

Nest construction behavior and variability in nest architecture & nest placement of the Spotted Barbtail (*Premnoplex brunnescens*)

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Abstract

The Spotted Barbtail (*Premnoplex brunnescens*) builds large, mossy, ball-shaped nests with downward facing entrance tubes. Nests are built along streams in a variety of situations including inside cavities, in hanging clumps of epiphytes, on rock faces, and under fallen logs. Nests are built by both adults over the course of more than 4 months, with some nests taking longer than 15 months to finish. After preparing an area by stuffing living moss into cracks and irregularities around the nest site, adults construct their enclosed nest. Nests are often formed in part by the surrounding substrate such as clay, wood, rocks, or epiphytes, and thus the entire ball is not always constructed by the adults. The moss-stuffing behavior of adults during early construction allows them utilize naturally formed partial cavities or to create their own cavities (or cavity-like situations), and may provide an example of how this, and other species of furnariids, have shifted from cavity to external nest building. Nests examined from Ecuador include an internal lining, which has not been reported from nests at higher latitudes, thus suggesting that there may be geographic variation in nest architecture.

Keywords: Andes, cloud forest, Ecuador, Furnariidae, nest architecture, reproductive biology.

Resumen

El Subepalo Moteado (*Premnoplex brunnescens*) construye nidos grandes, compuestos de musgo, con forma de bola inclinada hacia el túnel de entrada. Los nidos son construidos a lo largo de ríos y quebradas en una variedad de situaciones, en enmarañados de epifitas colgantes, en paredes rocosas y por debajo de árboles caídos. El nido es construido por los dos adultos durante el curso de más de 4 meses, algunos nidos tardan más de 15 meses en ser terminados. Después de preparar el área apiñando musgo vivo en las grietas e irregularidades alrededor del área del nido, los adultos construyen sus nidos cerrados. Los nidos son a menudo construidos en parte por los sustratos circundantes como arcilla, madera, piedras, o epifitas, y de esta manera no toda la bola es siempre construida por los adultos. El primer comportamiento de construcción, cuando los adultos apiñan los musgos, les permite utilizar cavidades formadas naturalmente o crear sus propias cavidades y puede proporcionar un ejemplo de cómo ésta y otras especies de furnáridos han cambiado la forma de construcción del nido de una cavidad a una construcción externa. Los nidos examinados en Ecuador, incluyen un recubrimiento interno que no ha sido reportado en nidos en latitudes superiores, lo cual sugiere que debe de haber variaciones geográficas en la arquitectura del nido.

Palabras claves: Andes, arquitectura del nido, biología reproductiva, bosque nublado, Ecuador, Furnariidae.

Introduction

This paper is part of a series of publications describing the natural history of the Spotted Barbtail (*Premnoplex brunnescens*). Recently, I reviewed the current state of knowledge of its taxonomy, distribution, behavior, and breeding ecology, as well as provided general observations on breeding in northeastern Ecuador (Greeney 2008a). In a separate study, I presented and analyzed data on their very specific nest-orientation preferences, without commenting in detail on their architecture and micro-site selection (Greeney

2008b). In this paper I present data on nest architecture and placement from 316 nests, found throughout Ecuador, at elevations from 1000 to 2500 m.a.s.l.

The Spotted Barbtail (Fig. 1-2) inhabits the interiors of montane forests from Costa Rica to Bolivia (Remsen 2003). Previous descriptions of Spotted Barbtail nests (Skutch 1967, Marin & Carrion 1994, Greeney & Nunnery 2006, Greeney & Gelis 2007, Areta 2007, Greeney 2008a) have provided insight into the variability of nest sites used across the species' geographic range. Most of these studies, however,

provided information on only a handful of nests at best. After 7 years of nest searching at one site, I am now able to describe the amazing flexibility this bird shows in nest-site selection. Here I describe the detailed architecture of Ecuadorian nests (ssp. *brunnescens*: *sensu* Ridgely & Greenfield 2001, Remsen 2003), the

variety of nesting sites occupied, and the various means of nest attachment shown by this remarkable bird. In addition, I provide observations on nest building behavior and discuss architecture and nest construction in a phylogenetic context.



Fig. 1. An adult Spotted Barbtail (*Premnoplex brunnescens*) peers out of the nest entrance at the Yanayacu Biological Station, Napo, Ecuador, 2000 m.a.s.l.



Fig. 2. An adult Spotted Barbtail (*Premnoplex brunnescens*) delivers food to nestlings at the Yanayacu Biological Station, Napo, Ecuador, 2050 m.a.s.l.

Methods

I made observations on 297 nests, from May 2001 to December 2007, in the vicinity of the Yanayacu Biological Station and Center for Creative Studies (00°36' S, 77°53' W, 1900-2400 m.a.s.l.) and Cabañas San Isidro (1900-2200 m.a.s.l.), 3-5 km west of Cosanga, Napo Prov., northeastern Ecuador. I also gathered information from nests at the following localities: Sumaco Volcano (1700-2400 m.a.s.l.), Napo Prov. (n = 5; Greeney & Gelis 2007); Mushullacta Community Reserve (n = 2; 00°50' S, 77°34' W, 1000-1150 m.a.s.l.), Napo Prov.; Tandayapa (n = 1; 00°00' N, 78°41' W, 1350 m.a.s.l.), Pichincha Prov., northwestern Ecuador; vicinity of Mindo (n = 5; 00°04' S, 78°43' W, 1600-1800 m.a.s.l.), Pichincha Prov. (Greeney & Nunnery 2006); Mindo Loma (n = 4; 00°00' S, 78°44' W, 1750-1800 m.a.s.l.), Pichincha Prov.; Tapichalaca Biological Reserve (n = 2; 04°30' S, 79°10' W, 1800-2500

m.a.s.l.), Zamora-Chinchipe Prov., southeastern Ecuador.

At each nest, when possible, I recorded the following measurements: nest height above the water's surface (n = 304), nest outside width (n = 50), nest outside height (Fig. 3a; n = 50), entrance width (n = 42), entrance height (Fig. 3b; n = 42), entrance tube length (Fig. 3c; n = 40), entrance overhang (Fig. 3d; n = 42). In addition I recorded the primary and secondary substrates to which nests were attached. For example nest "A" was attached to vines (2° substrate) hanging below a horizontal tree trunk (1° substrate). Often nests were attached directly to a primary substrate. I also scored the mobility of each nest as "hanging" or "fixed." If I was able to easily change the orientation of the nest entrance by more than 10°, then I considered the nest as "hanging" and, if not, I considered it "fixed." At each nest I also described which portions of the nest were attached to a substrate (i.e., attached by top and one side, or attached by back and top).

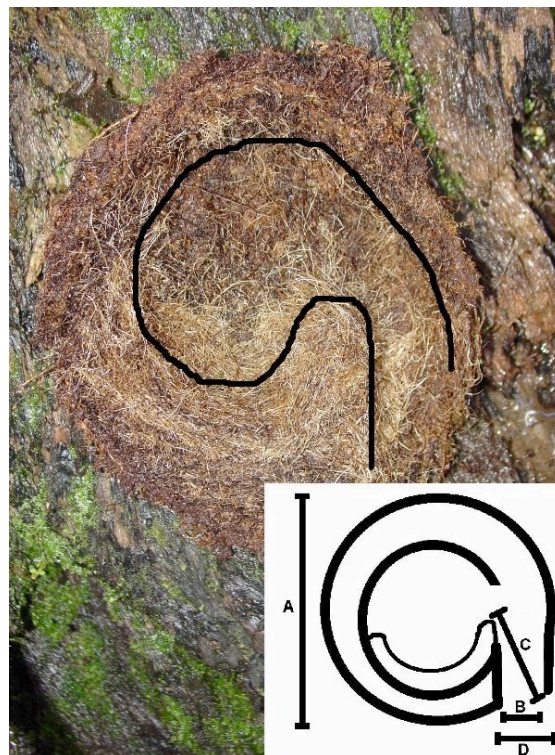


Fig. 3. Photograph of a nest of Spotted Barbtail (*Premnoplex brunnescens*) which has been cut in half to show the inner lining of pale fibers. The inner chamber and entrance tube of the nest have been outlined in black. Inset shows the measurements taken while describing barbtail nests: a, outside height; b, entrance height; c, entrance tube length; d, entrance hood overhang.

Results

Nest architecture. Although nest placement and attachment varied considerably (see *Nest-site selection*), most nests ($n = 287$) were of the same basic architectural design. They were large, globular, mossy balls with a downward facing entrance tube (Fig. 1-8). The downward entrance into the nest chamber was slightly wider than tall, with the entrance flaring laterally, but with the height of the entrance maintained along the length of the tube. The inner chamber held a thick cup of pale fibers with an elevated front lip that served to contain the nest contents as well as to form the inner portion of the entrance tube (Fig. 3). Although this description applies to the majority of nests, many nests were variously constructed such that one or several portions of the outer nest structure were actually formed by part of the surrounding substrate, in a similar manner to the nest illustrated by Skutch (1967). Thus, large portions of the inner chamber were often devoid of moss, and instead formed by the clay or wood to which the nest was attached (Fig. 4a). One fairly extreme example of this was a nest built wedged into a vertical crevice in a horizontal log. Only the front, top, and bottom portions of the nest were composed of moss, whereas both sides and the back were formed by the surrounding wood. Another example was a nest built just inside the entrance to an abandoned Highland Motmot

(*Momotus aequatorialis*) nest burrow. In this case the front of the nest was built as described above, forming a hood over the downward entrance tube, which opened just outside and below the burrow entrance. Other than this, moss had been tightly wedged into the inner portion of the tunnel, effectively blocking it off and creating a nest chamber formed on the sides, top, and bottom, by the earthen walls of the motmot tunnel. On the bottom of the nest chamber, resting directly on the floor of the tunnel was the typical inner cup of pale fibers, which held the eggs. In the case of two nests, both inside shallow, natural, earthen cavities, no moss was used in construction and the nest consisted of a thick cup of pale fibers that was entered directly through the cavity opening.

Using only those nests fully formed with moss, mean dimensions (cm \pm SD, Fig. 3) were: outer nest height, 15.3 ± 1.7 ; outer nest width, 16.1 ± 2.0 ; entrance width, 5.4 ± 0.8 ; entrance height 3.1 ± 0.4 ; entrance hood overhang, 5.9 ± 1.4 ; entrance tube length, 8.2 ± 1.7 ; entrance tube width, 3.7 ± 0.6 . Because nests are used for multiple breeding attempts (Greeney 2008a), I was able to measure the inner chamber (with lining removed) of only one nest. It measured 11.5 cm tall by 9 cm wide. By carefully removing the lining from 4 nests, I measured the dimensions of the egg cups. These were generally 1-2 cm thick with a mean inner width of 5.3 ± 0.5 cm by 3.0 ± 0.4 cm deep.

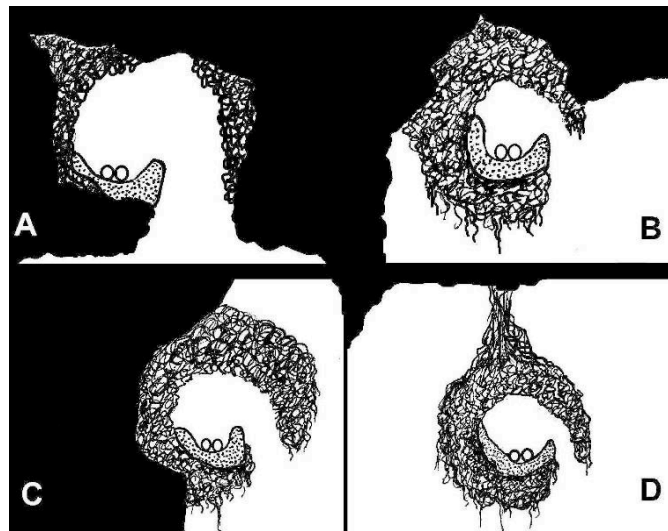


Fig. 4. Drawings in cross-section of Spotted Barbtail (*Premnoplex brunnescens*) nests illustrating a variety of nest placement strategies: a, fixed nest completely inside an earthen cavity with only sparse construction of the outer mossy shell; b, fixed nest built partially into a shallow cavity in the ceiling of a clay overhang; c, fixed nest built partially into a shallow cavity in the wall of a clay bank; d, hanging nest attached to a thin rootlet under a clay bank.

Nest-site selection. All nests were along well shaded streams (Fig. 5), the majority within primary forest. Of 316 nests, only five were not directly above flowing water. The streams below these nests, however, appeared to have recently shifted direction, and it is likely that they were over water at the time of construction. One such nest was never occupied during the course of my study, perhaps because the shifting of water caused abandonment. Two others were not occupied after initially being found active, and I do not know the fate of the final two. Mean nest height above the water was 1.7 ± 0.9 m (range = 0.25 - 5 m, n = 304). Nests showed a remarkable variety of substrates and means of attachment, a few of which are illustrated in Figures 4-8. Of 305 nests, 74% of nests were considered “fixed” and attached directly to an immobile primary substrate. The other 26% were attached to a mobile secondary substrate (such as a hanging clump of epiphytes), where I could easily alter the orientation of the opening, and thus were considered “hanging.” As primary substrates I recorded

horizontal tree trunks (36 %), tree trunks angled at $\approx 45^\circ$ (30 %), soil banks (17 %), rock faces (13 %), and vertical tree trunks (4 %), whereas secondary substrates included moss epiphyte clumps (85 %), single thin vines (8 %), multiple thin vines (3.5 %), and multiple small branches or tangled vines (3.5 %). Of 291 nests, 202 were located directly on the primary substrate (Figs. 4a-c, 5c-d, 6, 8), with the remaining 89 nests attached to secondary substrates (Fig. 4d, 5a-b, 7). Although many of the nests fixed into hanging epiphyte clumps were likely built into some sort of pre-existing vegetative niche, 20 of 291 nests were built into actual cavities (Figs. 2a, 8) such as crevices in rotting wood (45 %) or soil banks (55 %). One of these, as described previously (see *Nest architecture*) was built into the entrance of an abandoned Highland Motmot nest tunnel. In six cases, nests were built attached to some degree, and usually sharing at least one wall with, a previously constructed nest (Fig. 6b).

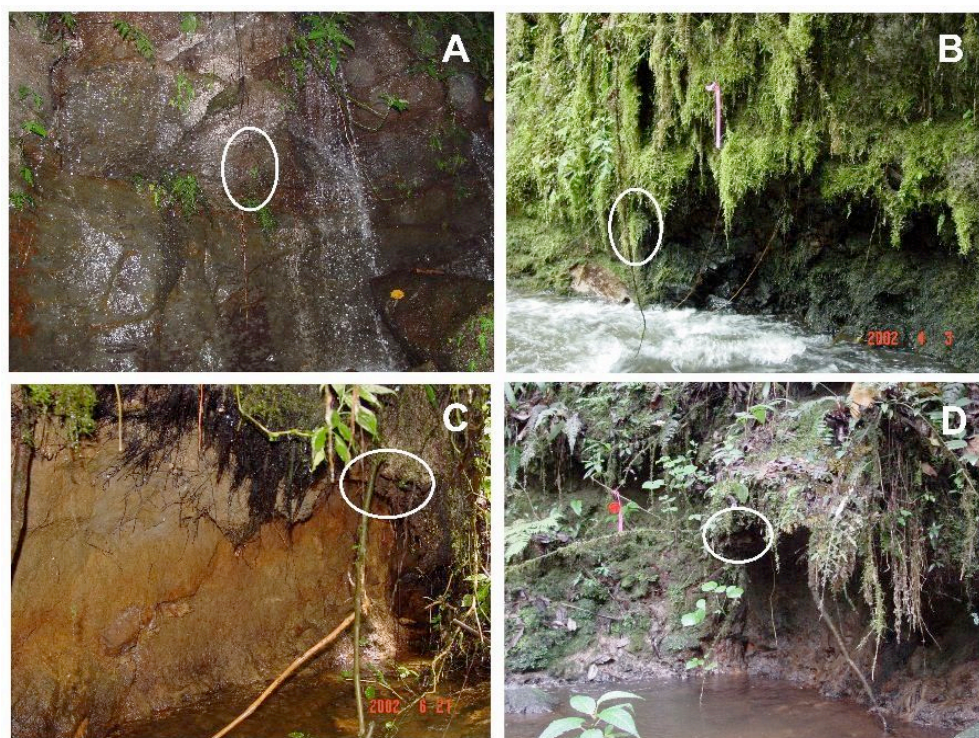


Fig. 5. Nests and nesting sites of Spotted Barbtail (*Premnoplex brunnescens*) at Yanayacu Biological Station, Napo, Ecuador, 1950-2200 m.a.s.l., white circles surround the nest in each photo: a, nest hanging by a thin vine adjacent to a small waterfall; b, nest hanging by a narrow attachment of moss and vines at the edge of a small rock overhang; c, fixed nest built partially into an earthen cavity of an overhanging bank; d, fixed nest attached from above to an overhanging dirt bank.

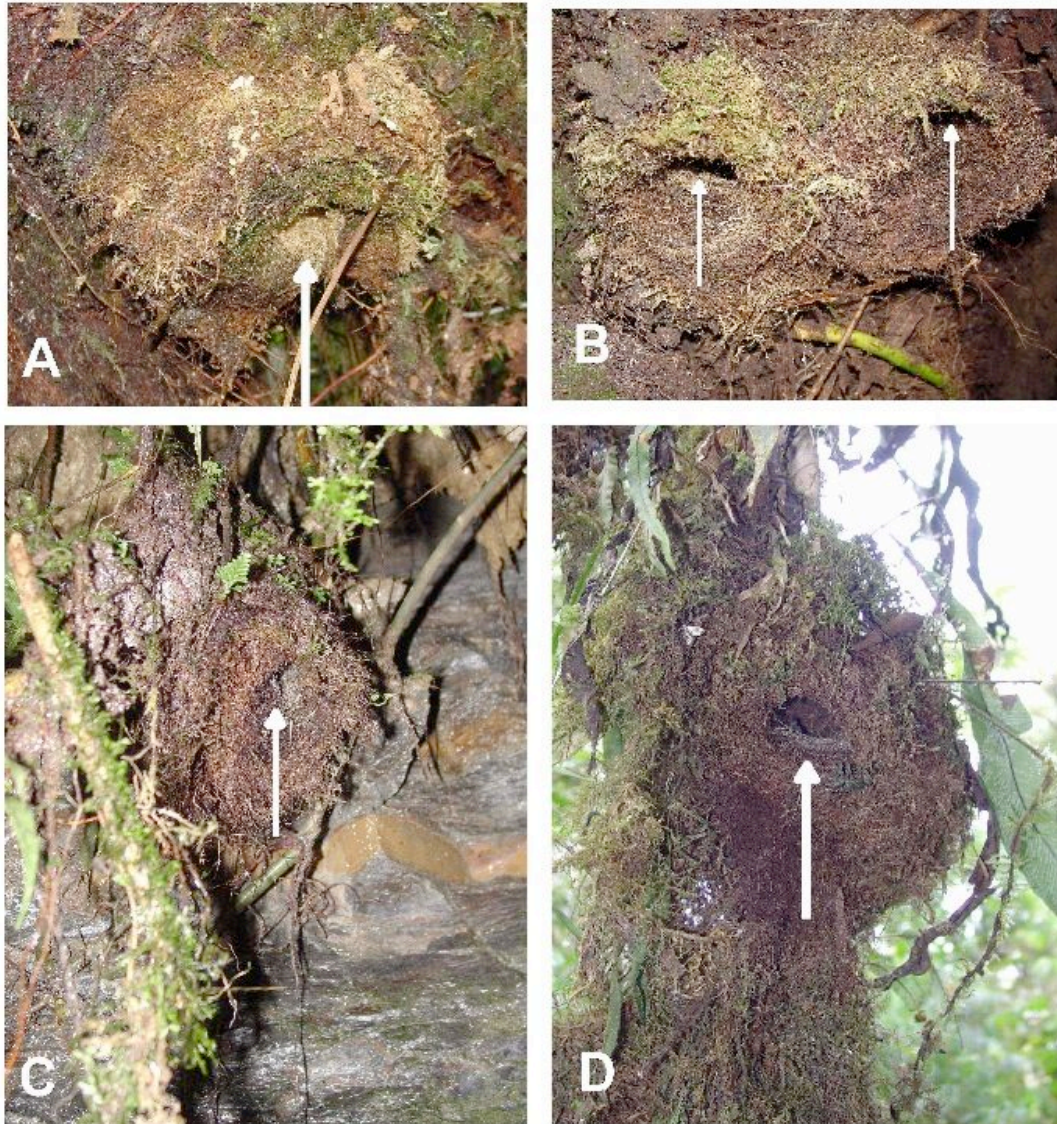


Fig. 6. Nests of Spotted Barbtail (*Premnoplex brunnescens*) at Yanayacu Biological Station, Napo, Ecuador, 1950-2200 m.a.s.l., arrows indicate nest entrances: a, fixed nest attached by the back and top to a mossy earthen bank; b, two fixed nests built adjacently, sharing a wall between them and attached by the back to an clay overhang; c, fixed nest attached by the back to a large clump of earth broken away from a dirt overhang; d, fixed nest attached by the side and the bottom to a large clump of mosses and epiphytes.

Nest construction behavior. Both sexes participate in nest construction, and from the first adult arrivals with beaks full of moss, the entire process can take over one year to complete. At one nest, which consisted of only a few scraps of fresh moss in early October 2006, the first clutch of eggs had not been laid as of January 2008. I am also still observing several nests started before October 2006 and still not finished as of January 2008. In three cases, however, I found nests begun and finished within 4 months. Six additional nests were completed within 7 months from when I first found them, but in all cases

there was already a substantial amount of moss present, forming most of the basic outer nest structure. Most nests I observed, probably long after completion, were mostly composed of living mosses and liverworts that had become so thickly interwoven over time that they appeared to be part of the surrounding vegetative material and had become host to epiphytic orchids and bromeliads. Often nests appeared to have been there so long that inner portions of the mossy walls had nearly decomposed into soil mixed with a thick network of living rootlets from surrounding plants.



Fig. 7. Nests of Spotted Barbtail (*Premnoplex brunnescens*) at Yanayacu Biological Station, Napo, Ecuador, 1950-2200 m.a.s.l., arrows indicate nest entrances: a, hanging nest attached by the top to the end of a large vine, the epiphytic bromeliad is growing on the outer wall of the nest; b, hanging nest attached narrowly at the top to the broken end of a thin, horizontal branch; c, hanging nest attached to a single thin vine; d, hanging nest attached by a thin sheet of moss to a U shaped vine which has become dislodged from its original large mossy tangle of vines and epiphytes.

Nest construction can be broken into three phases. The first involves placement of live mosses and liverworts into holes and cracks surrounding the area that will eventually hold the nest. Depending on the nest site selected, there may be cracks in the surrounding

clay, holes in the wood, or in the case of nests completely outside of cavities, irregularities in the surrounding epiphytic vegetation. The mosses and liverworts used to fill irregularities surrounding the nests' eventual attachment point create a partial cavity or

a more regular mossy surface to which the nest will be anchored. There is frequently a 1 week to 2 month delay before the second phase of construction begins. The second phase involves the formation of the outer nest structure, built of mosses, liverworts, and rootlets. This phase is often very protracted, lasting 2-8 months. During this phase the birds complete the globular outer structure of the nest. This is usually accomplished by first building a simple ring of moss. This two-dimensional ring is then added to, both forwards and backwards, until the three-dimensional, spherical structure of the outer nest is formed. Once the globular structure is complete, adults add material to the front, upper portion and work forward until the material forms the downward-facing entrance tube. At the single nest where I observed this entire process, the outer portion of the nest was completed in ca. 8 months. After 8 months of observation I blocked the entrance with a leaf, which remained untouched for 3 months. However, after 3 months (11 months after I first discovered the beginnings of this nest), adults began to visit the nest regularly, as evidenced by the continual removal of the leaf placed in the entrance. On several occasions I found an adult roosting in the nest, and I suspect that the nest was used as a nocturnal roost during most of this period. Finally, one year after construction commenced, the adults began the final phase, lining the nest with pale fibers over the course of 2 weeks. After this, adults occasionally roosted in the nest at night, but added little or no material to the nest. Now, five months later, the first clutch still has not been laid, giving a building period of over 17 months for this nest. In some instances, it appears that dormitory nests (Skutch 1967, Greeney 2008a) were augmented, eventually becoming breeding nests. Although additional observations on nest construction are needed, I suggest that most if not all nests are constructed in this manner. Those nests that are apparently hanging by few, or even a single, thin attachment point (Figs. 4d, 5a-b, 7) were likely built in the manner described above, but have subsequently become dislodged from their original, more fixed, attachment as the soil, vegetation, or wood was dislodged around them. Similarly, I suspect that the few nests found in situations such as small vine or branch tangles, where they appeared to have been attached by simply wrapping moss around small branches, were originally constructed into larger, denser clumps of vegetation that had subsequently fallen away from around the nest.

Because of the extremely slow rate at which nests are built, I have little information on adult behavior during construction. From videotaping behaviors at one nest during the lining phase, I found that adults may build at a rate of over 20 visits per adult per h, and then not return to the nest for several weeks or months. Most of my direct observations of nest construction were during the lining phase. While lining the nest, both adults frequently make their characteristic, loud, trilling call (Hilty & Brown 1986, Ridgely & Greenfield 2001, Areta 2007). Before reusing old nests (Greeney 2008a), the previous lining is removed and a new lining is added.

Discussion

The strikingly long period of nest construction seen at some nests of the Spotted Barbtail is, perhaps, what allows them to reuse nests over extended periods of time, in some cases up to 6 years (Greeney 2008a). By building the nest over the course of many months, barbtails allow the living mosses to grow and attach themselves to their new location. These new patches of moss also attract the growth of other plants, such as bromeliads and orchids which, in turn, aid in strengthening the integrity of the nest and its attachment point. Similarly, the mossy nests of other cloud-forest species (e.g., Grey-breasted Wood-Wren [*Henicorhina leucophrys*], Slaty-backed Nightingale Thrush [*Catharus fuscescens*]), although not reused, often grow onto the substrate and remain for several years as a living clump of moss (pers. obs.).

Spotted Barbtails are part of the ovenbird-woodcreeper clade (Furnariidae sensu Fjeldså *et al.* 2004), which are widely distributed and show as much variation in nest architecture and placement as the entire rest of the Passeriformes (Collias 1997, Zyskowski & Prum 1999). Some groups of furnariids show a great deal of geographic variation in nest architecture and placement (e.g., *Upucerthia*, *Asthenes*), but recent data suggest that genera such as these may be polyphyletic (Irestedt *et al.* 2006, Chesser *et al.* 2007), and some species may actually consist of several species (Remsen 2003, Chesser *et al.* 2007). Most taxa, however, are fairly consistent, especially in regards to nest materials used (Zyskowski & Prum 1999). Good examples include the use of leaf rachises in *Sclerurus* (e.g., Skutch 1969, Vaurie 1980, Denton & Blue-Smith 2000), sticks in *Synallaxis* (e.g., Bosque & Lentino 1987, Balchin 1996, Simon & Pacheco 1996), and tree fern scales in *Pseudocolaptes* (Skutch 1969, Solano-Ugalde & Arcos-

Torres 2007). Although sample sizes are low, especially within species, the consistent use of the same materials within genera appears to provide phylogenetically useful characters. As pointed out by Zyskowski & Prum (1999), however, if nest architecture is to be used in creating and testing phylogenetic hypotheses, then the appropriate characters must be selected when reconstructing phylogenies. Rarely, however, are the appropriate characters reported in nest descriptions (Zyskowski pers. comm.), often making it difficult to test phylogenetic hypothesis based on nest architecture. One good example in which nest architecture was used to test a phylogeny was in the furnariid genus *Thripadectes*, all of which build superficially similar nests (flat cups inside excavated tunnels) (Remsen 2003). A recent review of nest cup components and structure within *Thripadectes* reveals that nest materials

and their arrangement may be phylogenetically informative and conserved within species (Zyskowski & Greeney unpub.). In some cases, however, nest materials may vary geographically, most likely based on availability (Zyskowski & Prum 1999). Similarly, availability of common, widely distributed materials may lead to their use by many furnariids, as is certainly the case with moss, the primary component of *Premnoplex* nests and indeed the primary nest component of most birds living in mossy habitats (pers. obs.). Therefore, to understand the evolution of nest architecture in *Premnoplex* we must look past its nest description as a “globular, mossy ball” and explore such details as the ontogeny of nest construction, another character emphasized by Zyskowski & Prum (1999), as one that might ultimately provide informative characters.

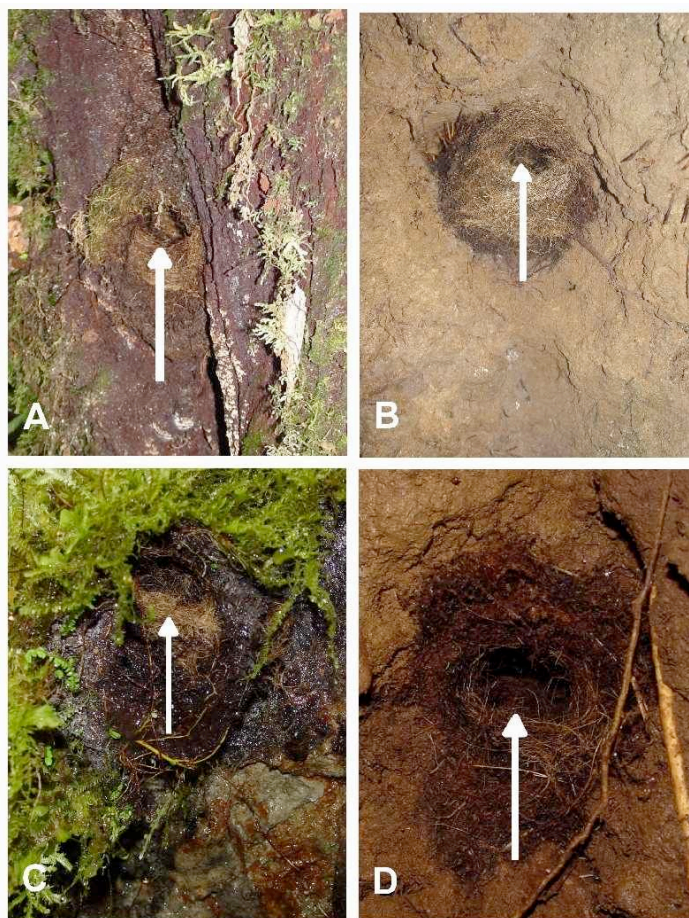


Fig. 8. Nests of Spotted Barbtail (*Premnoplex brunnescens*) built into natural cavities at Yanayacu Biological Station, Napo, Ecuador, 1950-2200 m.a.s.l., arrows indicate nest entrances: a, fixed nest wedged into a vertical crevice in a horizontal tree trunk; b, fixed nest built into the entrance of an irregular earthen cavity in a vertical bank; c, fixed nest built into a small niche in a rock wall; d, fixed nest built into a downward opening cavity in the ceiling of a dirt overhang (photo taken from below).

Until now, the ontogenetic steps involved in nest construction for *Premnoplex* have remained unknown. Perhaps the most telling is the “stuffing” behavior whereby crevices and holes surrounding the nests final position are filled by the birds prior to nest construction. As *Premnoplex* is currently thought to be part of the philydorine clade, derived from the cavity-enclosed cup-building ancestors of basal taxa (i.e., *Geositta*; Irestedt *et al.* 2006), the most parsimonious reasoning would suggest that *Premnoplex* evolved from an ancestor that built a cup or platform nests inside a cavity. Because enclosed nests within cavities may have evolved in response to radiations into colder, more humid climates (Remsen 2003: 228), *Premnoplex* may provide an extant example of how variation in nest architecture can lead from the construction of a simple cup to an entirely enclosed ball in a high-elevation nesting species. If stuffing moss into irregularities surrounding the nest site is a behavior simply performed until a suitable chamber is created, variation in the original chamber size and shape would naturally lead to variation in the amount and placement of moss. In some cases, where adults have found “the perfect nest site,” almost no stuffing is required, and the birds build a simple, ancestrally derived cup, consisting of nothing more than what we now consider the cup lining in more extensively built ball nests. In other cases adults are forced to bring more moss to the nest site, filling irregularities and leaks in a haphazard manner that results in the partially domed nests frequently observed here. This ability to fill spaces around the nest site with tightly compacted moss may also have promoted the gradual evolution of nests further and further from actual cavities, allowing them to create or augment cavities and releasing birds from the constraint of having to find an entirely naturally formed cavity. As the first step in building the actual nest ball, at least in some cases, appears to be the construction of a ring of moss attached on all sides, this early-construction stuffing may frequently result in modifications to a partial cavity that expand it slightly outward, giving this ring more secure attachment points. This then provides a more stable foundation from which to continue the attachment of additional moss to complete the dome in areas not protected within a cavity. Similarly, stuffing may have aided the evolution of nests entirely outside of cavities. The stuffing innovation has potentially allowed birds to build their own “cavities” even in exposed and extremely irregular situations such as hanging clumps of epiphytes. By first filling in gaps in the complex architecture of epiphyte, moss, and vine-laden tangles,

commonly found in Andean forest habitats, *Premnoplex* can create “cavities” outside of situations we would traditionally expect a “cavity nester” to build their nest. Greeney (2008a) suggested the possibility that Spotted Barbtail may be excluded from suitable nest sites, such as earthen banks, by both Highland Motmots and *Thripadectes* treehunters. Although the interactions of barbtails with other cavity nesters in the area (i.e., dendrocolaptines, woodpeckers, *Myiarchus* flycatchers, *Troglodytes* wrens, etc.) are not known, it is possible to speculate that competition for nesting sites may have been among the factors which led to barbtails’ shift away from cavity nesting. The ability of Spotted Barbtails to avoid direct dependence on pre-existing cavities possibly reduced competitive pressures for natural cavities, and may have been a key innovation leading to their currently broad distribution (Remsen 2003) and apparently high population densities in some areas, often greatly surpassing the abundance of other strictly cavity nesters (pers. obs.). While these speculations pertain specifically to barbtails, it is likely that the shift away from cavities occurred at a deeper node within the *Margarornis-Premnoplex* clade. Thus, it is important for future work to investigate nest construction in further detail for all members of this clade, before these speculations are given too much weight.

Interestingly, though nest construction was not observed, it has been suggested that the enclosed mossy nests of White-browed Spinetail (*Hellmayrea gularis*), which build in situations similar to many of the barbtail nests described here, may use a similar stuffing technique to anchor their nest into the partial cavities formed by clumps of moss and epiphytes (Greeney & Zyskowski in review). *Hellmayrea* is currently considered to belong to the synallaxine clade (Irestedt *et al.* 2006). Though their completed nests are structurally different from those of *Premnoplex*, it remains to be seen if this shared construction process is a convergent character independently derived by two genera adapting to the wet, mossy habitats of Andean cloud forests.

The stuffing innovation in nest construction also explains the findings of Zyskowski & Prum (1999), who grouped *Premnoplex* with other mossy, enclosed, pensile nest builders such as *Cranioleuca*. Although the nest ontogeny of *Cranioleuca* is well known to begin with moss “draping” that results in a roof from which the ball is built gradually downward (Zyskowski & Prum 1999, Zyskowski pers. com.), we now know that *Premnoplex*

is not a “draper,” as we also know it is not closely related to *Cranioleuca* (Irestedt *et al.* 2006). Thus, in this case, although the final nest forms are somewhat convergent in being mossy balls, the ontogeny of nest building has shown this character to be non-homologous, as Zyskowski & Prum (1999) predicted would be the case for many characters, once the details of nest ontogeny were better known. Even those nests of Spotted Barbtail described here, which were apparently pendant, were likely constructed using similar techniques as non-pendant nests, but subsequent natural changes in surrounding materials have “left them hanging.” Thus, as confusingly inadequate nest descriptions in other groups have led to potentially misguided suppositions of relationships based on nest architecture (e.g., Miller & Greeney 2008), I suggest that descriptions of pensile *Premnoplex* nests are most likely an error based on misinterpretation of the actual situation in which the nest was built.

Although all described Ecuadorian nests have fibrous internal nest-cup linings (Marín & Carrión 1994, Greeney & Nunnery 2006, Greeney & Gelis 2007, Greeney 2008a, this study), the detailed description of a nest in Costa Rica by Skutch (1967) did not include a description or illustration of any sort of differentiated lining. Similarly, Areta’s (2007) description of nests from Venezuela did not include a differentiated nest lining. As *Premnoplex*, part of the *Margarornis* clade, likely evolved from a South American ancestor, and

subsequently spread into Central America (Remsen pers. com.); perhaps the loss of an internal nest lining in Central American populations reflects latitudinal climate differences that have released birds from needing a thick, insulating inner egg cup. While it is possible that nest cup linings have been overlooked by previous authors, perhaps due to geographical variation in color which made them less obvious, I suggest that it would be very informative to carefully describe nests of *Premnoplex brunnescens*, both northward and southward from Ecuador, to examine the possibility of latitudinal patterns in nest architecture.

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