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NEST SITES OF TERMITARIUM NESTING BIRDS IN SE PERU

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Resumen. – Nidos de aves en termiteros arbóreos en el sureste del Perú. – En todas las áreas tropicales del mundo hay aves que anidan en los nidos arbóreos de termitas. Este comportamiento de anidamiento en termiteros está poco documentado y ha sido objeto de pocos estudios científicos. Este artículo reporta la estación de anidamiento y las características de los nidos de seis especies de aves que anidan en termiteros arbóreos en el bosque húmedo tropical del suroeste de la cuenca Amazónica. El Jacamar grande (*Jacamerops aurea*) excavó nidos en termiteros hechos por la termita *Constrictotermes cavifrons*, este representa el primer registro de aves de este género anidando en termiteros. El Jacamar castaño (*Galbalcyrhynchus purusianus*), el Trogón colinegro (*Trogon melanurus*), el Trogón coroniazul (*T. curucui*), el Pihuicho tui (*Brotogeris sanctithomae*) y el Pihuicho alicobalto (*B. cyanoptera*) usaron termiteros de *Nasutitermes corniger*. También se reporta un nido del Jacamar frentiazulada (*Galbula cyanescens*) en el margen de una pequeña quebrada. Las excavaciones hechas por todas las especies de aves en los termiteros de *N. corniger* consistieron de un túnel angosto con inclinación positiva que lleva a cámaras de anidamiento casi hemisféricas. Las excavaciones de los pihuichos *Brotogeris* tuvieron entradas significativamente mas angostas y con un mayor ángulo de inclinación que las del Trogón colinegro. Las excavaciones de los pihuichos *Brotogeris* fueron similares a las reportadas en la literatura para otros miembros de este mismo género. Las excavaciones del Trogón colinegro y el Trogón coroniazul fueron similares entre ellas y similares las de otros miembros del "violaceous subclade" del género *Trogon* pero difieren de las excavaciones poco profundas hechas por miembros del "elegant subclade" de este mismo género.

Abstract. – In all tropical areas of the world there are birds that nest in the arboreal nests of termites. The termitarium nesting behavior is poorly documented and has been the object of few scientific studies. This paper reports on the nesting season and nest characteristics of six species of termitarium nesting birds from moist tropical forests in the southwestern Amazon Basin of Peru. Great Jacamar (*Jacamerops aurea*) excavated nests in termitaria made by *Constrictotermes cavifrons*; this represents the first record of birds nesting in termitaria of this genus. Purus Jacamars (*Galbalcyrhynchus purusianus*), Black-tailed (*Trogon melanurus*) and Blue-crowned (*T. curucui*) trogons, Tui (*Brotogeris sanctithomae*) and Cobalt-winged (*B. cyanoptera*) parakeets used *Nasutitermes corniger* termitaria. A single nest for Bluish-fronted Jacamar (*Galbula cyanescens*) in a stream bank is also reported. Nest excavations made by all species in *N. corniger* termitaria consisted of narrow up sloping tunnels leading to roughly hemispherical nesting chambers. Excavations of *Brotogeris* parakeets had significantly narrower entrance tunnels and entered at significantly steeper angles than those of Black-tailed Trogons. The excavations of *Brotogeris* parakeets were similar to those reported in the literature for other members of this genus. The excavations of Black-tailed and Blue-crowned trogons are similar and similar to other members of the "Violaceous subclade" of the genus *Trogon* but differ from the shallow excavations made by members of the "Elegant subclade" of this genus. *Accepted 24 January 2004*.

Key words: *Galbalcyrhynchus purusianus, Trogon melanurus, Trogon curucui, Brotogeris cyanoptera, Brotogeris sanctithomae, Jacamerops aurea, Galbula cyanescens,* nest site characteristics, nest excavation, termite, *Nasutitermes corniger, Constrictotermes cavifrons.*

INTRODUCTION

The great structural complexity of tropical lowland forests provides birds with many nesting niches not available to temperate species (Koepcke 1972, Terborgh 1985). One structural element of these forests exploited by nesting birds throughout the tropics is arboreal termite nests or termitaria (Hindwood 1959). Despite its global distribution, termitarium nesting has been subject to few scientific investigations and comparatively little is known about this behavior (Reed & Tidemann 1994, Brightsmith 2000). Termitaria nesters include species from the predominantly burrow nesting families Galbulidae (Jacamars), Coraciidae (Kingfishers), and Bucconidae (Puffbirds), and species from the predominantly tree nesting families Trogonidae (Trogons) and Psittacidae (Forshaw 1989, Fry *et al.* 1992, Collar 1997, 2001; Rasmussen & Collar 2002, Tobias 2002). This suggests that there are at least two paths by which birds made the evolutionary transition to nesting in termite mounds (Brightsmith 1999a). Unfortunately, detailed analysis of the ecological importance and evolutionary history of termitaria nesting is inhibited by a lack of basic nest site descriptions. To help fill this gap in our knowledge, I report on the nesting of six species of birds that used arboreal termite mounds in a moist tropical lowland forest in southeastern Peru.

METHODS

This study took place in mature and late successional tropical floodplain forest surrounding Cocha Cashu Biological Station in Manu National Park, Peru (11°54'S, 71°18'W; Terborgh *et al.* 1984). This site lies at about 400 m elevation on the boundary between tropical and subtropical moist forest (Holdridge 1967). The mature forests of this site are estimated to be over 200 years old and have canopies 35–40 m high, with emergents reaching 60 m (Robinson *et al.* 1990, Terborgh & Petren 1991). Over 560 bird species have been recorded in the 15 km^2 surrounding the station (Terborgh *et al.* 1984). Alpha diversity, defined here as the number of species with overlapping home ranges, exceeds 160 species in some areas of the mature forest, making this one of the most diverse avian communities in the world (Terborgh *et al.* 1984, 1990; Gentry 1988, Karr *et al.* 1990, Robinson *et al.* 1990).

Data were collected from September to November 1993, 1995, 1996, and 1997. As a result, only species nesting during this time of the year were recorded. Additional species likely use termite mounds at other times of year. Nests were found using three methods: 1) checking all termitaria located in 13 ha of plots; 2) walking trails and systematically checking each termitarium found; and 3) following the characteristic sounds of calling adult and nestling birds (Brightsmith 1999a, 2000).

Termitarium length, width and depth were measured directly with tape measurers or estimated from the ground using 5-cm diameter PVC tubes with 1.5 x 1.5 mm grid on one end. These values were then converted to cm using the height and distance from the termitaria (Brightsmith 2000). The volume of the termitarium was calculated assuming it was an ellipse with diameters equal to the measured height, width and depth (Lubin *et al.* 1977). Entrance angle for excavations was measured with a clinometer. Cavity characteristics were measured using a rigid metal tape measure. Nests visibility was recorded from the ground and each nest was scored as clearly visible, obscured by leaves or in the shadows at the bottom of the termitarium. Characteristics of the nest excavations were compared among species using t-tests and differences in nest visibility among species were tested with c^2 tests (Gibbons 1985).

Data are presented as mean ± SD unless otherwise reported; *P*-values < 0.05 are considered significant.

RESULTS

Six bird species were found using termite mounds during this study: Purus (*Galbalcyrhynchus purusianus*), and Great (*Jacamerops aurea*) jacamars, Black-tailed (*Trogon melanurus*) and Blue-crowned (*T. curucui*) trogons, Tui (*Brotogeris sanctithomae*) and Cobalt-winged (*B. cyanoptera*) parakeets. Each is discussed below in detail.

Purus Jacamar. I observed a group of at least six Purus Jacamars excavating a cavity in a termitarium on 20 October 1997. The termitarium was in open swamp forest dominated by *Ficus trigona*, with a dense *Heliconia* understory (see Terborgh 1983 for a description of this swamp). At night, the group roosted in the cavity together. On 6 November, I checked the termitarium for the last time; the birds were still attending it but I could not confirm the presence or absence of eggs because the entire interior of the chamber was not visible. The termitarium was 4.7 m above the ground, 143 l in volume, built and inhabited by *Nasutitermes corniger* termites (subfamily Nasutiterminae). The birds' tunnel ran about 15 cm into the mound at a vertical angle of +40°. At the entrance the tunnel had a diameter of 7 cm which narrowed to 5 cm before opening into a chamber, approximately 15 cm in diameter by 13 cm high. The entrance to the tunnel was partly obscured from view by leaves. The mound was inhabited by a large colony of biting *Dolichoderus* sp. ants that made cavity inspection difficult.

Great Jacamar. Two active nests of this species were found during the study and each had two chicks that fledged in mid-October. Both nests were in termitaria made by *Constrictotermes cavifrons* (subfamily Nasutiterminae). One mound was still occupied by the termites whereas the other was not. The nests of Great Jacamars were 7.0 and 3.8 m above the ground in termitaria that were 82 and 201 l in volume. The one nest that could be measured had an entrance 10 cm high and 6 cm wide. The floor sloped down from the entrance at 30° into a chamber about 8 cm wide and 25 cm long that hugged the side of the tree. In the other nest, the tunnel sloped up at an angle of +40° into the chamber. Both nest holes were clearly visible and not obstructed by leaves or other vegetation.

Termitaria made by *C. cavifrons* were extremely rare in the study area, I found only two in 13 ha of forest surveyed, and only seven in total. These termite mounds were also spatially clumped. All seven were within a 7-ha triangular-shaped area, despite the fact that searches were conducted throughout an area over 1500 ha. The architecture and placement of *C. cavifrons* termitaria was nearly identical for all seven encountered: all were attached to the main boles of large living *Dipteryx micrantha* trees (diameter at termitarium height = 67 ± 12.1 cm, range = 51–81 cm, N = 6) with no branches or lianas passing through or near the mounds. The mounds were on average 7.3 ± 1.91 m above the ground (range = 5.3–10.4 m, N = 7), 43 ± 15 cm wide (range = 21–62 cm, N = 7), 189 ± 69 cm long (range = 109–310 cm, N = 7) and 13 ± 1.9 cm deep (range 10–15 cm, N = 7). Of the seven *C. cavifrons* mounds located, two had active nests of Great Jacamars, three had old bird excavations but no active nests, and two showed no signs of bird excavation. Small sample sizes prevented statistical comparisons of mound characteristics among these groups (Table 1). The elongate shapes of *C. cavifrons* mounds were different in structure from the elliptical mounds of *N. corniger* used by all other nesting birds in this study.

TABLE 1. Characteristics of *Constrictotermes cavifrons* termitaria. Data were collected from September to November 1993, 1995, 1996, and 1997 in Cocha Cashu Biological Station, Madre de Dios, Peru. Data are presented for termitaria with confirmed Great Jacamar nests, bird excavated cavities, and no cavities.

	Mean (min–max, N)	
	Height above ground (m)	Volume (l)
Great Jacamar nest	7.1 (6.2–8.0, 2)	142 (82–201, 2)
Bird excavation	8.0 (5.0–10.4, 3)	67 (51–85, 3)
No excavation	6.5 (5.3–7.7, 2)	87 (19–156, 2)

Blue-crowned Trogon. I saw Blue-crowned Trogons excavating at two *N. corniger* termitaria but in neither of these cases was the excavation very deep and no nests resulted. On 27 July 1998, I was shown a nest of this species on a small farm along the Tambopata river, less than 250 km from the Cocha Cashu site (Table 2). The nest was in a 25-l *N. corniger* termitarium, 2.3 m above the ground in a citrus tree. The tunnel was 5.7 cm in diameter, 14 cm long, and entered the mound at a vertical angle of +72°. The entrance to the nest was clearly visible from a distance. The chamber appeared similar in form to those of Black-tailed Trogons and *Brotogeris* parakeets (see below), but could not be measured. The nest contained three white eggs. The termitarium contained termites but not ants.

Black-tailed Trogon. I located eight nests of Black-tailed Trogons during this study, all in termitaria constructed by *N. corniger*. Three contained partially destroyed clutches, four had clutches of two eggs, and one had a clutch of three eggs. Birds excavated chambers from early September to early October, and eggs were laid in late September through early October. At one nest, two young fledged on 13 October 1996. I saw adults excavating or leaving deep excavations at an additional 12 mounds. All but one of the 20 termitaria used by Black-tailed Trogons was in mature or late successional floodplain forest; the other mound was on the edge of a lake over the water. Measurements of the termitaria used by this species are presented in Brightsmith (2000). Tunnels excavated by this species averaged 7.3 cm in diameter, 19 cm long and sloped up at an average of 56° (Fig. 1). The nest chambers averaged 18 cm in diameter and 15 cm high (see Table 3 for standard deviations, ranges and sample sizes). All holes were clearly visible from a distance and were not obstructed by leaves or other vegetation.

One year later, I rechecked four termitaria used by Black-tailed Trogons and found no evidence of renesting. These checks revealed that two chambers were completely refilled by the termites, one remained intact but empty and the other contained a roosting marsupial (*Micoureus* sp.).

Tui Parakeet. I located seven termitaria used by Tui Parakeets and all were made by *N. corniger*. The mounds were within 15 m of a lake or river edge (N = 5), in early or mid-successional forest (N = 1), or both (N = 1). In six nests, I confirmed the presence of chicks by the sounds of their begging calls or direct observations. One brood contained three young. I found chicks from late September to mid-November. Characteristics of the termitaria used by this species are presented in Brightsmith (2000). The nest excavations (N = 2) were similar to those of Cobalt-winged Parakeets with long (30 cm), steep (+68°), narrow (3.5 cm) tunnels running up, and opening into a 15 cm diameter and 15 cm high chamber (Table 3).

Tui Parakeets occasionally reused termitaria: one of five contained nests in successive

TABLE 2. Characteristics of *Nasutitermes corniger* termitaria used by birds. For each bird species, data are presented for mounds where active nests were confirmed ("Nests") and all termitaria where individuals were seen excavating, leaving deep holes, or where nests were confirmed ("All"). Termitaria were scored as "on palm" if they were on *Scheelia* or *Astrocaryum* palms. "Termites present" indicates whether or not termites were still living in the mound or if it was abandoned. The height is the height of the termitarium above the ground and the substrate diameter is the diameter of the largest substrate (usually a tree) supporting the mound. Data are presented as mean ± SD, sample size (N). Sample sizes differ within a category if not all data could be accurately collected for each mound. Data were collected at Cocha Cashu Biological Station, Madre de Dios, Peru during September to November 1993, 1995, 1996, and 1997.

Nesting bird species	% on	% termites		Mean ± SD (N)		% Ants
	palm (N)	present (N)	Height (m)	Substrate (cm)	Volume (l)	
Blue-crowned Trogon						
Nests	0 (1)	100(1)	2.3 (1)	12 (1)	25 (1)	0 (1)
All	33 (3)	66 (3)	4.0 ± 2.3 (3)	12 0.3 (3)	28 ± 23 (3)	67 (3)
Purus Jacamar						
Excavation	0 (1)	100 (1)	5.0 (1)	18 (1)	143 (1)	100 (1)

nesting seasons. The birds were not marked, so I do not know if the same birds nested in the mound in both years. Of the four termitaria that were not reused by nesting birds, the termites had refilled the nest cavity in two, and left the other two nest cavities untouched.

Cobalt-winged Parakeet. I located 30 arboreal termite mounds used by Cobalt-winged Parakeets and all were made by *N. corniger*. In 26 of these, I confirmed the presence of chicks by the sounds of their begging calls or through direct observation. Of three broods seen, one had two chicks and two had four chicks. I found chicks in nests from late September through mid-November, but the observation of recently fledged young on 8 October, coupled with the 24-day incubation period for members of the genus (Harris 1985), indicates that hatching may have started as early as mid-September.

Most nests were in mature and late-successional floodplain forest, but three were within 10 m of a lake edge. Measurements of the termitaria used by this species are presented in Brightsmith (2000). Nest excavations made by the birds consisted of long narrow tunnels (length 22 cm, diameter 4.8 cm) sloping steeply upward (+67°). Nest chambers averaged 17 cm in diameter and 16 cm high, and the tunnel entered through the floor of the chamber near one side (see Table 3 for sample size and range). In 14 of 24 cases, the entrances to the nests were clearly visible. In the remaining 10 cases, the nest entrances were obscured from view by vegetation (leaves, lianas or small vines) near the nest (N = 3), in the shadowed area at the bottom of the mound (N = 6), or both (N = 1).

Cobalt-winged Parakeets occasionally reused nesting termitaria: two of 14 contained active nests in successive nesting seasons. Of the remaining 12, the termites completely filled the chamber in five, partially refilled the chamber in two, and left the chamber unfilled in five. One termitarium was used in 1993 and again in 1997. In this case it is known that the termites had refilled the 1993 nest chamber, indicating that the birds excavated a new chamber in 1997.

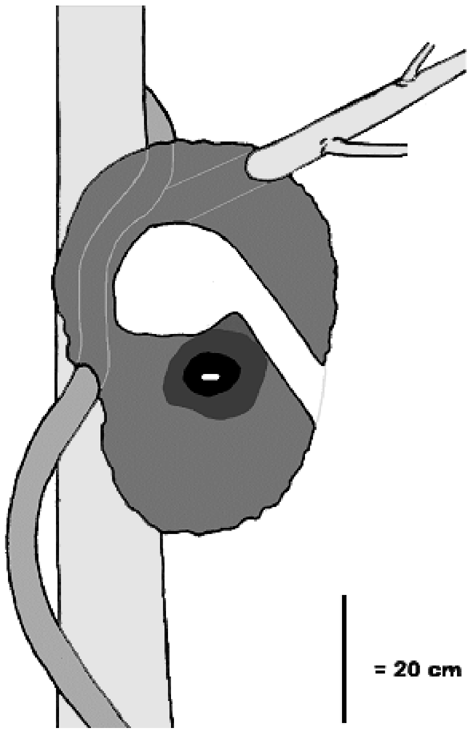

FIG. 1. Typical Black-tailed Trogon (*Trogon melanurus*) nest in an arboreal *Nasutitermes corniger* termitarium (to scale) based on data from Cocha Cashu Biological Station, Madre de Dios, Peru. The nest is shown on a tree with a woody liana running through the upper left of the termitarium. The small white section surrounded by black is the chamber of the queen termite. This area is exceedingly hard and not usually damaged by the excavating birds. The average excavation and termitarium measurements on which this illustration is based are presented in Table 3 and Brightsmith (2000) respectively.

Excavations by Cobalt-winged Parakeets and Black-tailed Trogons. The nest excavations made by Cobalt-winged Parakeets had significantly narrower tunnels than those of Black-tailed Trogons (t-test: $mean_{cwp}$ = 4.8 ± 0.22 cm, N_{cwp} = 13, $mean_{btt}$ = 7.3 ± 0.41 cm, N_{btt} = 6, t = 14.03, $P < 0.0001$) that entered at significantly steeper angles (t-test: $mean_{cwp}$ = 67° ± 14.5°, N_{cwp} = 20, $mean_{btt}$ = 56° ± 5.2°, N_{btt} = 9, t = 2.99, $P = 0.006$) than those made by Black-tailed Trogons. Tunnel length and nest cavity diameter did not differ significantly ($P > 0.1$), but sample sizes for both were small (Table 3). Black-tailed Trogon nest entrances were significantly more visible from a distance than Cobalt-winged Parakeet nest entrances (10 of 10 obvious for Black-tailed Trogons, 10 of 18 for Cobalt-winged Parakeets, $c^2 = 6.24$, df = 1, $P = 0.0125$).

DISCUSSION

Jacamar nesting. Jacamars nest in burrows in the ground, stream banks, termite mounds or rarely rotting trees (Skutch 1968, 1983; Tobias 2002). To date, nesting in termitaria has been reported for three of the five genera of jacamars: *Jacamerops*, *Galbalcyrhynchus* and *Galbula* (Haverschmidt 1968, Skutch 1968, 1983; Hilty & Brown 1986, Styles & Skutch 1989, Sick 1993, Tobias 2002). Use of termitaria by each of these genera will be discussed in turn.

This work provides the most detailed nest site description for Great Jacamars published to date. This species nests in rotting trees (Brazil; Sick 1993) and arboreal termitaria, 3–15 m high, in March–June (Costa Rica; Styles & Skutch 1989). The nests I found fledged in October, indicating that the nesting in Peru and Costa Rica are separated by 6 months. These nests represent the first records of any bird nesting in termitaria constructed by *Constrictotermes* termites. The genus *Constrictotermes* contains three species, all of which are endemic to South America (Araujo 1970). The range of Great Jacamars extends from Costa Rica, to northern Bolivia and the western Amazon basin of Brazil (Hilty & Brown 1986, Styles & Skutch 1989, Sick 1993, De la Peña & Rumboll 1998), indicating that Great Jacamars must nest in termitaria of other genera in Costa Rica.

TABLE 3. Bird nest excavations in *Nasutitermes corniger* termitaria. Data are in centimeters and are presented as mean ± SD (mini–max, sample size). Data were collected from September to November 1993, 1995, 1996, and 1997 at Cocha Cashu Biological Station, Madre de Dios, Peru.

	Tunnel			Chamber	
	Diameter	Vertican angle	Length	Diameter	Height
Cobalt-winged Parakeet	4.8 ± 0.22 (4.0–5.0, 18)	67 ± 14.5 (14–90, 20)	21.8 ± 11.3 (5–40, 6)	17.0 ± 3.6 (13–20, 3)	16 (N = 1)
Tui Parakeet	3.5 (N = 1)	68	30	15	15 (N = 1)
Purus Jacamar	5 (N = 1)	40	15	13	18 (N = 1)
Blue crowned Trogon	5.7 (N = 1)	72	14	–	–
Black-tailed Trogon	7.3 ± 0.41 (6.8–8.0, 6)	56 ± 5.2 (47.5–63.5, 9)	19.1 ± 11.9 (8–33, 5)	17.9 ± 1.8 (15–20, 5)	15.0 ± 1.6 (13.3–16.5, 3)

This is the first nest site description for Purus Jacamars. The only nesting record for any member of this genus is a presumed nest of White-eared Jacamar (*G. leucotis*) in Ecuador, in an arboreal termitarium 3 m above the ground (Hill & Greeney 2000). I could not confirm the presence of eggs or young in the cavity I located, so it is possible that it was only a roost. My observation that birds remained in the cavity during the day after the completion of excavation suggests that the cavity was not just a roost. The entire cavity was not visible during the nest checks and the final check was made less than 17 days after excavation was complete. These facts suggest that eggs could have been in a part of the chamber that was not visible or that the birds were preparing to lay eggs. My observation of six birds attending this potential nest cavity is consistent with observations that Purus Jacamars forage and defend territories in groups (Robinson 1997), and suggests that this species may breed cooperatively.

Members of the genus *Galbula* excavate nesting cavities in termitaria (N = 4 spp.), vertical banks (N = 1) or both (N = 2; Skutch 1968, 1983; Haverschmidt 1968, Hilty & Brown 1986, Sick 1993, Tobias 2002). The nest sites for three members of the genus are apparently unknown. In his review of the family Tobias (2002) lists no known nest sites for Bluish-fronted Jacamars (*Galbula cyanescens*), so I will briefly describe a nest that I found during this study. On 26 September 1995, one young bird with its head fully feathered was in a nest in a vertical bank by a small seasonal stream. The entrance was approximately 5 cm in diameter and there was a 36-cm long tunnel leading to a 23-cm diameter chamber. The habitat was early successional, river-edge forest dominated by *Cecropia* spp.

Forces affecting nest site selection by jacamars have not been investigated. Work on trogons and parrots indicates that termitarium nesting species arose from tree cavity nesting ancestors and that high predation rates on nests in old tree cavities favor the transition to termite mounds (Brightsmith 1999a). A similar analysis of the ecology and evolution of jacamar nesting behavior would provide insight into the evolutionary transitions between nesting in banks and termitaria and further test the role of predation in molding avian nesting behavior.

Trogon nesting. My report provides the first detailed nest site descriptions for both Black-tailed and Blue-crowned trogons (see also Brightsmith 2000). New World trogons have been recorded nesting in tree cavities only (N = 12 spp.), arboreal termitaria only (N = 3), or both (N = 8 Skutch 1972, 1981, 1983, 1999; Wills & Eisenmann 1979, Hilty & Brown 1986, Styles & Skutch 1989, Howell & Webb 1995, Hall & Karubian 1996). The Violaceous Trogon (*T. violaceus*) nests in tree cavities, termite mounds, vespiaries, ant nests and epiphyte root masses (Collar 1997). The nest site for one species, the Blue-tailed Trogon (*Trogon comptus*), is unknown.

The cavities excavated by Black-tailed and Blue-tailed trogons are similar to those constructed by other members of the "Violaceous subclade" of the genus *Trogon* [Violaceous, Black-tailed, Citrolene (*T. citreolus*), Baird's (*T. bardii*), and Slaty-tailed (*T. massena*) trogons, phylogeny from Espinosa de los Monteros 1998]. Regardless of the substrate used (rotting trees or termitaria), these species excavate up-sloping tunnels leading to large spacious chambers (Skutch 1972, 1983). The form of these chambers contrasts with the small shallow excavations made by the members of the "Elegant subclade" of the *Trogon* genus: Mountain (*T. mexicanus*), Black-throated (*T. rufus*) and Collared (*T. collaris*) trogons, that leave the contents of the nests clearly visible from outside (Skutch 1983).

Brotogeris *nesting*. The genus *Brotogeris* contains eight species, all of which are reported to use cavities in trees and termitaria, (American Ornithologists' Union 1997, 1998; Collar 1997, Juniper & Parr 1998, Brightsmith 1999b). *Brotogeris* parakeets also use previously existing tree cavities and excavate cavities in the bases of palm fronds and rotting dead trees (Forshaw 1989, Styles & Skutch 1989, Collar 1997, Juniper & Parr 1997; Brightsmith 1999b, this study). Despite the fact that multiple nests of each *Brotogeris* species have been located, detailed descriptions of nest sites and relative proportions of nests in different substrates are lacking. Lubin *et al*. (1977) reported that Orange-chinned Parakeets (*B. jugularis*) made excavations in mounds of *N. corniger* and mounds of another *Nasutitermes* species in Panama, but details on whether these excavations led to nests were not reported.

The only nest description for Cobalt-winged Parakeets published to date is that of Collar (1997) who reports pairs attending tree cavities but gives no further details. The failure to locate nests in tree cavities during this study was not likely because of inadequate searching. I conducted extensive tree cavity searches in 1997 and located most nests by acoustic and behavioral cues given by the birds (Brightsmith 1999a). If this species commonly used tree cavities, it should have been detected. The lack of tree cavity nests in my study area suggests that nest site selection by this species may differ geographically, or with different ecological conditions.

Published nest site descriptions for Tui Parakeets are limited to brief accounts of a single nest in a hollow in the bend of a branch about 6 m high in northeastern Peru, and reports of pairs seen at holes in termite mounds in Columbia (Hilty & Brown 1986, Forshaw 1989).

Comparison of nest excavation characteristics. The excavations made by Tui and Cobalt-winged parakeets in this study are similar in general form to excavation made in termitaria by White-winged Parakeets (*B. versicolurus*; Hindwood 1959), and in cork "termitaria" by captive Orange-chinned Parakeets (Power 1967). In all cases, the excavations start on the lower part of the substrate and have steeply inclined tunnels leading to relatively large nesting chambers. This pattern is also followed by feral *Brotogeris* parakeets that excavate nests in the rotting bases of Canary Island date palm fronds in Miami (Schroads 1974, Brightsmith 1999b). Small sample sizes prohibit statistical comparison of excavations made by Tui Parakeet and Cobalt-winged parakeets. The narrower tunnel diameter (3.5 cm for Tui and 4.8 cm for Cobalt-winged) likely holds as Tui Parakeets (64 g) are smaller than Cobalt-winged Parakeets (67 g, Terborgh *et al.* 1990), and neither species excavates holes larger than necessary to enter.

Brotogeris nest excavations had smaller entrance diameters, steeper entrance tunnels and lower visibility than the holes made by Black-tailed Trogon. These characteristics likely reduce the relative predation rates on parakeet nests, but the small sample size of Black-tailed Trogon nests prevented statistical comparisons of predation rates (Van Balen *et al.*1982, Major & Kendall 1996, Brightsmith 1999a).

Reuse of nest sites. Reuse of nest sites in subsequent years by parrots is common (Arrowood 1981, Snyder *et al.* 1987, Sparks 1990, Waltman & Beissinger 1992, Reed & Tideman 1994, Abramson *et al.* 1995). In Australia, 43% of 52 nests of the Hooded Parrot (*Psephotus dissimilis*) in terrestrial termite mounds were in chambers that had been reused (Reed & Tideman 1994). *Brotogeris* parakeets reused only 16% of the termitaria rechecked in successive years (3 of 19, this study). I did not confirm that parakeets reused the old chamber in any of these cases. In one case, a termitarium was used in 1993 and parakeets nested in a newly excavated cavity in the same mound in 1997. The low rate of nest reuse also held for Black-tailed Trogons, which did not reuse any of the four termitaria I rechecked. Previous work suggests that nests in old cavities suffer higher predation rate than those in newly excavated cavities or newly erected nest boxes (Sønerud 1993, Brightsmith 1999a). This may be one reason why birds in the predator rich rain forest community studied here do not usually reuse old cavities for nesting.

Nest site characteristics. Detailed comparison of the termitaria used by Black-tailed Trogon, Cobalt-winged and Tui parakeets are discussed by Brightsmith (2000). That study showed that only 1% of apparently suitable termite mounds were occupied, suggesting that nest site availability was not limiting reproduction. It also showed that the two *Brotogeris* parakeets used different habitats for nesting (Tui Parakeets used river and lake edge, whereas Cobalt-winged Parakeets used forest interior) and that Black-tailed Trogons used lower and larger termite mounds than the two parakeets. Whether or not a termite mound was on a palm was apparently not important. However, all species apparently preferred to nest in termite mounds with termites and biting *Dolichoderus* ants (Brightsmith 2000). Whereas sample sizes are too small for statistical comparisons, the three species added in this study, Purus Jacamar, Great Jacamar, and Blue-crowned Trogon, apparently have nest selection criteria that separate them from the other termitarium nesting species at the site. Great Jacamar was the only species that nested in the structurally distinct termitaria of *C. cavifrons.* The other two species used termitaria of *N. corniger.* Purus Jacamar used a large low termite termitarium and was the only species found nesting in the *Ficus trigona* swamp. Blue-crowned Trogon used low termitaria in floodplain forest, and used the smallest termitaria of any species recorded in this study. Also of note was the finding that most bird nests were in termitaria with both active termite colonies and active *Dolichoderus* sp. ant colonies (except those of Great Jacamar). The presence of the termites is undoubtedly an advantage because their constant maintenance activities reduce the risk of the termitarium falling to the ground before the birds fledge (Hindwood 1959). The reason why birds select termitaria with ants remains untested but could be due to the biting ants' ability to repel predators or the "olfactory camouflage" provided by the strong scent of these ants (Brightsmith 2000).

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