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Authors: Sánchez†, Julio E., Conejo-Barboza, Karla, Sánchez, César, Fonseca Arce, Ariel A., Tenorio, Javier, et al.

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Nest architecture and parental care in Ruddy Treerunner *Margarornis rubiginosus*

by Julio E. Sánchez[†], Karla Conejo-Barboza, César Sánchez,
Ariel A. Fonseca Arce, Javier Tenorio & Luis Sandoval

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SUMMARY.—We complement the only existing nest description for Ruddy Treerunner *Margarornis rubiginosus* and include observations of nestbuilding and breeding behaviour. We also compare our data with existing information on nest architecture and breeding biology of the closely related Pearled Treerunner *M. squamiger* and Spotted Barbtail *Premnoplex brunnescens*. The nest of Ruddy Treerunner was a pendant closed nest below a single tree branch and was mostly constructed of moss. In the nest base there was a circular entrance and a second cavity. The inner chamber was spherical and the egg cup was mostly constructed of roots, fern scales and other plant fibres. Both adults build the nest and care for chicks. We observed a nest helper and removal of faecal sacs by both adults. Many aspects of nest structure and parental behaviour are similar to those of its sister species, thereby supporting existing genetic data.

Ovenbirds (Furnariidae) exhibit a high diversity of nest architecture (Zyskowski & Prum 1999, Remsen 2003). Some adopt or excavate cavities in trees, subterranean burrows or other animal constructions (i.e., *Xenops*, *Philydor* and *Pseudocolaptes*). Others construct platforms (i. e., *Sclerurus*) and cups (i.e., *Thripadectes*) inside cavities (Zyskowski & Prum 1999). *Furnarius*, *Synallaxis* and *Cranioleuca* build domes ('closed nest' *sensu* Simon & Pacheco 2005) using clay, sticks or moss (Zyskowski & Prum 1999, Greeney 2008a). These features and others that describe nest design, such as materials and perch type, reflect phylogenetic relationships between genera and species of Furnariidae, and other bird families (Sheldon & Winkler 1999, Zyskowski & Prum 1999, Irestedt *et al.* 2006, Greeney *et al.* 2013). Thus, complete and detailed nest descriptions are necessary to help establish such relations (Sheldon & Winkler 1999, Simon & Pacheco 2005).

Within the *Premnoplex*–*Margarornis* clade (Rudge & Raikow 1992, Derryberry *et al.* 2011) Spotted Barbtail *Premnoplex brunnescens* and Pearled Treerunner *Margarornis squamiger* share similar architecture and parental behaviour. Adults of both species construct large mossy oval or ball-shaped nests, usually with an entrance followed by a tunnel that leads to a nest chamber (Greeney 2008a,b, Greeney & Gelis 2011). Another species within this clade is Ruddy Treerunner *M. rubiginosus*. Data on its breeding biology are limited to a single event where possible bi-parental care was observed. The nest, however, was not collected and data on the internal structure were not provided (Mennill & Doucet 2005).

Ruddy Treerunner is endemic to the highlands of Costa Rica and western Panama, occurring in premontane and montane forests above 1,000 m (Stiles & Skutch 1995). Here we describe the nest structure and include details of nestbuilding and breeding behaviour based on two collected nests and field observations at two active nests. Additionally, we compare our data with nest architecture and breeding biology of the closely related Pearled Treerunner and Spotted Barbtail.

Methods

We found three nests, all in Costa Rica. The first (nest 1; Fig. 1) was found inactive on 20 May 2003, at Jaboncillo, Dota, San José province (09°35'55"N, 83°47'55"W; elevation 2,910 m) in a mature forest fragment. It was collected and deposited at the Museo Nacional de Costa Rica (MNCR 269), San José. We observed active nest 2 on 22 March 2009 at Villa Mills, Paraíso, Cartago province (09°34'06"N, 83°42'20"W; 2,775 m) in secondary forest. We found and observed the active nest 3 (Figs. 2–3) between March and June 2015, at Cerro Chompipe, Heredia province (10°05'25"N, 84°04'45"W; 1,885 m) in a secondary forest adjacent to pasture. This nest was collected after the juvenile fledged and deposited at the Museo de Zoología, Universidad de Costa Rica (MZUCR AN419), San José. Habitats where we observed the three nests involved premontane and montane forest dominated by trees and shrubs of *Alnus acuminata* (Betulaceae), *Quercus* sp. (Fagaceae), *Ocotea* sp. (Lauraceae), *Drimys granadensis* (Winteraceae), *Cyathea* sp. (Cyatheaceae), *Citharexylum donnell-smithii*, *Blakea grandiflora* (Melastomataceae) and introduced *Cupressus lusitanica* (Cupressaceae). We found a dead chick and no eggs inside nest 1 and we heard two chicks each in nests 2 and 3.

From nests 1 and 3 we took nine measurements (in cm; Figs. 1, 3): (1) max. external height, (2) max. external diameter, (3) max. entrance diameter, (4) minimum entrance diameter, (5) tunnel depth from the entrance to the ceiling of the inner chamber, (6) tunnel depth from the entrance to the front rim of the egg cup, (7) max. height of the inner chamber and (8) max. horizontal diameter of the inner chamber. For nest 1 we also measured (9) an extra max. external height and, max. (3) and minimum (4) entrance diameter and tunnel depth (5) to accurately describe the shape of the second cavity (Fig. 1A). We recorded nest measurements using a metallic ruler (BEIFA ± 0.025) and digital callipers (OEM 25363, ± 0.01 mm). We used a camera (PEC-VE300) with an articulation probe (Baito) to visualise egg cup materials inside nest 1. We made two radial cuts in the inferior part of nest 3 to analyse the

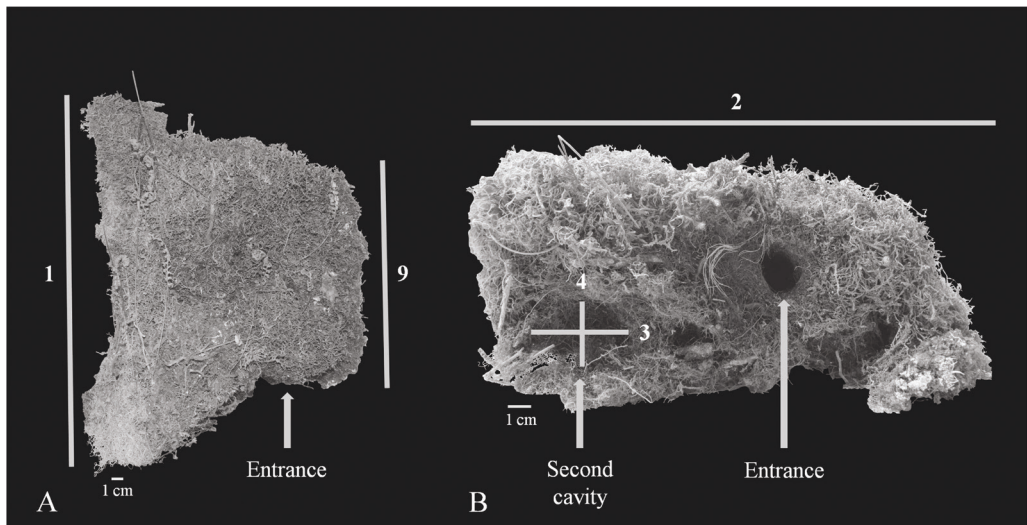


Figure 1. (A) Lateral and (B) underside views of a Ruddy Treerunner nest *Margarornis rubiginosus*, collected on 20 May 2003 at Jaboncillo, Dota, San José province, Costa Rica (nest 1). Only the entrance is connected to the inner chamber. Numbers correspond to (1) max. external height, (2) max. external diameter of the nest, (3) entrance or cavity max. diameter (4) entrance or cavity minimum diameter, and (9) extra max. external height (Karla Conejo-Barboza)



Figure 2. Nest of Ruddy Treerunner *Margarornis rubiginosus*, collected on June 2015, at Cerro Chompipe, Heredia province, Costa Rica (nest 3) (Ariel A. Fonseca-Arce)

materials of the inner chamber and tunnel, study the wall surroundings and measure the inner chamber dimensions (measurements 7–8, Fig. 3).

We observed nest 2 for *c.*15 minutes and observed nest 3 at 10–30-minute intervals over nine days (13 total hours). At nest 3, we observed nest construction (17–22 March 2015), parental care and adult behaviour (14 April–26 May 2015).

Results

Nest architecture.—All three nests were pendant structures attached to the main trunks of trees, always below a single branch. Height above ground was not available for nest 1. Nest 2 was *c.*7 m above ground and nest 3 was sited at *c.*10 m. According to the nest classification system of Simon & Pacheco (2005), nests 1 and 2 had an ovoid external shape. Nest 1 had straight sides; however, the external shape was more similar to a rectangle than an ovoid (Fig 1A). The opposite external sides of nest 1 differed (Fig. 1A). The longest side was 54.8 cm corresponding to max. external height (measurement 1). The shorter side was 34.0 cm (measurement 9), opposite to the longest side and next to the entrance to the inner chamber. We could not determine the shape of nest 3 because it was embedded in a large aggregation of mosses, liverworts, multiple epiphytic orchids and ferns on a branch (Fig. 3). In addition to mosses, live epiphytes and ferns, the external layer of all three nests contained small sticks and roots.

Nest 1 had a circular entrance, connected directly to the inner chamber by a tubular tunnel, and a second cavity at the nest base. The entrance and the cavity were separated by an 8.0 cm-wide wall (Table 1, Fig 1B). Nest 3 had a circular entrance connected directly to

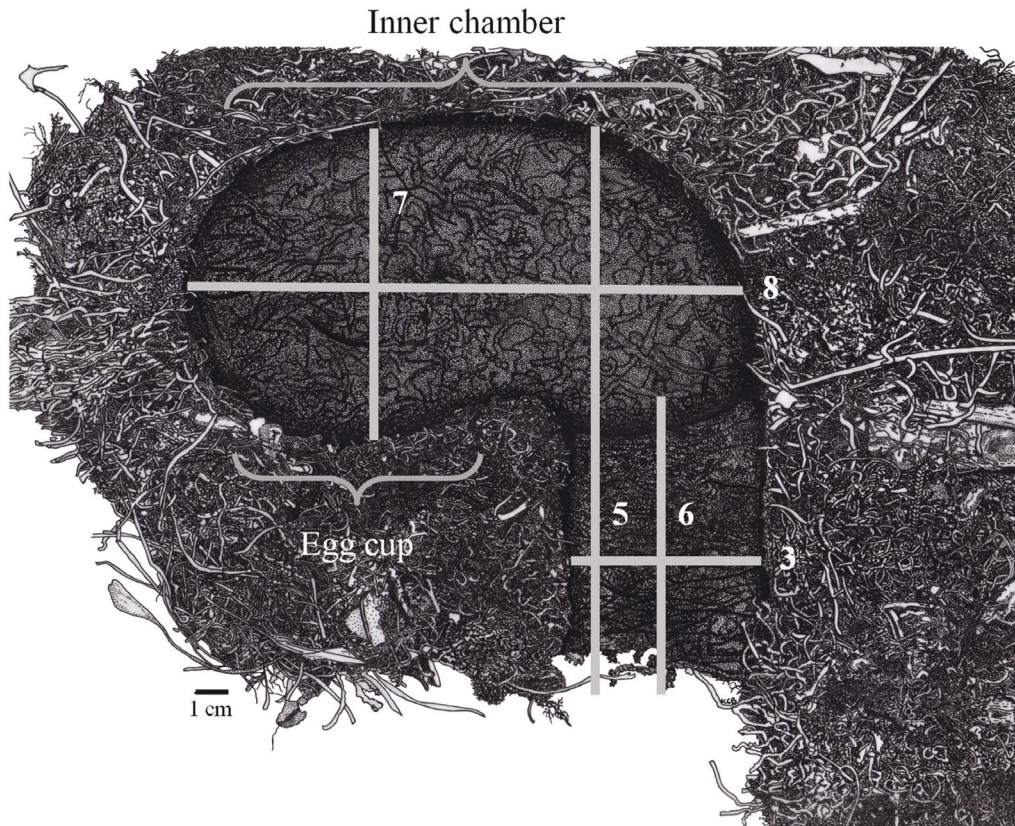


Figure 3. Internal view (inner chamber, egg cup and tunnel) of a nest of Ruddy Treerunner *Margarornis rubiginosus*, collected on June 2015, at Cerro Chompipe, Heredia province, Costa Rica (nest 3). Numbers correspond to (3) entrance max. diameter, (5) tunnel depth from the entrance to the ceiling of the inner chamber, (6) tunnel depth from the entrance to the front rim of the egg cup, and (7) max. height and (8) max. horizontal diameter of the inner chamber (Karla Conejo-Barboza)

the inner chamber via a tubular tunnel but no visible external cavities. The interior lining of the tunnel of nest 3 comprised dark plant fibres and fern scales (Fig. 2).

The inner chambers of nests 1 and 3 were spherical (Fig. 3). In nest 3, the inner chamber was surrounded by a discontinuous layer, 1.0–2.5 cm thick, of tightly compacted mosses, roots and dark vegetal fibres (Fig. 3). This layer was strongly adhered to the nest's walls and to the vegetation surrounding the nest (moss, ferns and epiphytes). The egg cups of nests 1 and 3 were sited in the basal portion of the inner chamber (Fig. 3), they were constructed of roots, fern scales, mosses and black fibres of unknown origin, and in the egg cup of nest 3 we also found some fibres of lichens (*Usnea* sp., Parmeliaceae) and sticks. In nest 3, the egg cup could not be separated structurally from the inner chamber.

Nest construction.—Nest construction behaviour is based on our observations at nest 3. At 12.00 h on 17 March 2015 we observed three Ruddy Treerunners simultaneously, near a large mass of moss (Fig. 3). We determined that all three were adults as they had whitish throat feathers and none had throat feathers with faint sooty fringes as in juvenile plumage (Stiles & Skutch 1995). The three adults were carrying fine mosses and lichens in their bills, which they deposited in a cavity within the moss. The birds entered the cavity with the material one at a time. On 22 March 2015 we observed three adults carrying mosses and lichens into the same cavity, but occasionally adults exited with apparently the same

TABLE 1

Dimensions of Ruddy Treerunner *Margarornis rubiginosus* nests observed in Costa Rica. Nest 1 was collected at Jaboncillo, Dota, San José province (MNCR 269), nest 3 was collected at Cerro Chompipe, Heredia province (MZUCR AN419) and dimensions estimated by Mennill & Doucet (2005), named nest 4 herein. All measurements in cm. Only the entrance is connected to the inner chamber. Measurements taken as described in the text. Diam. = diameter, Hori. = horizontal, Max. = maximum, Min. = minimum, Tun. = tunnel.

Nest	External		Entrance				Inner chamber		Second cavity		
	Height	Max. diam.	Max. diam.	Min. diam.	Tun. Depth ⁵	Tun. Depth ⁶	Max. height	Max. hori. diam.	Max. diam.	Min. diam.	Tun. Depth ⁵
1	54.8	36.4	4.6	3.8	7.7	-	-	-	4.4	4.1	2.0
3	-	-	5.5	3.3	12.7	5.1	9.2	11.1	-	-	-
4	30.0	20.0	10.0	-	-	-	-	-	-	-	-

material they had carried inside. Ten days later, we observed just two adults entering the nest without material, and we assumed that construction had been completed. One of the adults spent more time inside the nest than the other.

Parental care.—Our information concerning parental care was based on nests 2 and 3. On 22 March 2009, we observed two adults arriving simultaneously with food at nest 2. Both perched on different branches of the nest tree (close to the nest). One flew to the nest entrance and introduced the anterior half of the body into the nest; three seconds later it flew to the main trunk of the nest tree and perched without food in its bill. Meanwhile, the second bird waited until the first had flown away before visiting the nest entrance. After two seconds, the second bird flew to another tree without food in its bill and the first one followed it. We heard chicks calling inside when the adults arrived at the nest.

Between 1 April and 26 June 2015 we conducted observations at nest 3 at different times on six days. On six occasions, we observed both adults enter the nest and after a few minutes only one left, to forage in the same patch of secondary forest where we had observed both adults foraging previously. On several occasions after 9 May we observed adults spend between five and seven minutes foraging in the same secondary forest near the nest before entering. If both adults arrived simultaneously, as occurred at nest 2, one perched next to the nest and waited until the other had departed before delivering food (no. of observations = 25). Prey included beetles, spiders and unidentified arthropods. Both adults introduced the anterior half of the body into the nest entrance. During one feeding bout, an adult brought food to the nest on three occasions, while the other remained inside (we are certain it was the same individual as it never entered completely). On three occasions we observed both adults leave the nest with faecal sacs immediately after provisioning the chicks. The last time that we heard the chicks vocalising inside the nest was on the morning of 26 May 2015. We visited the nest on 26 June but did not see activity inside or near it.

Discussion

Our observations of three Ruddy Treerunner nests augment the previous description (Mennill & Doucet 2005), providing detailed nest measurements (Table 1), a description of nest materials, the structure of the egg chamber, and observations of parental behaviour. In general, the nest structure of this species is similar to that of nests of its sister species, Pearled Treerunner and Spotted Barbtail, which also construct closed nests of moss attached below a single branch (Meyer de Schauensee & Phelps 1978, Stiles *et al.* 2000, Remsen 2003, Greeney

2008a, Greeney & Gelis 2011). The external shape of the nest of Ruddy Treerunner appears variable, as also reported for Spotted Barbtail (Greeney 2008a). External nest variation can be related to site characteristics (Nickell 1958, Pacheco & Simon 1995), or to the ontogeny of nest construction (Greeney 2008a, Greeney & Gelis 2011). Nest 3 was completely embedded in the vegetation that surrounded it, suggesting that it was constructed within a natural, pre-existing mass of moss. This behaviour has been reported previously for Pearled Treerunner and Spotted Barbtail, although these species might also transplant and compact moss to construct their nest (Greeney 2008a, Greeney & Gelis 2011). In both scenarios, the moss can continue to grow and provide a substrate for epiphytic plants such as orchids and ferns, which partially determine the external shape of the nest.

Although we did not witness the construction of nest 1, the presence of a second cavity in the nest has been reported previously in some species of Furnariidae (Zyskowski & Prum 1999, Greeney 2008a). In Pearled Treerunner nests there can be a second cavity that functions as an adult dormitory during the breeding season (H. F. Greeney pers. comm.) and in one nest of Spotted Barbtail the second cavity led to an inner, inactive nest chamber (Greeney 2008a; Table 2). In Plain Softtail *Thripophaga fusciceps* the second cavity served as an additional nest entrance (Zyskowski & Prum 1999). In one Rufous-fronted Thornbird *Phacellodomus rufifrons* nest, Skutch (1969) found more than two cavities each with an individual chamber at the end. These might be old nests or dormitories (Skutch 1969, Carrara & Rodrigues 2001, Rodrigues & Carrara 2004). We suggest that the second cavity in nest 1 might have served as an adult dormitory. It is unlikely that the second cavity was created by a predator (despite that we found a dead chick inside nest 1) because the nest exhibited no signs of damage. Contrary to the external structure, the shape and materials of the nest chamber and egg cup were similar in the two collected nests and among sister

TABLE 2

Summary of the reproductive biology, specifically nest architecture and parental breeding behaviour for Spotted Barbtail *Premnoplex brunnescens* (Greeney 2008a,b), Pearled Treerunner *Margarornis squamiger* (Greeney & Gelis 2011) and Ruddy Treerunner *M. rubiginosus* (Mennill & Doucet 2005). ¹Based on Meyer de Schauensee & Phelps (1978), Stiles *et al.* (2000) and Rensen (2003). ²Based on Simon & Pacheco (2005). ³Except one nest that was reused (Greeney 2008a). ⁴Some nests, H. F. Greeney pers. comm. ⁵Not confirmed.

	Spotted Barbtail	Pearled Treerunner	Ruddy Treerunner
Nest architecture			
Perch	Rocks, trees or roots	Horizontal branch	Horizontal branch
Nest position ¹	Pendant and bottom	Pendant ¹ and bottom	Pendant
Substrate (mass of mosses)	Built or modified natural mass	Built or modified natural mass?	Built or modified natural mass?
Nest form ²	Globular	Globular	Globular, ovoid or irregular
Principal material	Moss	Moss	Moss
Number of entrances	One ³	One or two ⁴	Two
Entrance position	Below	Below	Below
Entrance form	Tubular	Tubular	Tubular
Inner chamber form	Spherical	Spherical	Spherical
Breeding behaviour			
Bi-parental nestbuilding	Yes	Yes	Yes
Bi-parental nestling care	Yes	Yes	Yes
Parental removal of faecal sacs	Yes	Unknown ⁵	Yes

species (Greeney 2008a, Greeney & Gelis 2011; Table 2). The only difference between the egg cup of Ruddy Treerunner and those of its sister species is that in both Pearled Treerunner and Spotted Barbtail the structure is independent of the inner chamber (Greeney & Gelis 2011, Greeney 2008a; Table 2).

The third bird observed during the construction of nest 3 was perhaps a helper. Such behaviour during the breeding season is widespread among Neotropical birds (Skutch 1935), enhancing the fitness of kin offspring (Brouwer *et al.* 2012). Among Furnariidae, Rufous-fronted Thornbird appears to have more than two helpers that assist in nestbuilding, territory defence or feeding nestlings (Skutch 1935, Rodrigues & Carrara 2004). Based on our observations, it is probable that Ruddy Treerunner also employs a helper during nest construction. Similar to Pearled Treerunner and Spotted Barbtail, in Ruddy Treerunner both adults build the nest, feed the nestlings and remove faecal sacs; the latter is also reported in Spotted Barbtail (Greeney 2008b), but has not been confirmed for Pearled Treerunner (Areta 2007, Greeney & Gelis 2011; Table 2). For incubation behaviour, we could not confirm whether one of the adults spent more time incubating than the other, but it is probable that both adults incubate the eggs, as is true for Spotted Barbtail (Greeney 2008b).

Many aspects of nest structure and parental behaviour are similar among Spotted Barbtail, Pearled and Ruddy Treerunners (i.e. nest placement, materials, nest entrance position, the shape of the inner chamber, bi-parental care and removal of faecal sacs by both adults; Table 2). Until now, some nest characteristics were shared by just two species of the *Margarornis–Premnoplex* clade. For example, Pearled Treerunner and Spotted Barbtail nests can be placed over a horizontal branch (Greeney 2008a, Greeney & Gelis 2011), and some Ruddy and Pearled Treerunners nests possess a second cavity in the base (H. F. Greeney pers. comm.; Table 2). Based on our observations, only Ruddy Treerunner employs a helper during nest construction. Information concerning breeding biology reinforces the genetic relationships reported previously for the *Margarornis–Premnoplex* clade (Derryberry *et al.* 2011).

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Addresses: Julio E. Sánchez†, Asociación de Ornitólogos Unidos de Costa Rica, San José, Costa Rica, 11695-1000. Karla Conejo-Barboza, Escuela de Biología, Universidad de Costa Rica, Montes de Oca, San José, Costa Rica, 11501-2090, e-mail: k.conejobarboza@gmail.com. César Sánchez, Asociación de Ornitólogos Unidos de Costa Rica, San José, Costa Rica, 11695-1000, and Dept. of Biological Sciences & Museum of Natural Science, Louisiana State University, Baton Rouge, LA 70803, USA. Ariel A. Arce, Asociación Ornitológica de Costa Rica, San José, Costa Rica, 572-1250, and Escuela de Ciencias Biológicas, Universidad Nacional de Costa Rica, Heredia, Costa Rica, 86-3000. Javier Tenorio, Escuela de Ciencias Biológicas, Universidad Nacional de Costa Rica, Heredia, Costa Rica, 86-3000. Luis Sandoval, Asociación de Ornitólogos Unidos de Costa Rica, San José, Costa Rica, 11695-1000, and Escuela de Biología, Universidad de Costa Rica, Montes de Oca, San José, Costa Rica, 11501-2090.