club* 126:38–45.
- HARTMAN, F. A. 1957. Some additions to nesting data on Panamanian birds. *Condor* 59: 269–271.
- HILTY, S. L., AND W. L. BROWN. 1986. Birds of Colombia. Princeton University Press, Princeton, NJ.
- IHERING, H. VON. 1914. Novas contribuições para a ornitologia do Brasil. *Revista do Museu Paulista* 9:420–448.
- IRESTEDT, M., J. FJELDSÅ, AND P. G. P. ERICSON. 2006. Evolution of the ovenbird–woodcreeper assemblage (Aves: Furnariidae)—major shifts in nest architecture and adaptive radiation. *Journal of Avian Biology* 37:261–272.
- JUDZIEWICZ, E. J., L. G. CLARK, X. LONDOÑO, AND M. J. STERN. 1999. American bamboos. Smithsonian Institution Press, Washington, D.C.
- KIFF, L. F., M. MARÍN A., F. C. SIBLEY, J. C. MATHEUS, AND N. J. SCHMITT. 1989. Notes on the nests and eggs of some Ecuadorian birds. *Bulletin of the British Ornithologists' Club* 109:25–31.
- MARÍN, M., AND J. M. CARRIÓN B. 1994. Additional notes on nest and eggs of some Ecuadorian birds. *Ornitología Neotropical* 5:121–124.
- MORALES R., A., D. E. ARZUZA B., J. C. VERHELST, C. BOHÓRQUEZ, N. CLEERE, P. SALAMAN, S. DE LA ZERDA, AND L. ROSSELLI. 2007. Las colecciones ornitológicas en Colombia: una fuente importante de información sobre la biodiversidad de nuestro país. *Código (Boletín Científico y Cultural del Museo Universitario, Universidad de Antioquia)* 814:6–11.
- MOYLE, R. G., R. T. CHESSER, R. T. BRUMFIELD, J. G. TELLO, D. J. MARCHESE, AND J. CRACRAFT. 2009. Phylogeny and phylogenetic classification of the antbirds, ovenbirds, woodcreepers, and allies (Aves: Passeriformes: infraorder Furnariides). *Cladistics* 25:386–405.
- REMSEN, J. V., JR. 2003. Family Furnariidae (ovenbirds), p. 162–357. In J. del Hoyo, A. Elliott, and D. Christie [EDS.], *Handbook of the birds of the world*, Vol. 8. Lynx Edicions, Barcelona.
- RIDGELY, R. S., AND P. J. GREENFIELD. 2001. The birds of Ecuador, Vol. 1: status, distribution, and taxonomy. Cornell University Press, Ithaca, NY.
- RIDGELY, R. S., AND G. TUDOR. 1994. The birds of South America, Vol. 2: the suboscine passerines. University of Texas Press, Austin, TX.
- SCHÖNWETTER, M. 1967. *Handbuch der oologie*, Vol. 14. Akademie-Verlag, Berlin.
- SCLATER, P. L., AND O. SALVIN. 1879. On the birds collected by the late Mr. T. K. Salmon in the State of Antioquia, United States of Colombia. *Proceedings of the Zoological Society of London* 1879:486–550.
- SKUTCH, A. F. 1969. Life histories of Central American birds, Vol. 3. Pacific Coast Avifauna 35.
- STREWE, R. 2001. Notes on nests and breeding activity of fourteen bird species from southwestern Colombia. *Ornitología Neotropical* 12:265–269.
- VAURIE, C. 1980. Taxonomy and geographical distribution of the Furnariidae (Aves, Passeriformes). *Bulletin of the American Museum of Natural History* 166:1–357.
- WETMORE, A. 1972. The birds of the Republic of Panamá, part 3. Smithsonian Institution Press, Washington, D.C.
- WORTH, C. B. 1939. Nesting of some Panamanian birds. *Auk* 56:306–310.
- ZYSKOWSKI, K., AND R. O. PRUM. 1999. Phylogenetic analysis of the nest architecture of neotropical ovenbirds (Furnariidae). *Auk* 116:891–911.