

## THE NEST, NESTING BEHAVIOR, AND FORAGING ECOLOGY OF THE RUSTY-WINGED BARBTAIL (*PREMNORNIS GUTTULIGERA*)

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**ABSTRACT.**—We discovered and monitored a nest of the Rusty-winged Barbtail (*Premnornis guttuligera*) on the eastern slope of the Andes in Napo Province, Ecuador. The nest, in a hollow *Cyathea* tree-fern snag, was a deep cup composed entirely of *Cyathea* tree-fern petiole scales (ramenta). A single nestling fledged successfully on 13 March 2002. During the latter half of the nestling period, adults visited the nest with food a mean of  $4.7 \pm 1.9$  (SD) times/h and removed fecal sacs  $2.2 \pm 1.1$  times/h. Nest visitation rates generally decreased throughout the day. Adult Rusty-winged Barbtaills foraged by gleaning from or probing into suspended dead leaves or moss, often while hanging onto the substrate, and did not hitch up trunks or creep along branches. Nest structure, composition, and location, and foraging behavior all raise doubts about the taxonomic placement of *Premnornis* in the *Margarornis* treerunner-barbtail assemblage. *Received 18 March 2003, accepted 25 June 2003.*

The Rusty-winged Barbtail (*Premnornis guttuligera*) is an uncommon and poorly known Neotropical ovenbird (Furnariidae) that inhabits lower growth of montane forest from western Venezuela to southern Peru (Fjeldså and Krabbe 1990, Ridgely and Tudor 1994, Remsen 2003). In Ecuador, the species is locally distributed in the subtropical zone, primarily between 1,600 and 2,300 m on the eastern slope of the Andes (Ridgely and Greenfield 2001). Little has been published on the natural history of the Rusty-winged Barbtail, and virtually nothing is known of its breeding biology (Remsen 2003).

Based on general morphology (e.g., size, wing shape, tarsus:toe length ratio, plumage coloration and pattern) and hindlimb musculature, the Rusty-winged Barbtail appears to be most closely related to *Premnoplex* and *Roraimia* barbtails and *Margarornis* treerunners, collectively known as the *Margarornis* assemblage (Vaurie 1980; Rudge and Raikow 1992a, 1992b). Ecologically and behaviorally, however, the Rusty-winged Barbtail differs strongly from those species, some of which (i.e., *Margarornis*; little data exists for *Premnoplex* and *Roraimia*) typically forage by hitching up tree trunks and along branches in a manner similar to woodcreepers (Dendro-

colaptidae) and creepers (Certhiidae). In contrast, Rusty-winged Barbtaills forage by moving along branches and through dense vegetation (e.g., vine tangles) and probing dead leaves and moss, much like many foliage-gleaners and some *Cranioleuca* spinetails (Miller 1963, Fjeldså and Krabbe 1990, Ridgely and Tudor 1994, Ridgely and Greenfield 2001). Despite the common assumption that the Rusty-winged Barbtail shares scansorial (tree climbing) habits with other species of the *Margarornis* assemblage (Wetmore 1972; Vaurie 1980; Rudge and Raikow 1992a, 1992b), this is not the case (Fjeldså and Krabbe 1990, Ridgely and Tudor 1994, authors pers. obs.).

Nest structure and placement represent behavioral traits that have proven informative in reconstructing phylogenetic relationships within Furnariidae (Zyskowski and Prum 1999). *Premnoplex* barbtails and *Margarornis* treerunners exhibit similar nest architecture and nest placement; species in both genera build mossy, globular nests, placed beneath logs, against banks, or are suspended from vegetation (Hilty and Brown 1986, Ridgely and Tudor 1994, authors pers. obs.). Thus, morphological, ecological, and behavioral characteristics are consistent in suggesting that *Premnoplex* and *Margarornis* are very closely related (Rudge and Raikow 1992b, Zyskowski and Prum 1999). Information of nest structure and placement of the Rusty-winged Barbtail may yield important insights into the species' phylogenetic relationships and, hence, how to interpret the morphological, ecological, and behavioral differences be-

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tween *Premnornis* and virtually all other species of the *Margarornis* assemblage. Here we provide the first description of a nest and nest site of the Rusty-winged Barbtail, as well as details on nestling appearance, parental care, and adult foraging behavior.

### METHODS

We observed a Rusty-winged Barbtail nest during February and March 2002 in primary montane evergreen forest at 2,100 m on the eastern slope of the Andes, near Yanayacu Biological Station ( $00^{\circ} 36' S$ ,  $77^{\circ} 54' W$ ), about 3 km southwest of Cosanga, Napo Province, Ecuador. This humid "cloud" forest is characterized by heavy epiphytic growth, a canopy 20–25 m in height, and gently rolling topography. We based species identification on a combination of plumage pattern (scalloped breast pattern, lack of bold back streaking), morphology (thin bill and decurved culmen), and high-pitched, thin vocalizations, which separate the species from all other sympatric furnariids.

We documented nestling appearance on 28 February, and again on 3 March when we also recorded nestling mass and linear measurements. To access the nest, which was in a tree cavity (see below), we cut away a panel of bark at the level of the nest. We used mud the same color as the bark to cement the panel of bark back into its original position. This disturbance did not appear to affect the adult birds, which apparently remained absent during our presence at the nest and resumed normal activity soon after our departure from the immediate area. We measured nest dimensions on 3 March and immediately following fledging on 14 March, when we removed the nest from the cavity for examination.

We observed and quantified adult behavior at the nest during three 3-h periods per day (07:00–10:00, 11:00–14:00, 15:00–18:00 EST), every other day from 2 to 12 March, for a total of 54 h of observation comprising the majority of six days. We conducted an additional 7.9 h of observation at other times (e.g., at dusk to determine roosting activity). We conducted nest watches from a concealed position in the understory, 20 m away from the nest site. The observer's presence did not appear to affect the birds' behavior. Quantified behaviors included nest visitation rate, method

of nest approach and entrance, time present inside and outside the nest, and fecal sac removal rate. We also described less common behaviors and activity patterns (e.g., nest defense, adult interactions, roosting behavior).

We also collected data opportunistically on Rusty-winged Barbtail foraging behavior. Between 17 March and 11 April 2002, and on 5 February 2003, we followed and observed adults of unknown breeding status as we encountered them in the forest. While observing a foraging individual, we dictated its actions into a microcassette recorder. For each prey attack, we noted the bird's height, distance to canopy, type of attack maneuver, and prey substrate (following Remsen and Robinson 1990). For analysis of height variables, we included only data from the first attack observed for a given bird.

### RESULTS

*Nest discovery and phenology.*—We discovered the nest on 22 February 2002 by observing adults taking food into the nest cavity. Adults visiting the nest with food always remained within the cavity for 5–25 min, and often left with fecal material. On 22 February, adults spent approximately 80% of three observation hours inside the cavity, apparently brooding young. A single nestling showed little development and was largely naked when examined on 28 February. The nestling fledged on 13 March before 14:50.

*Nest site and habitat.*—The nest was in a 4.53-m tall, dead (standing) *Cyathea* tree-fern stump. Three openings in the bark allowed access to the completely hollow interior of the snag. One opening was a slender, natural crack in the bark that measured  $19.5 \times 4.0$  cm, faced a  $30^{\circ}$  orientation, and was near the top of the snag, 4.08 m above the ground. Two other holes in the bark were rectangular in shape, with rough and irregular edges, and appeared to have been made by a bird. The larger of these, which was the entrance most often used by the birds, measured  $3.0 \times 5.5$  cm, had an  $80^{\circ}$  orientation, and was located 3.44 m above the ground. The third and least-used entrance measured  $2.0 \times 3.7$  cm and was approximately the same height as the main entrance hole, but on the opposite side of the snag, facing  $210^{\circ}$ .

The nest site was midway up a drainage

slope, about 30 m from a small stream, inside primary forest. Canopy height was about 20 m. Live tree-ferns and mid-sized trees formed a subcanopy 8–10 m in height above the nest site. The understory was relatively thick with 1- to 2-m tall saplings and ferns. Two live, 8- to 9-m tall tree-ferns were located <3 m of the nest snag; the next closest tree was 7 m away from the nest site.

**Nest description.**—The nest was an open cup (Fig. 1), the rim of which was located 2.82 m above the ground and 62 cm below the main entrance hole. Nest material filled the entire cylinder of the hollow snag for 22.5 cm vertically, from the rim of the cup to the bottom exterior of the nest. Material at the bottom of the nest did not rest on the bottom of a cavity, but was supported by thin strands of bark that had peeled away from the inner walls of the snag. The nest, however, appeared to be supported primarily by the bulk of the material itself, which was packed into the cavity such that outward pressure against the walls of the snag provided support. The outer diameter of the cup, equivalent to the inner diameter of the snag, measured 12.4 cm. The inner diameter of the cup, which did not change in size or shape from early to late in the nestling period, measured 6.6 cm. The inner depth of the cup changed dramatically as the nestling grew. Early in the nestling period (28 February), cup depth was 7.9 cm, which resulted in a very narrow, deep, and almost cone-shaped inner cup. By fledging (14 March), cup depth was only 3.2 cm, resulting in a shallow cup.

The nest consisted completely of *Cyathea* tree-fern petiole scales (ramenta), which are thin, soft, and flexible. No distinct lining was placed in the bottom of the cup.

**Nestling description.**—We documented the appearance and took measurements of the nestling on 3 March, an estimated 9–11 days after hatching and 10 days before fledging. At 12:00, the primary pin feathers were exposed 1.5 mm from their sheaths and the nestling weighed 16.2 g. Tarsus length was 18.6 mm, wing chord was 29.3 mm, culmen length was 10.2 mm, and gape width was 14.2 mm. Although capable of opening its eyes slightly while begging, the nestling generally kept its eyes closed. Skin on the body was pinkish with a slight orange tinge. Legs and feet were

mauve and the bill was grayish black in color. Flanges of the gape were whitish yellow and the mouth lining was yellowish orange. Pin feathers with gray sheaths were coming in on all feather tracts. Rust-colored pin feathers had broken their sheaths on dorsal and ventral tracts and on wing coverts. Secondary and primary pin feathers had recently broken their sheaths and were grayish brown in color. Sparse downy plumes were present on the head and back.

**Nest attendance.**—We observed the nest for a total 61.9 h, primarily during the latter half of the nestling period (2–12 March). Adults always carried food (arthropods) in their bills when going to the nest. Adults typically approached the nest through the understory, making a final short flight upward to a cavity entrance, or through a series of incrementally closer flights between trees with a final horizontal flight to a cavity entrance. When approaching or leaving the nest, adults flew directly to or away from a cavity entrance, or within 10 cm of a cavity entrance, rather than creeping up or down the trunk before entering or leaving the cavity. Flights away from the nest typically were long (>20 m) horizontal flights and occasionally were preceded by looking out of the hole (for up to 50 s).

Overall nest visitation rate (mean  $\pm$  SD) by the adults was  $4.7 \pm 1.9$  nest visits/h (range 1–8;  $n = 54$  h). Among days, mean nest visitation rate ranged from 4.1–5.6 nest visits/h and did not appear to vary with nestling age. Within each day, nest visitation rate tended to decrease throughout the day, with a slight increase late in the afternoon (Fig. 2). An adult arriving to find its mate already inside the nest cavity typically perched outside and waited for its mate to leave before entering the cavity. Both adults were present at the nest site simultaneously during only 3% (7) of 254 nest visits, and both were inside the cavity simultaneously only once. Of the three nest cavity entrances, the adults clearly favored the larger rectangular hole, using it for 96% of 424 nest cavity entrance and exit events.

Time spent inside the nest cavity by adults, presumably brooding, did not show a consistent pattern throughout the day. However, time (% of observation time) spent in the cavity appeared to decrease as the nestling grew, from approximately 80% on 22 February to



FIG. 1. Rusty-winged Barbtail nest inside hollow tree-fern snag, with section of bark cut away to show nest structure. Photograph by B. Swift, Napo Province, Ecuador, 14 March 2002.

30% on 2 March, 8% on 4 March, 5% on 6 March, 4% on 8 March, 2% on 10 March, and 3% on 12 March. Mean time spent in the nest cavity per visit declined from 3.3 min on 2

March to 0.3 min on 12 March, whereas maximum duration of time spent in the nest cavity decreased from 15.6 min to 1.1 min over that same period. Adults always entered the nest

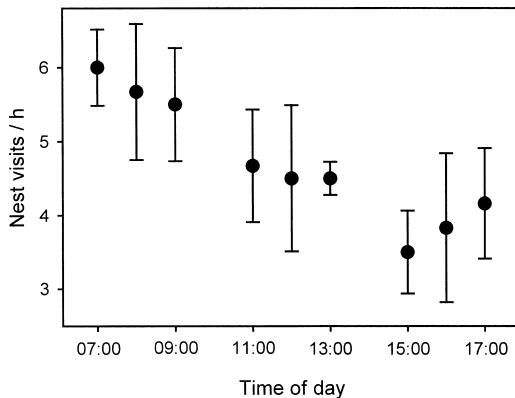


FIG. 2. Diurnal pattern of Rusty-winged Barbtail nest visitation was generally decreasing during the latter half of the nestling period. Symbols represent mean ( $\pm$  SE) number of nest visits/h ( $n = 54$  h, 9 h/day for six days). Data are from Napo Province, Ecuador, 2002.

cavity, spending  $\geq 7$  s inside, during nest visits and never were observed feeding the nestling from outside the cavity.

One adult slept inside the nest cavity during the nights of 2, 4, 6, 8, and 10 March, entering the cavity (with food) for the last time between 18:08 and 18:21 (mean = 18:14). The roosting adult had left the nest by 06:45 each morning, and by 06:17 one morning. No adult roosted in the nest cavity the night of 12 March, just prior to fledging (13 March).

Adults removed fecal sacs from the nest after 46% of nest visits ( $n = 254$  nest visits). Overall, adults removed fecal material  $2.2 \pm 1.1$  times/h (range 0–5). There was no consistent pattern in fecal sac removal rate with respect to time of day or nestling age (within the latter half of the nestling period). Adults carried fecal sacs in their bills and flew  $\geq 20$  m away from the nest before disposing of them, the exact method of which was not determined.

Nestling begging, audible from a distance of 20 m on 4 March, was a sustained, high-pitched, insect-like vocalization with pulses of emphasis. The nestling typically begged 1–2 s after an adult arrived and entered the cavity and again as it left the cavity, quickly becoming quiet after the adult's departure. The nestling did not beg when an adult perched outside the cavity entrance.

*Nest defense.*—We observed two nest de-

fense events by adult Rusty-winged Barbtauls when woodcreepers (Dendrocolaptidae) perched on the nest snag. On 8 March a Montane Woodcreeper (*Lepidocolaptes lacrymiger*) flew to and perched on the nest snag, 20 cm below the main nest cavity entrance. Within 2 s of the woodcreeper landing on the nest snag, a single adult barbtail flew in, displaced and chased the (larger) woodcreeper  $> 20$  m away from the nest site. Nestling provisioning resumed 7 min later.

On 12 March, at 07:54, a Strong-billed Woodcreeper (*Xiphocolaptes promeropirhynchus*) flew to and perched on the nest snag, landing near the main entrance and moving up to the natural hole. Within 5 s both adult barbtails, one carrying food, began diving at the (much larger) woodcreeper, making 10–12 dives during 20 s, at which time the woodcreeper flew away. Neither adult barbtail appeared to hit the woodcreeper, but each approached it closely during each dive and one chased it approximately 10 m as it flew. Both barbtails remained agitated near the nest for 13 min, repeatedly diving over the nest site, flicking wings when perched, and giving emphatic, high-pitched, and slightly downslurred “tsep” alarm calls. One adult made several brief visits to the main cavity entrance, but was immediately displaced and chased by its mate. Both adults left the area at 08:07 and remained absent for 25 min, returning at 08:32. At 08:35, 41 min after the woodcreeper left the nest site, nestling provisioning resumed. Adults remained agitated, giving alarm calls and often flying past the nest site before going to it, until 08:40.

*Foraging behavior.*—Rusty-winged Barbtauls foraged with mixed-species flocks, primarily in vine tangles and among mossy branches and live foliage, from the understory to the subcanopy. Mean foraging height was  $6.6 \pm 3.5$  m (range 1.8–10.7;  $n = 6$ ); mean distance to canopy was  $11.9 \pm 4.7$  m (range 6.1–16.8). Rusty-winged Barbtauls gleaned arthropods from surfaces and probed into crevices of substrates, often while hanging-up (i.e., clinging to a substrate in a vertical, head-up position) or hanging-sideways (i.e., hanging in a horizontal posture; see Remsen and Robinson 1990) on a moss-covered branch or large dead leaf (e.g., *Cecropia* sp.). Rusty-winged Barbtauls frequently hopped and made

short flights between perches while searching for prey, and did not hitch up vertical branches or trunks in the manner that both Spotted Barbtails (*Premnoplex brunnescens*) and Pearled Treerunners (*Margarornis squamiger*) frequently do (RCD pers. obs.). The Rusty-winged Barbtail appears to be a regular dead leaf forager (*sensu* Remsen and Parker 1984), with 53% of attacks directed at prey in or on suspended dead leaves, which ranged from 3 × 5 cm to 40 × 40 cm in size. Other prey substrates included small, dead or live moss-covered branches (37%), suspended moss (3%), vine stems (3%), and live leaves (4%;  $n = 30$  attacks by six birds). Rusty-winged Barbtails typically searched small (e.g., 1- to 5-cm diameter) moss-covered branches.

## DISCUSSION

The Rusty-winged Barbtail nest described here was active in February and March, and probably as early as late January, which is consistent with timing of breeding evidence recorded elsewhere in the northern Andes. Fledglings have been observed in January and February in northeastern Ecuador and during January in the western Andes of Colombia (Fjeldså and Krabbe 1990); adults in breeding condition have been collected during March in the western Andes of Colombia (Miller 1963). Records of fledglings in northeastern, northwestern, and southern Ecuador (Fjeldså and Krabbe 1990) indicate that the species also breeds from September to November on the eastern slope of the Ecuadorian Andes.

The nest of the Rusty-winged Barbtail was a cup composed of tree-fern petiole scales, built in the hollow column of a tree-fern snag. Thus, nest structure, composition, and placement set *Premnornis* apart from its allies, *Premnoplex* barbtails and *Margarornis* treerunners, which use mosses and liverworts to construct globular nests with side or bottom entrance holes, placed against banks, under logs, or in suspended vegetation (Skutch 1967, Vaurie 1980, Hilty and Brown 1986, Fjeldså and Krabbe 1990, Marín and Carrión 1994). In contrast, the Rusty-winged Barbtail is similar to several other furnariid taxa, also in the subfamily Philydorinae, with respect to nest structure and placement. *Anabazenops*, some *Philydor*, and at least two species of *Syndactyla* foliage-gleaners build cup-shaped

nests with pliable materials in tree cavities, as do species of *Xenops* (Skutch 1969, Vaurie 1980, Belton 1984, Hilty and Brown 1986, Kratter 1994, Zyskowski and Prum 1999).

The nest of the Rusty-winged Barbtail may be most similar to nests of *Pseudocolaptes* tuftedcheeks, which also nest in tree cavities and use tree-fern petiole scales exclusively upon which to lay their eggs (Slater and Salvini 1879, Skutch 1969, Zyskowski and Prum 1999). The exclusive use of tree-fern petiole scales in nest construction is known only in *Premnornis* and *Pseudocolaptes*, and may be a synapomorphy uniting the two genera (K. Zyskowski pers. comm.). Nest architecture, however, is poorly known in *Pseudocolaptes*. Zyskowski and Prum (1999) classified a single *Pseudocolaptes* nest specimen as a "platform" based on its current shape and because tree-fern petiole scales are too short to be interwoven (a criterion in their "cup" classification scheme). It is important to note, however, that the *Pseudocolaptes* nest could have been cup-shaped prior to being removed from the nest cavity. In fact, the shape of the Rusty-winged Barbtail nest described here changed from a deep cup to a shallow cup as the nestling grew and, because tree-fern petiole scales were not interwoven, the nest did not hold its shape well after being removed from the cavity (authors pers. obs.). Detailed structure and measurement data from a *Pseudocolaptes* tuftedcheek nest inside (i.e., prior to being removed from) its nest cavity could clarify potential nest architecture similarities between *Premnornis* and *Pseudocolaptes*.

Unlike the scansorial habits of *Margarornis* treerunners, Rusty-winged Barbtails searched for arthropod prey by hopping through vine tangles and tree branches, often through dense foliage. Rusty-winged Barbtails acquired prey primarily by gleaning from and probing into dead leaves and moss. Foraging ecology of the Rusty-winged Barbtail, therefore, is similar to that of some foliage-gleaners and *Cranioleuca* spinetails (see Remsen and Parker 1984, Rosenberg 1997), as noted previously by Fjeldså and Krabbe (1990) and Ridgely and Tudor (1994). Quantitative data on the foraging behavior of *Premnoplex* barbtails could yield further insight into ecological variation within the *Margarornis* assemblage.

The unique nesting ecology, and potentially

unique foraging ecology, of the Rusty-winged Barbtail within the *Margarornis* assemblage may imply genetic divergence from the *Margarornis* assemblage or reflect ecological convergence with other furnariiid taxa (e.g., *Pseudocolaptes*, various foliage-gleaner genera). Species of the *Margarornis* assemblage, including the Rusty-winged Barbtail, possess numerous myological variations in hindlimb musculature, which appear to be adaptive for tree climbing (Rudge and Raikow 1992a). Based on a series of derived characters, Rudge and Raikow (1992b) hypothesized that the *Margarornis* assemblage represents a monophyletic group and, further, that *Premnornis* and *Premnoplex* are sister taxa. Although resolving the phylogenetic relationships of the Rusty-winged Barbtail is beyond the scope of this paper, we suggest that ecological characteristics of the species are incongruous with its traditional taxonomic position and warrant attention in future phylogenetic analyses.

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