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A NOVEL NEST ARCHITECTURE WITHIN THE FURNARIIDAE: FIRST NESTS OF THE WHITE-BROWED SPINETAIL

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Abstract. The White-browed Spinetail (*Hellmayrea gularis*), of the Andean cloud forests, is the sole member of the genus *Hellmayrea*, and its phylogenetic relationships are still unresolved. The diversity of nest architectures in the family Furnariidae provides many phylogenetically informative characters; however, information on the nest of this enigmatic genus is lacking. Here, we describe four nests of *Hellmayrea* discovered in Ecuador. All nests were embedded within hanging masses of epiphytic moss, but were not pendulous, being supported from below or by stems incorporated in side walls. All nests were balls with a side entrance, externally built of green moss and internally of dry bamboo leaves. The bottom of the chamber was lined with *Tillandsia* seed down and, in one nest, tree-fern scales were also used. These first nests of *Hellmayrea* represent a type of nest architecture previously unknown in the family Furnariidae.

Key words: bamboo, Chusquea, *cloud forest, Ecuador,* Hellmayrea gularis, *moss, ovenbird.*

Una Arquitectura Novedosa de los Nidos de los Furnáridos: los Primeros Nidos de *Hellmayrea gularis*

Resumen. *Hellmayrea gularis*, un taxón del bosque nublado andino, es el único miembro del género *Hellmayrea*, y sus relaciones filogenéticas no están aún resueltas. La diversidad de la arquitectura de los nidos en la familia Furnariidae provee muchos caracteres que brindan información filogenética, pero aún no existe información acerca del nido de este género enigmático. En esta nota describimos cuatro nidos de *Hellmayrea* descubiertos en Ecuador. Los nidos eran bolas incrustadas dentro de masas colgantes de musgos epífitos. Los nidos no estaban suspendidos, sino que estaban soportados por debajo o por tallos incorporados en las paredes laterales. Todos los nidos eran bolas con una entrada lateral, externamente construidos con musgo verde e internamente con hojas secas de bambú. La parte inferior de la cámara estaba forrada de semillas con apéndices plumosos de *Tillandsia* y, en un nido, también escamas de helechos arbóreos. Los primeros nidos de *Hellmayrea* presentan una arquitectura previamente desconocida entre los nidos de otras especies de Furnariidae.

Neotropical ovenbirds and woodcreepers (Furnariidae; Remsen et al. 2008) represent one of the most diverse avian radiations in the New World. In addition to remarkable morphological, ecological, and behavioral diversification, this group is characterized by the evolution of diverse nest architectures (Collias 1997, Zyskowski and Prum 1999). Certain evolutionary innovations in nest placement and structure in the ovenbird-woodcreeper clade are thought to have facilitated its diversification into new habitats and encouraged the evolution of new morphological specializations (Irestedt et al. 2006). However, a thorough understanding of furnariid nest evolution has been impeded by the lack of data on nest architecture and nesting behavior for several key species and genera in this family (Zyskowski and Prum 1999, Remsen 2003, Irestedt et al. 2006). The enigmatic White-browed Spinetail (*Hellmayrea gularis*) is among the key taxa for which knowledge of nest architecture is integral to elucidating hypothesized shifts in furnariid nest evolution (Irestedt et al. 2006).

Although originally described in *Synallaxis* and superficially similar to members of this genus, the White-browed Spinetail is unique in several aspects of its morphology and behavior. As noted by Hellmayr (1925), its tail is shorter than the wing and the bill is more slender and depressed than in *Synallaxis*. Based on these autapomorphies the species was placed in its own genus, *Hellmayrea* (Sztolcman 1926). Subsequent authors either maintained

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it in this monotypic genus (Peters 1951, Wolters 1977) or returned it to *Synallaxis* (Meyer de Schauensee 1970, Vaurie 1980). It was not until Braun and Parker (1985) provided new data on its vocalizations, behavior, and the electrophoretic properties of its proteins that the uniqueness of this species was fully appreciated. These authors suggested that *Hellmayrea* is more closely related to species in the genus *Cranioleuca* or *Schizoeaca* than to *Synallaxis* spinetails. More recently, the molecular study of García-Moreno et al. (1999) indicated that *Hellmayrea* was closer to *Cranioleuca* than to *Asthenes*, although clearly distinct from them (but no *Synallaxis* species were included in this study). Finally, according to a more recent molecular phylogeny, *Hellmayrea* remains part of the synallaxine clade but is not closely related to *Synallaxis* or *Cranioleuca* (Irestedt et al. 2006).

Hellmayrea inhabit the wet undergrowth of Andean evergreen forests from western Venezuela south to central Peru (Remsen 2003). They favor *Chusquea* bamboo thickets and stunted elfin forest near the treeline. These energetic and agile foragers usually stay close to the ground and forage singly or in loosely associated pairs, only rarely joining mixed-species flocks (Hilty and Brown 1986, Fjeldså and Krabbe 1990, Ridgely and Greenfield 2001, Remsen 2003).

Populations of White-browed Spinetails in Ecuador represent the nominate subspecies and occur on both slopes of the Andes at altitudes ranging from 2500 to 3700 m (Ridgely and Greenfield 2001). We studied this form on the eastern slopes of the Andes in southern and north-central Ecuador. Here, we describe the architecture of four nests and discuss the phylogenetic significance of these findings. A detailed description of eggs, nestlings, incubation, and parental behavior are the subject of a separate publication (Greeney and Zyskowski 2008).

METHODS

We made observations of three nests of the White-browed Spinetail from 12 October to 8 November 2004 at the Tapichalaca Biological Reserve (4°30′S, 79°10′W), located on the east slope of the Andes, ca. 11 km north of Valladolid in the southeastern Zamora-Chinchipe Province of Ecuador. Nests were studied at altitudes ranging from 2550 to 2650 m. The habitat in this area is steep, montane evergreen forest, with a 15–20 m canopy and an understory dominated by tree ferns (Cyathaceae) and *Chusquea* bamboo (Poaceae). Most trees are clad with thick masses of dripping wet epiphytic bryophytes. In December 2006, Paul Martin (Queens University) collected a fourth nest in the vicinity of the town of Papallacta (0°36′S, 78°15′W), Napo Province, at an altitude of 3340 m. The habitat here is dominated by epiphyte-laden *Polylepis* and *Gynoxis* trees interspersed with *Chusquea* bamboo growing on a steep mountain slope. The two study sites are separated by ca. 480 km. We present measurements as means ± SD.

RESULTS

The three nests found in Tapichalaca Biological Reserve were situated 1.5 to 2.4 m above the ground (mean = 2.1 ± 0.4 m), either within a dense understory of *Chusquea* bamboo on a steep slope or (nest 2 in Table 1) over a small stream in an area of tangled tree regeneration and young tree ferns adjacent to a recent landslide. Each nest was attached to 2–4 supporting stems, either the distal portions of lower tree branches or thin lianas. The nest collected near Papallacta was situated in the small branches of a *Phyllanthus* (Euphorbiaceae) shrub. Being cryptically embedded within hanging masses of epiphytic mosses and trapped debris, the nests appeared pendulous (Fig. 1 and 2), but in each case the primary support was provided by woody stems incorporated into the side walls or passing below the nest. The entrances of the three Tapichalaca Biological Reserve nests were oriented to 240°, 275°, and 140°. In the case of nest 2, the entrance was perpendicular to the axis of the stream below.

All four nests were neat balls with a centrally located side entrance and they varied little in external and internal dimensions (Table 1). Nest materials were arranged in three distinct layers (Fig. 3). Externally, nests were constructed of living green moss representing several species of moss growing abundantly on the branches and vines surrounding the nests. Nest walls were thickest in the floor (ca. 6.5 cm) and thinnest in the roof (ca. 2.5 cm), with side walls being intermediate (ca. 4.0–5.0 cm). Loose strands of moss, 8.5–32.0 cm in length, formed a "beard" below each nest, making the nests perfectly camouflaged (Fig. 1).

The chamber inside the mossy ball was entirely lined with dry leaves of *Chusquea* bamboo. These leaves were up to 11 cm long and 4 cm wide. Leaves were criss-crossed, and were compacted to form a layer ca. 0.5 cm thick. The egg cup alone was lined with the brown seed down of *Tillandsia* sp. (Bromeliaceae) and other silky-white plant fibers. These materials were compressed, and formed a distinct cup that retained its integrity even when pulled from the nest. The inner portion of this cup was ca. 5–6 cm in diameter and up to 2 cm thick near the center. The surface of one of the cups was additionally covered with 10–20 narrow, glossy *Cyathea* tree-fern petiole scales (ramenta).

DISCUSSION

The four nests described here represent the first nests of the White-browed Spinetail known to science. They were all balls of green moss, bamboo leaves, and seed down cryptically embedded within hanging masses of epiphytic mosses. They showed little intraspecific variation in all aspects of architecture studied and are thus likely to be phylogenetically informative.

Although *Hellmayrea* has formerly been considered to belong in *Synallaxis* (Meyer de Schauensee 1970, Vaurie 1980), be a sister

TABLE 1. Variation in size among four nests of the White-browed Spinetail found in southeastern Ecuador.

	Outside diameter (cm)			Inside diameter (cm)		Entrance diameter (cm)	
Nest	Top to bottom	Side to side	Front to back	Vertical	Horizontal	Vertical	Horizontal
1	15.0	17.0	17.0	9.0	8.5	3.5	3.5
2	18.0	18.0	15.0	8.5	8.5	3.0	4.5
3	17.0	17.0	16.0	9.5	8.5	3.0	3.5
4	16.0	16.0	15.0	8.0	8.0	3.0	3.5

FIGURE 1. An adult White-browed Spinetail (*Hellmayrea gularis*) perched outside the entrance of a nest just after feeding nestlings in southeastern Ecuador.

FIGURE 2. A White-browed Spinetail (*Hellmayrea gularis*) nest built into a hanging clump of vines and epiphytes in southeastern Ecuador. The arrow indicates the nest entrance.

species to *Cranioleuca* (Braun and Parker 1985, García-Moreno et al. 1999), or to form part of a clade including other synallaxine genera (*Anumbius*, *Coryphistera*, and *Phacellodomus*; Irestedt et al. 2006), its nest architecture does not support any of these relationships. With the exception of *Cranioleuca*, the aforementioned synallaxines form a clade based on detailed nest synapomorphies (Zyskowski and Prum 1999), none of which are shared with *Hellmayrea*. In contrast to *Hellmayrea*, these synallaxines construct domed nests of dry sticks; some have long entrance tubes, thatch, and lining of pubescent leaves (*Synallaxis*); some are entered from above and adorned with conspicuous objects around the entrance (*Anumbius*, *Coryphistera*); and some are semipensile with a constricted entrance tunnel (*Phacellodomus*; Zyskowski and Prum 1999). Although it is possible that some of these nest characters are the result of these birds inhabiting dry, open environments, the architecture of *Hellmayrea* nests is dissimilar in too many respects to hypothesize a sister relationship with the aforementioned genera based on nest architecture.

The sister relationship between *Hellmayrea* and *Cranioleuca* is also not supported by nest architecture. Nests of *Cranioleuca* spinetails lack bamboo leaves, *Tillandsia* seed down, and tree-fern scales, and instead incorporate other plant materials, such as woody twigs, rootlets, bark strips, and grass (Remsen 2003; KZ, pers. obs.). Although pensile mossy nests of some montane *Cranioleuca* species superficially resemble those of *Hellmayrea* (Remsen 2003; KZ, unpubl. data), the former typically drape strands of live moss from a branch or over a vertical fork, resulting in a campanulate, shaggy mass supported at or near the top and entered from underneath (KZ, pers. obs.). In contrast, *Hellmayrea* appear to construct their nests by stuffing strands of live moss into preexisting hollows within hanging masses of epiphytes and woody stems, and the resulting sphere is supported near the bottom and entered from the side. This form of nest placement and material manipulation has recently been described for the Spotted Barbtail (*Premnoplex brunnescens*; Greeney 2008a), and may also be employed by *Schizoeaca* thistletails. The few *Schizoeaca* nests described to date were supported by bushes or dense grass, entered from the side or near the top, and possibly constructed by stuffing *Sphagnum* moss into a framework of twigs or grass stems (Zyskowski and Prum 1999, Remsen 2003).

Since *Hellmayrea*, *Premnoplex*, and *Schizoeaca* do not appear to be closely related to each other (Irestedt et al. 2006), the "stuffing" behavior probably evolved independently as many as three times within the family Furnariidae. This behavioral innovation is also thought to occur outside the furnariid clade in the Tyrannidae, including *Pseudotriccus* pygmy-tyrants, *Zimmerius* tyrannulets, and the *Silvicultrix* clade of *Ochthoeca* chat-tyrants

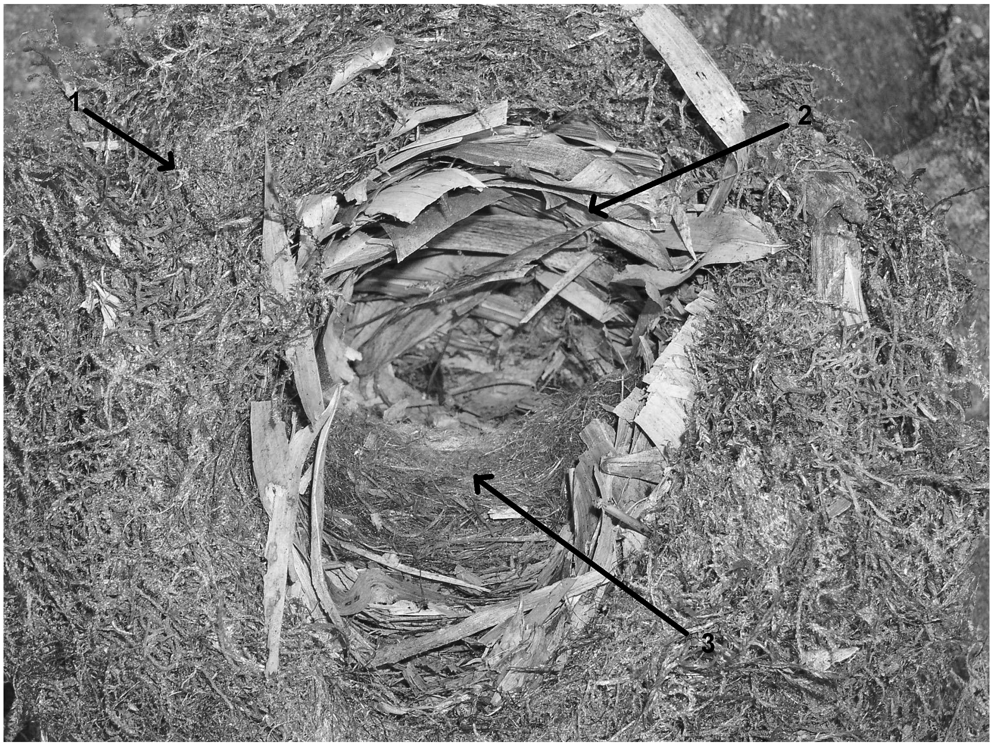

FIGURE 3. **Cross-section of a White-browed Spinetail** (*Hellmayrea gularis*) nest from southeastern Ecuador. Arrows indicate: (1) outer mossy layer, (2) inner chamber lining of bamboo leaves, and (3) inner cup lining of seed down.

(Fitzpatrick 2004, Greeney et al. 2005, Greeney 2006, Miller and Greeney 2008). The feature uniting the taxa known to use moss-stuffing is their humid, epiphyte-laden, montane habitat, further supporting the hypothesis of multiple origins of stuffing behavior.

The composition of *Hellmayrea* nests is unique in the Furnariidae. No other furnariid nest combines a shell of green moss, inner sphere of dry bamboo leaves, and a distinct cup of *Tillandsia* seed down at the bottom of the nest chamber. Notably, however, the construction of a sphere of dry *Chusquea* bamboo leaves, criss-crossed and compacted to form a layer impervious to water, is shared by the Sharp-tailed Streamcreeper (*Lochmias nematura*), another furnariid representing a monotypic genus and inhabiting wet forest undergrowth. However, streamcreepers construct their bamboo spheres inside self-excavated subterranean burrows or natural rock crevices (Goeldi 1894, Narosky et al. 1983; KZ and HFG, unpubl. data). Outside the Furnariidae, two other passerines nesting in extremely wet environments in the Andes, the White-capped Dipper (*Cinclus leucocephalus*, Cinclidae) and Olive Finch (*Arremon* [*Lysurus*] *castaneiceps*, Emberizidae), also appear to use a thick lining of bamboo leaves in this manner (Greeney and Gelis 2006, Greeney 2008b). In all cases, the function of the bamboo leaves seems to be to isolate the nest contents from the wet surroundings. For each of these, including *Hellmayrea* and *Lochmias*, this character is shared more likely as a result of convergence than common origin. Based on DNA sequencing, *Lochmias* is only distantly related to *Hellmayrea* (Irestedt et al. 2006).

Finally, it is also noteworthy that one *Hellmayrea* nest was additionally lined with tree-fern scales (ramenta). The use of ramenta is rare in the Furnariidae and has been reported only in the tuftedcheeks (*Pseudocolaptes* spp.; Skutch 1969, Zyskowski and Prum 1999, Solano-Ugalde and Arcos-Torres 2007), Rusty-winged Barbtail (*Premnornis guttuligera*; Dobbs et al. 2003), and two species of *Thripadectes* treehunters (KZ and HFG, unpubl data). More nests from a wider geographical area are needed to establish whether the use of this special material by the furnariids, including *Hellmayrea*, is occasional or routine, and to evaluate the potential function and phylogenetic significance of this nest character.

In summary, nests of *Hellmayrea* represent a unique type of nest architecture in the family Furnariidae, which does nothing to further the resolution of the phylogenetic position of this enigmatic taxon. Most of the potential nest synapomorphies discussed above are more likely a result of convergence than common origin. Nest features that make the nest impermeable to water are likely to have evolved as an adaptation to extremely wet Andean environments, and the choice of nest materials appears to be correlated with environmental variation in material availability. All nest characters discussed in this paper will need to be reevaluated when a more taxonomically complete molecular phylogeny of the Furnariidae becomes available. In addition, data are needed on nest ontogeny, i.e., the type and sequence of events during nest construction, to test homology of various nest construction behaviors (e.g., moss-stuffing). As shown by Zyskowski and Prum (1999), nest ontogeny may reveal additional information about the homology of cryptically homologous or superficially similar but analogous nest characters.

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