ABSTRACT

The Brown Nunlet (N. brunnea) is one of six species of small puffbirds in the genus Nonnula. Here, we describe a nest of Brown Nunlet from Amazonian Ecuador. The nests’ architecture diverges from that of other bucconids, built neither in a subterranean burrow nor in a termitarium, but rather is a flattened, dome-shaped structure composed of leaf litter above a shallow depression. Structural integrity of the leafy dome is created with carefully placed sticks and the inner chamber is entered through a short tunnel. We also provide observations that clarify uncertainties in nest placement of White-chested Puffbird (Malacoptila fusca) and observations on the breeding of other Bucconidae in Amazonian Ecuador.

Key words: Bucconidae, Ecuador, Malacoptila fusca, nest architecture, Nonnula brunnea, Puffbirds.

INTRODUCTION

Nest placement and architecture provide phylogenetically informative characters in a variety of avian groups (e.g., Winkler & Sheldon 1993, Zyskowski & Prum 1999, Miller & Greeney 2008). Most species-rich groups, however, lack data for key taxa and incomplete nest descriptions make interpretation difficult (e.g., Zyskowski & Prum 1999). In contrast, relatively small and well-
defined clades provide us with an opportunity to use
est architecture for reconstructing and testing
phylogenies. One such clade is the puffbird family
(Bucconidae).

The phylogeny and generic taxonomy of the
puffbirds remains largely unresolved (Rasmussen &
Collar 2002). Sclater (1882) and Ridgway (1914)
first evaluated intra-familial relationships using
morphological features. Peters (1948) and Cottrell
(1968) later lumped 15 species into what is likely a
polyphyletic genus, Bucco. Rasmussen & Collar
(2002) and the molecular studies of Witt (2004)
suggest reverting to older generic names for all but
the nominate species B. capensis, but a revised
classification of the group has not yet been widely
adopted (Remsen et al. 2010). As currently defined,
the Bucconidae includes 11 genera and 37 species
divided into two subfamilies, the Malacoptilinae and
Bucconinae (Witt 2004). For all but eight taxa,
published accounts of nest placement are available.
The nests of these species fall into two general
categories: some are placed in tunnels excavated in
termitaria and some are excavated in the ground
(Rasmussen & Collar 2002).

Here we present observations clarifying nest
placement and architecture in two species, Brown
Nunlet (Nonnula brunnea) and White-chested Puff-
bird (Malacoptila fusca). In the former species, the
only described nest was not examined closely
(Dauphiné et al. 2007), and in the latter only vague
data were presented (Rasmussen & Collar 2002).
Additionally, we present breeding information
gathered in Ecuador for four additional bucconids,
White-fronted Nunbird (Monasa morphoeus),
Black-fronted Nunbird (M. nigrifrons), Spotted
Puffbird (Bucco tamatia), and Swallow-winged
Puffbird (Chelidoptera tenebrosa). We interpret
this information in light of what is known about
bucconid phylogeny.

MATERIALS & METHODS

We studied nests of Brown Nunlet and White-
chested Puffbird from 22 to 24 January 2008. The
nests were found in Ecuador’s northeastern Orellana
Province, at 230 m elevation near the Tiputini
Biodiversity Station (TBS, 00° 38’S, 76° 08’W).
The habitat in the area is terra firme forest, typical
of the western Amazon; Freiberg & Freiberg (2000)
give a complete site description. We made
observations on the nesting of four additional
species at the Shiripuno Research Center (SRC, 01°
06’S, 76°43’W, Pastaza Province, c. 220 m
elevation). Habitat at Shiripuno is similar to the
area surrounding Tiputini.

RESULTS

The nest of Brown Nunlet was built on the ground,
in a relatively flat area near the top of a small hill. The
nest was an igloo-shaped structure of leaf litter and
sticks that formed a roof over a shallow
deression (Fig. 1). There was an obvious semi-
circle of cleared ground surrounding the entrance.
The entrance to the nest was 6 cm wide by 3.5 cm
tall (Fig 1). A horizontal, 10 cm long tunnel led
into a circular chamber with internal dimensions of
roughly 12 cm in diameter and 6 cm in height.
Externally, the nest appeared as a roughly circular

![Figure 1. Photograph of Brown Nunlet (Nonnula brunnea)
nest near Tiputini, Orellana, Ecuador. Note the carefully
arranged sticks forming an arch at the entrance. Inset shows a
stylized view of the nest in cross section.](image)
mound of leaf litter, 7 cm tall and 30 cm in diameter. We saw no evidence of any excavation (i.e. small piles of dirt or material), and it appeared that the roof had been constructed over a shallow, natural depression. This depression was either naturally or intentionally lined with leaf litter. On 22 January an adult flushed silently from in front of nest and perched nearby with a small leaf fragment in its bill. The nest was empty, but appeared to be in the final stages of construction. On 24 January the nest was still empty, but a few sticks had been added to further support the entrance tunnel.

On 23 January we flushed an adult White-chested Puffbird from a partially excavated tunnel near the top of a low (1 m), gently sloping bank beside a small drainage at TBS. The adult flushed quietly and perched nearby, where it was immediately joined by its mate. The tunnel was slightly down-sloping, and already at least 45 cm long. We were unable to determine if a terminal chamber had yet been excavated, but we do not believe so. The entrance measured 10 cm wide by 12 cm tall.

At SRC we found two nests of Swallow-winged Puffbird on 7 January 2007. Both were still being excavated, as evidenced by the adults repeatedly emerging while pushing material out of the entrance. We were unable to reach the back of the single nest we approached, even after using a ca. 1 m long stick. Both nests were excavated on gently sloping riverbanks composed of lightly compacted sandy soil.

Also on 7 January 2007, we discovered a pair of White-fronted Nunbirds feeding two nestlings in a small chamber at the end of a 55 cm-long tunnel. The entrance was roughly circular and 9 cm in diameter. The floor of the nest chamber was covered with a thin layer of dead and decaying leaves, but was otherwise clean. The nest was excavated about 40 m from the edge of a small stream in an area of seasonally flooded forest. The nest, however, was at least 5 m above regular annual high-water levels. The nestlings had pink skin, white bills, white gapes, and pale pink-white mouth linings (Fig. 2). During our visit both adults arrived with food, one carrying a ca. 4 cm-long green katydid (Tettigoniidae). Contour pinfeathers were well developed, with those on the dorsal tracts beginning to break their sheaths.

On 2 February 2006, we found a nest of Black-fronted Nunbird with a single well-feathered nestling. The following day the nest was empty and there were no signs of disturbance. The nest was a 60 cm long tunnel excavated in gently sloping

![Figure 2. Photo of nestling of White-fronted Nunbird Monasa morphoeus nesting, 7 January 2007, Shiripuno Research Center, Pastaza, Ecuador.](image)

![Figure 3. Nest entrance of Black-fronted Nunbird Monasa nigrifrons, 2 February 2006, Shiripuno Research Center, Pastaza, Ecuador.](image)
ground about 20 m from the Shiripuno River. The tunnel sloped downward, dropping an estimated 15 cm before opening into a chamber 20 cm wide, 15 cm front to back, and 12 cm tall. The floor of the chamber was covered with a thin layer of dead leaves but otherwise clean. The entrance to the nest was 9 cm wide and 6 cm tall (Fig. 3). An adult arrived at the nest on our first visit and fed the nestling a ca. 5 cm-long green katydid.

Jarol F. Vaca B. described to us his observations on Spotted Puffbird nesting at the SRC. On 8 January 2009 he flushed an adult from a burrow excavated in a termite mound built flush with the ground. The presumed nest tunnel was empty but showed fresh signs of excavation. It was in the lower portion of the termite mound, only several centimeters above the ground. The following day he observed copulation of a pair of Spotted Puffbirds nearby, suggesting they were preparing for breeding.

DISCUSSION

Rasmussen & Collar (2002) mentioned a dubious association between White-chested Puffbird and a cavity in an arboreal termitarium. In contrast, our observations demonstrate that this species does, at least in some cases, excavate a burrow in the ground. Further data are needed to confirm the nest architecture of this species but it is likely that White-chested Puffbird nests in the ground as do other species of *Malacoptila* (Skutch 1958, Rasmussen & Collar 2002).

The nest of Brown Nunlet described here suggests that it builds a nest that differs from those of other Buccoindae. Because we did not observe the construction of the nest, our interpretation that it was built by piling material over a natural concavity (as opposed to excavating an existing pile of material) should be used cautiously. Based on many years of experience in lowland Ecuadorian forests, however, we feel that the material appeared piled rather than naturally fallen. Furthermore, we clearly observed the addition of small sticks that were used as structural support for the overhead material. Based on the excavating behavior of other puffbirds, we believe it is most likely that leaf litter is piled up, then later excavated by the adult and the roof is strengthened by the addition of small sticks. Alternatively, the nest we observed could have been in the early stages of construction and further excavation into the ground had yet to begin. Again, however, we feel this is unlikely because the internal bowl of the nest appeared smoothed and ready to hold eggs. Regardless of nest construction methods, this is the first record of a puffbird building a nest in any situation other than an earthen or termitaria tunnel.

One other nest of the Brown Nunlet was recently described by Dauphiné *et al.* (2007), who did not examine the chamber portion closely because the nest was partially hidden among the roots of a palm tree. Their description suggested that the nest was a subterranean tunnel with a small collar of leaf litter, but actual architecture was not confirmed. Based on their description and the photos provided, however, it is likely that their nest was similar in architecture to the one we observed. If the nest of Brown Nunlet described by Dauphiné *et al.* (2007) was indeed at least partially subterranean, this suggests some degree of intra-specific variation representing a continuum from subterranean to above-ground nesting. A brief mention in Rasmussen & Collar (2002) that Rusty-breasted Nunlet (*N. rubecula*) nests in holes in either earthen banks or trees suggests that flexibility in nest placement may be common within *Nonnula*. A predisposition for variability in nest architecture and placement, both within and between species, has been suggested to be a factor promoting the evolution of novel nest architectures (Zyskowski & Prum 1999, Greeney 2008).

Within the Malacoptilinae, there is one detail of nest architecture, either absent or undescribed for most species, which is shared by *Monasa* and *Nonnula*. Fig. 1 clearly shows the placement of sticks in the form of an arch at the nest entrance, and these sticks obviously helped to support the leaf litter above the entrance tunnel. Skutch (1972) also noted (and illustrated) a similar placement of sticks at the entrance to the subterranean burrows of *Monasa morphoeus*. Similarly, Cherrie (1916) described a substantial amount of material arranged at the entrance of *M. nigrifrons* nests and F. Gary Stiles (pers. com.) found a nest of *M. morphoeus* in Costa
Rica that had a ring of material built around the entrance. Neither of the Monasa nests described in this study, however, showed any signs of intentional placement of material at burrow entrances. Skutch (1972) observed some variation in this character, and further detailed nest descriptions of Monasa spp. nests are needed to see if such variance has a geographic component or if it may be an artifact of the descriptive interpretations of the observers. In any event, the molecular studies of Witt (2004) indicate that Monasa and Nonnula are only distantly related, which suggests that “collar” construction has likely arisen independently in these genera.

Species of Monasa consistently excavate horizontal burrows in nearly flat ground as opposed to doing it on hills or banks as other tunnel nesters (Skutch 1972, this study), a trait apparently shared with Chelidoptera (Cherrie 1916, this study). The other three genera included within the Malacoptilinae (Micromonacha, Hapaloptila, and Malacoptila; Rasmussen & Collar 2002) all appear to favor steeper slopes or vertical banks (Todd & Carriker 1922, Skutch 1948, 1958, Freile & Endara 2000, Athanas & Davis 2004). However, there seems to be some geographic variation within Malacoptila. Two nests of M. panamensis collected by F. Gary Stiles in Costa Rica (Western Foundation of Vertebrate Zoology coll. # FGS 343/2 and 661/3) were horizontal burrows excavated into small, apparently natural mounds of earth, covered by leaf litter, on nearly flat ground and both included a short tunnel of sticks and material extending out from entrance to the burrow. The nest of M. fusca described here, while still under construction, was on a slope appearing too steep to have supported any sort external construction. We suggest future studies should take careful notes on both nest collars and the slope into which nests are built.

Puffbirds are considered the sister group to the jacamars (Galbulidae) (Johansson & Ericson 2003, Ericson et al. 2006). Based on the nest placement in jacamars, in earthen banks or termitaria (Rasmussen & Collar 2002), it is likely that the ancestral state for nest placement in puffbirds was one (or both) of these situations. Although too few puffbird nests are described to say for certain, there seems to be some flexibility in nest location with relation to ground slope for some terrestrial-nesting groups (see Cherrie 1916, Skutch 1958). We hypothesize that competition for uninhabited, vertically oriented earthen banks may have favored the construction of burrows in flatter ground in some lineages. Not having a sharp drop-off in front of the entrance has subsequently allowed the evolution of entrance tunnel extension. The nest of Brown Nunlet described here may represent an extension of this trait, with the evolution of constructed or partially constructed entrances (i.e. in Monasa) leading to the ability to entirely construct the upper portion of the nest and completely avoid the need to excavate.

Although nest placement remains unknown for a number of bucconid species, nest construction characters appear to fit well with our current understanding of generic relationships in the family (Rasmussen & Collar 2002, Witt 2004). One notable exception is Nystalus, which is the only genus within the Bucconinae known to nest in the ground (Rasmussen & Collar 2002, Greeney et al. 2004). Interestingly, along with Bucco, Nystalus shares the lack of a bifid bill with members of the Malacoptilinae (Ridgway 1914, Rasmussen & Collar 2002). This suggests that Nystalus may be better placed with the malacoptilines or, as suggested by a phylogeny based on nuclear genes (Witt 2004), as basal to other puffbirds along with Bucco. Conversely, mtDNA analyses in Witt’s (2004) study placed Nonnula as basal, with neither tree being the clear choice. Given what we feel is the most logical character evolution for nest architecture, we feel that our data support the placement of Nystalus/Bucco as basal, with Nonnula showing the derived traits of nesting in flat ground and of well developed entrance collars.

Although nest placement and architecture are well known to be useful characters for testing phylogenetic hypotheses (e.g., Lanyon 1986, Prum 1993, Winkler & Sheldon 1993, Greeney 2009), these data remain unavailable for many species, and sample sizes are low for most. Such is unfortunately the case for Nonnula and other puffbirds. As the ontogeny of nest structure may be an informative, yet often unreported, character (e.g., Greeney & Zyskowski 2008), we encourage others to publish further observations on this and other
species, particularly any information regarding the methods involved in nest construction.

ACKNOWLEDGEMENTS

We thank Lori and Juan Miguel Espinoza, the staff of Andean Studies Program, and the staff of Tiputini Biodiversity Station and Shiripuno Research Center for their logistical support. Juan Fernando Vaca B. and F. Gary Stiles graciously contributed their unpublished observations and Chris Witt contributed to useful discussions. The field work of HFG is supported by Matt Kaplan and John V. Moore through the Population Biology Foundation, Field Guides Inc., the PBNHS, and the Maryland Ornithological Society. During the preparation of this manuscript HFG was supported by National Geographic Grant W08-38 and NSF grant DEB-0346729. This is publication number 183 of the Yanayacu Natural History Research Group. We thank Krystof Zyskowski, Daniel Cadena, and two anonymous reviewers for suggested improvements to earlier versions of this manuscript.

LITERATURE CITED


SACCBaseline.html.


Recibido: 05 mayo 2009
Aceptado: 27 enero 2010