USE OF ARBOREAL TERMITARIA BY NESTING BIRDS IN THE PERUVIAN AMAZON[1]

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Abstract. I documented the use by nesting birds and availability of arboreal termite nests (termitaria) in the Peruvian Amazon. Birds occupy about 1% of the termitaria annually, suggesting that termitarium availability does not limit reproductive output. Birds choose termitaria that are larger and higher than average, and the three most common termitarium-nesting species differ in their use of termitaria. Two species of *Brotogeris* parakeets use termitaria with similar characteristics, but Tui Parakeets (*B. sanctithomae*) nest in young forests and edge habitats whereas Cobalt-winged Parakeets (*B. cyanoptera*) use mature forests. Termitaria used by Black-tailed Trogons (*Trogon melanurus*) are larger and lower than those used by the two *Brotogeris* species. The contention that birds usually nest in termitaria still occupied by termites was upheld, but the presence or absence of termites did not explain a significant proportion of the difference between used and available termitaria after removing the effects of height, volume, and substrate type. Birds choose to nest in termitaria inhabited by both termites and aggressive biting ants (*Dolichoderus* sp.). These ants may be protecting the birds' nests by attacking predators or by providing a sort of "olfactory camouflage."

Key words: Brotogeris cyanoptera, Brotogeris sanctithomae, cavity nesting, Dolichoderus ants, Nasutitermes termites, parakeet, Trogon melanurus.

Resumen. En el presente estudio se documenta el uso de termiteros arbóreos por tres especies de aves (*Brotogeris cyanoptera, B. sanctithomae,* y *Trogon melanurus*) y su disponibilidad en un bosque no intervenido en la Amazonía Peruana. Los resultados revelaron que las aves estudiadas anidaron en 1% de los termiteros encontrados anualmente, lo cual sugiere que la disponibilidad de termiteros no está limitando la reproducción. Las aves seleccionaron los termiteros que, en altitud sobre el nivel del suelo y volumen, sobre pasan los valores promedios. Las tres especies de aves más comunes que anidan en termiteros presentan diferentes nichos de anidificación. Las dos especies de pericos *B. cyanoptera* y *B. sanctithomae* usan termiteros con características similares. Sin embargo, *B. sanctithomae* anida en bosques sucesionales tempranos y hábitats de borde, mientras que *B. cyanoptera* usa termiteros en bosque maduro. Los termiteros usados por *Trogon melanurus* son más grandes y bajos en altitud que los usados por las dos especies de *Brotogeris.* Se ha confirmado que las aves normalmente anidan en termiteros aún ocupados por termites (activos), sin embargo la presencia de termites no explica una parte significativa de la variancia entre termiteros usados y no usados después de sacar los efectos de altura, volumen y tipo de substrato. Las aves seleccionan los termiteros que están ocupados por termites y hormigas agresivas del género *Dolichoderus.* Se presume que estas hormigas estarían protegiendo los nidos de ataques por parte de depredadores. Se sugiere que olores intensos características en este tipo de hormigas podrían estar sirviendo como ≪camuflaje olfatorio≫ a los nidos.

INTRODUCTION

Bird species from all tropical regions of the world use arboreal termite nests (termitaria) for nesting (Hindwood 1959). For some taxonomic groups, the percentage of termitarium-nesting species is considerable: at least 11% of all parrots (Juniper and Parr 1998), 32% of all New World trogons (Willis and Eisenmann 1979, Hilty and Brown 1986), and 45% of all kingfishers (Fry et al. 1992). Despite the frequency and global distribution of this behavior, termitarium

nesting has received little attention other than the general review by Hindwood (1959) and brief mention in reviews of bird nesting and termite biology (Krishna and Weesner 1970, Collias and Collias 1984). The work presented here is the first to compare used and available termitaria and nest-niche differentiation by a community of termitarium-nesting birds.

Anecdotal observations suggest that a large volume and presence of a healthy termite colony are important selection criteria for arboreal termitarium-nesting birds, but no quantitative comparisons of use and availability have been conducted. Qualitative observations also suggest

that breeding birds occupy a substantial percentage of the suitable termitaria (Hindwood 1959, Hardy 1963). I investigated these contentions by comparing used and available termitaria in a pristine forest in Amazonian Peru. I also discuss my discovery of a novel three species interaction among nesting birds, termites and aggressive, biting *Dolichoderus* ants.

METHODS

STUDY SITE

This study took place in mature and late successional tropical floodplain forest in the vicinity of Cocha Cashu Biological Station, 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 in the Holdridge system (Holdridge 1967). The mature forest at Cocha Cashu has a canopy 35–40 m high, with emergents reaching 60 m. The mature forest is estimated to be over 200 years old, but younger patches are present due to the natural meandering of the whitewater Manu River (Terborgh 1983). The plant and animal communities at this site have been almost completely free from human disturbance.

MEASUREMENTS OF TERMITARIA

I located and measured arboreal termite nests (termitaria) in 13 1-ha plots regularly distributed throughout a 15-km^2 area of mature and late successional floodplain forest. The plots, 200 × 50 m were bisected lengthwise by a trail. In October 1996, a team of three investigators systematically searched each plot and measured all termitaria larger than approximately 6 L. This value was chosen because it was less than the approximate minimum needed to hold the tunnels and nesting chambers made by Cobalt-winged Parakeets (*Brotogeris cyanoptera*) and Black-tailed Trogons (*Trogon melanurus*) (pers. observ.). This estimation was conservative because I found no bird nests in termitaria smaller than 8.9 L. Small and broken termitaria were ignored. For each termitarium, I recorded the following data: location, height above ground, length, width, and depth of the termitarium, diameter of supporting substrate, and presence of termites.

The estimates of termitarium length, width, and depth were made using 5-cm diameter PVC tubes with a 1.5 × 1.5 mm grid in one end. Observers rested the tubes on monopods, looked through them, and estimated the dimensions of the termitaria by counting the number of grid squares occupied by the termitarium. These grid values were then converted to centimeters using the height and distance from the termitaria. Under ideal conditions this system was found to have an error rate of about 5%. The volume of each termitaria was calculated by assuming that it was an ellipse with radii equal to the measured height, width, and depth (Lubin et al. 1977).

Presence of termites was determined at ground level by locating all termite trails leading from the termitarium and breaking them open to check for the presence of termites (Lubin et al. 1977). This technique is based on the premise that all arboreal termites still maintain trails that make contact with the ground (Hogue 1993). I recorded which termitaria were on palm trees of the genera *Astrocaryum* or *Scheelia*. I hypothesized that birds would avoid termitaria on these palms because both are heavily visited by nest-depredating *Cebus* monkeys while foraging for fruit and insects (Terborgh 1983, Robinson 1997).

I searched for bird nests in termitaria by checking all termitaria in the plots, walking trails outside of plots and systematically checking each termitarium found, and following the characteristic sounds of calling adult and nestling birds. I checked all holes in termitaria for vertebrates by using flashlights, a 2-cm diameter micro-video camera on a 9-m pole, or by observing the hole for 1 hr starting at sunrise. This last method successfully detected the presence of birds as they left in the early morning. If birds were seen in the vicinity of termitaria, then I would confirm the presence of a nest by seeing or hearing nestlings or seeing eggs. Termitaria with bird nests were measured in the same way as those in plots.

To determine whether birds preferentially choose termitaria with active colonies of *Dolichoderus* sp. ants, I checked all active bird nests and a sample of 100 termitaria in November 1997. Because I checked nests for ants in 1997, active bird nests from 1995 and 1996 could not be scored for presence of ants (except for nests to which I climbed during the active period and noted the presence or absence of ants). I checked for ants from the ground by watching all pathways to and from the termitarium for a total of 1–2 min using binoculars. If I saw ants entering or leaving, I confirmed the identification by either taking specimens or checking them for their

characteristic odor. Although small colonies of ants may have been under-reported, large colonies of ants like those that inhabited bird nests were clearly visible.

STATISTICAL ANALYSES

To test the hypothesis that termitaria used by parakeets and trogons differ significantly from unused termitaria, I combined data from bird nests across years and compared them to unused termitaria from the 13 1-ha plots using canonical discriminant analysis (SAS Institute 1989). The variables included in the analysis were supporting substrate diameter, substrate type (*Astrocaryum/Scheelia* palm or other), presence or absence of termites, height above ground, and termitarium volume. Termitaria were included in the analysis only if values for all five variables were obtained. I compared the canonical coefficients of termitaria using *t*-tests and stepwise Bonferroni corrections to determine which groups (parakeet nests, trogon nests, or unused) differed significantly (Sokal and Rohlf 1995). Potentially useable termitaria were defined as those that fell within the ranges of canonical coefficients for termitaria used by each species.

I conducted χ^2 analyses to determine whether birds used termitaria with termites and with ants more or less than expected. Sample sizes for these analyses differ from those in the discriminant function analysis because bird nests missing values for some of the measurements were excluded from the discriminant function analysis but included in the χ^2 test. Data are presented as mean $\pm$ SD unless otherwise reported; *P*-values < 0.05 are considered significant.

RESULTS

NESTS

I located 40 termitaria containing confirmed nests, and 17 termitaria where birds were excavating or attending cavities but nesting was not confirmed. Of these 57 termitaria, 30 were used by Cobalt-winged Parakeets (26 confirmed nests), 7 by Tui Parakeets (*Brotogeris sanctithomae*, 6 confirmed nests), and 20 by Black-tailed Trogons (8 confirmed nests). All nests of these species were located in termitaria, although both species of *Brotogeris* are known to use additional substrates in other areas (Collar 1997). I also found a smaller number of nests of Great Jacamar (*Jacamerops aurea*), Blue-crowned Trogon (*T. curucui*), and Purus Jacamar

(*Galbalcyrhynchus purusianus*), but these are discussed elsewhere (Brightsmith 1999a).

All *Brotogeris* and *Trogon* nests located during this study were in termitaria built by *Nasutitermes corniger* (Termitidae, subfamily Nasutiterminae). On average, birds used large termitaria (93 $\pm$ 86 L), occupied by termites (97%) and *Dolichoderus* sp. ants (79%) in the subcanopy (10.1 $\pm$ 4.8 m high, see Table 1 for data for each species). Most termitaria used by birds were well within mature or late-successional forest (82% of 57, habitat terminology follows Terborgh and Petren 1991). For *T. melanurus* and *B. cyanoptera*, 95% (*n* = 20) and 90% (*n* = 30) of the termitaria were > 10 m from the nearest edge in mature or late successional forest, respectively. The remaining nests for both species were located where mature forest bordered on a lake. In contrast, all *B. sanctithomae* termitaria were in either early or mid-successional forest (*n* = 1), within 15 m of a lake or river edge (*n* = 5), or both (*n* = 1).

TERMITARIUM AVAILABILITY

Five termite species made arboreal nests sufficiently large to hold bird nests: *Nasutitermes corniger*, *N. ephratae*, *N. surinamensis*, *Constictotermes cavifrons*, and *Microcerotermes* sp. Thirteen hectares of forest surveyed in 1996 contained 214 termitaria: 205 of *Nasutitermes corniger*, 7 of *N. ephratae*, and 2 of *Constrictitermes cavifrons* (these figures only include arboreal termitaria greater than 6 L). There were no *N. surinamensis* or *Microcerotermes* sp. termitaria in the plots. Birds were not seen using or visiting termitaria of *N. ephratae*, *N. surinamensis*, or *Microcerotermes* sp., so these are excluded from the subsequent discussion and analyses.

Constrictitermes cavifrons termitaria were extremely rare in the study area. I found two in 13 hectares of forest surveyed and only seven in total. *Jacamerops aurea* nested in two of these, and this is discussed elsewhere (Brightsmith 1999a).

The termitaria of *N. corniger* large enough to hold bird nests (> 6 L) averaged 15.8 $\pm$ 4.2 ha^{-1} in the plots (range 10–26). The number of termitaria greater than the minimum size actually used by a nesting bird (8.9 L) was 14.7 $\pm$ 4.4 (range 7–25, Table 2). Birds occupied small fractions of the available termite nests each year. In 1995, checks of 24 ha of forest revealed 387

TABLE 1. Characteristics of used and available *Nasutitermes corniger* termitaria. For each bird species, data are presented for mounds where active nests were confirmed ("Nests") and for mounds where individuals were seen excavating, leaving deep holes or nesting ("All"). Termitaria were scored as "On palm" if they were located 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. Sample sizes differ within a category if not all data could be accurately collected for each mound.

Nesting bird species	% On palm (n)	% Termites present (n)	Height (m) mean ± SD (n)	Substrate diameter (cm) mean ± SD (n)	Volume (L) mean ± SD (n)	% Ants present (n)
Brotogeris cyanoptera						
Nests	27 (26)	92 (26)	10.9 ± 4.2 (26)	41 ± 34 (20)	85 ± 54 (23)	60 (10)
All	27 (30)	97 (30)	11.7 ± 5.1 (30)	42 ± 32 (23)	83 ± 58 (27)	66 (12)
B. sanctithomae						
Nests	0 (6)	83 (6)	11.9 ± 5.8 (6)	36 ± 25 (5)	126 ± 125 (4)	66 (3)
All	0 (7)	86 (7)	11.6 ± 5.3 (7)	35 ± 23 (6)	105 ± 118 (5)	66 (3)
Trogon melanurus						
Nests	75 (8)	100 (8)	6.1 ± 1.9 (8)	27 ± 11 (8)	63 ± 56 (8)	100 (2)
All	60 (20)	100 (20)	7.2 ± 2.3 (20)	35 ± 19 (20)	103 ± 110 (20)	89 (9)
All birds combined						
Nests	33 (40)	93 (40)	10.1 ± 4.5 (40)	37 ± 28 (33)	85 ± 66 (35)	67 (15)
All	35 (57)	97 (57)	10.1 ± 4.8 (57)	38 ± 26 (49)	93 ± 86 (52)	79 (24)
Unused						
All	43 (204)	85 (204)	7.3 ± 4.7 (204)	39 ± 13 (204)	47 ± 49 (204)	10 (100)[a]

[a] The 100 termitaria evaluated for ants are different than the 204 termitaria used in the other analyses.

termitaria large enough to hold bird nests and only 4 (1.0%) contained bird nests. In 1996, the percent occupied was even lower because the 205 termitaria checked contained only one bird nest (0.5% occupancy).

BIRD USE OF AVAILABLE TERMITARIA

Termitaria used by *T. melanurus, B. cyanoptera,* and *B. sanctithomae* (data from all years pooled) differed significantly from the unused termitaria (canonical discriminant analysis, $F_{15,671} = 4.6$, $P < 0.001$). The first canonical coefficient, which summarizes the difference between used and un-

TABLE 2. Densities of termitaria potentially suitable for nesting birds. Densities in number ha⁻¹. Termitaria were considered similar to those used if they fell within the minimum convex polygon produced by the canonical discriminant analysis.

Termitaria	*Brotogeris*	*T. melanurus*
Greater than 6 L	15.6[a]	15.6[a]
Greater than minimum size used	14.7	12.7
Similar to those used by each species	5.4	5.7

[a] Numbers are average density per hectare from 13 hectares surveyed.

used termitaria, showed that termitaria used by birds were higher and greater in total volume than those that were not used, but the diameter of the substrate and presence or absence of termites were not significant. Because presence or absence of ants was not scored in the plots, that factor is analyzed independently below. Although they differed significantly, the first canonical coefficients for used and unused termitaria showed great overlap. Nearly 70% (141 of 203) of the unused termitaria had first canonical coefficient values within the range used by nesting birds.

The second canonical coefficient showed that termitaria used by *Brotogeris* parakeets were higher, smaller, and less likely to occur on *Astrocaryum* or *Scheelia* palms than those used by *T. melanurus* (canonical discriminant analysis, $F_{8,488} = 2.82$, $P < 0.005$, Fig. 1). Despite this significant difference, there was still substantial overlap in the characteristics of termitaria used by these species. The canonical coefficient scores for 30% (6 of 20) of *T. melanurus* nests were within the range of scores recorded for nests of *B. cyanoptera,* and 35% (8 of 23) of the *B. cyanoptera* nests were within the range of
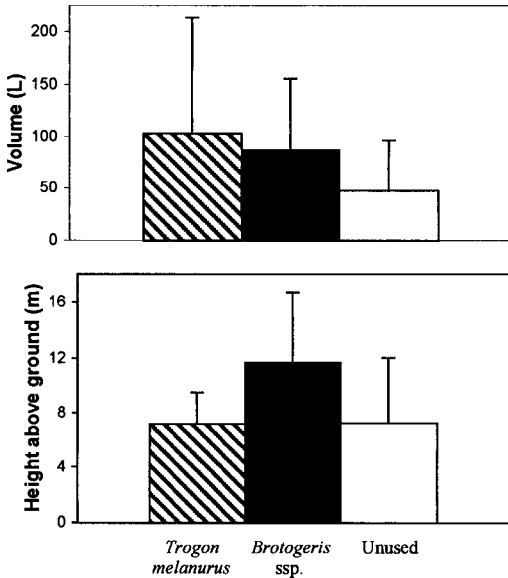
FIGURE 1. Volume and height of used and available termitaria for *Trogon melanurus* ($n = 21$), *Brotogeris* parakeets ($n = 37$), and termitaria unused by birds (n = 204). Error bars represent one standard deviation above the mean.

canonical coefficient scores recorded for *T. melanurus*. In fact, I saw both species excavating in the same termitarium and on numerous occasions old termitaria showed evidence of excavation by both *Brotogeris* and *Trogon*. The finding that *Brotogeris* nests were less likely to occur on palms is apparently because this variable is not independent of height. Because of the palms' growth form, termitaria on palms occurred in a range from 3–12 m high. I compared the proportions of bird nests and available termitaria on palms in this height range and found that *Brotogeris* nests occurred on palms less than expected and *T. melanurus* nests occurred more than expected, but the trend was not significant (on palms *Brotogeris* 6 of 17, *T. melanurus* 12 of 19, available 85 of 158, $\chi^2_1 = 1.4$, $P = 0.24$). The third canonical axis that separated the termitaria used by the two species of *Brotogeris* was not significant (canonical discriminant analysis, $F_{3,245} = 0.3$, $P = 0.81$).

Of the unoccupied termitaria in the plots, 35% (70 of the 203) and 37% (74 of 203) had first and second canonical coefficient scores within the ranges used by parakeets and trogons, respectively. This indicates that approximately 35% of the unused termitaria were potentially

suitable for birds and that unoccupied termitaria potentially useable by parakeets and trogons occur at a density of over 5 ha^{-1}.

The presence or absence of an active colony of termites did not account for a significant amount of variation among used and unused termitaria (canonical discriminant analysis $R^2 = 0.023$, $P = 0.13$). Despite this, the proportion of termitaria with termites was higher among termitaria used by birds (0.96, $n = 51$) than those not used by birds (0.85, $n = 205$, $\chi^2_1 = 4.5$, $P < 0.05$).

Dolichoderus sp. ants occurred in a significantly higher proportion of termitaria with bird nests than termitaria without bird nests (15 of 20 termitaria with bird nests had ants, 10 of 100 without nests had ants, $\chi^2_1 = 42.7$, $P < 0.001$). The termites also were present in 93% of the termitaria inhabited by ants (26 of 28). Where both occurred, the ants apparently live in parts of the termitarium that do not contain termites (pers. observ.). It is unknown whether the ants invade and take over part of the termitarium, or whether the ants move into sections of the termitarium that the termites had previously abandoned. On six occasions, birds were seen beginning excavations in termitaria, and in five of these cases the termitaria contained ants. This observation indicates that the birds were actively choosing ant-occupied termitaria and not that ants were invading termitaria that had bird nests.

DISCUSSION

Nesting birds occupied only a small fraction of the available termitaria and chose ones that were higher and larger than average. The three most common species of termitarium-nesting birds partitioned the nesting resource as follows: *B. sanctithomae* in young forests and along edges; *B. cyanoptera* in small, high termitaria in old forests; and *T. melanurus* in large, low termitaria in old forests, although there was extensive overlap in the characteristics of termitaria used by *B. cyanoptera* and *T. melanurus*. All three species of birds show an apparent preference for termitaria inhabited by *Dolichoderus* ants.

TERMITARIUM AVAILABILITY

Birds nested in termitaria constructed by two species of termites from the subfamily Nasutiterminae: two nests of *Jacamerops aurea* were located in *Constrictotermes cavifrons* termitaria (Brightsmith 1999a), and the rest were in *Na-*

sutitermes corniger nests. *N. corniger* is a common species that occurs in habitats as diverse as open pastures and mature moist forests from Mexico to Venezuela and south to Bolivia (Araujo 1970, Thorne 1980). Evidence from Panama and Costa Rica (Lubin et al. 1977, Skutch 1983) suggests that this termite is exploited by nesting birds over a broad geographic area. My failure to locate bird nests in termitaria of other termite species may be due to their relative scarcity at the site or that the termitaria of different species have different structural characteristics that may make them more or less attractive to birds (Thorne 1980).

The low occupancy rates I found suggest that termitarium availability does not limit the reproductive output of *T. melanurus* or the two *Brotogeris* parakeets. The home range size of *T. melanurus* is approximately 5 ha (Terborgh et al. 1990), and termitaria sufficiently large to hold bird nests occur at a density of 12.7 ha^{-1}, giving each pair an average of over 60 termitaria to choose from. If only the potentially suitable termitaria are considered, then there are still over 28 5-ha^{-1} home range (Table 2). The nonterritorial parakeets range over areas that far exceed the 5 ha reported for trogons and therefore also have a large number of potential nest-sites to choose from. The abundance of termitaria found here apparently provides the birds with ample nesting opportunities.

Birds prefer termitaria occupied by *Dolichoderus* ants, and only about 10% of all termitaria contain these ants. This suggests that not all available termitaria are equally attractive to birds. Despite a preference for ants, their absence does not make a termitarium unusable by birds because all species in this study used termitaria without ants (except *G. purusianus,* for which only one excavation was found, Brightsmith 1999a).

The apparent abundance of termitaria reported here may not hold for all areas. On Barro Colorado Island, Panama (BCI), 19 large arboreal nests of *N. corniger* were monitored for one year, and damage by nesting birds was recorded 25 times. This suggests occupancy rates on BCI are greater than the 1% recorded in my study (Lubin et al. 1977). However, the BCI study made no attempt to distinguish between the small scrapes made by prospecting birds and active nests. Near Sydney, Australia, birds occupy most termitaria of sufficient size during the breeding season, indicating high occupancy rates (Hindwood 1959). I found that five of seven *Constrictotermes cavifrons* termitaria had bird-made holes, and two of these holes had active nests of *J. aurea* (Brightsmith 1999a). Similarly in northern Mexico, 4 of 10 large *Nasutitermes nigriceps* termitaria had active nests of Orange-fronted Parakeets (*Aratinga canicularis*) giving an occupancy rate of 40% (Hardy 1963). These lines of evidence suggest that in some areas birds may face a shortage of termitaria suitable for nesting. Additional work is needed to determine whether the high occupancy rates suggested by the anecdotes or the low occupancy rates found in my systematic surveys are the norm for termitarium-nesting birds.

NEST SITE CHARACTERISTICS

The termitaria used by birds are larger and higher than those that remained unused. The minimum size used by birds, 8.9 L, also is much larger than the 1.8 L nest chambers that the birds excavate (Brightsmith 1999a). This large minimum size is likely due to the fact that the interior of the termitarium is not uniformly soft and excavatable. All termitaria contain a very hard queen's chamber located near the center (Noirot 1970), and most are traversed by tree trunks, branches, and lianas (pers. observ.). Both the queen's chamber and woody vegetation are likely too hard for parrots and trogons to excavate. As a result, only larger termitaria may have sufficient volume to be used by nesting birds. The finding that termitaria used by birds in general were higher than unused termitaria is likely due to *Brotogeris* parakeets' use of high termitaria, as those used by *T. melanurus* are similar to those that are unused (Table 1, Fig. 1, see section "Niche Differentiation," below).

Birds usually nest in termitaria where the termites are still present (Hindwood 1959, Hardy 1963, Collias and Collias 1984). My findings confirm this, but also show that *Brotogeris* parakeets will occasionally occupy abandoned termitaria. The presence of termites may be important to nesting birds because abandoned termitaria break and fall at a higher rate than active ones (Hindwood 1959; unpubl. data). If a nest falls before young fledge, it is unlikely that any young will survive; however, no bird nests failed due to this factor during my study. I found that birds used active termitaria at a significantly higher rate than expected, but that termite activ-

ity did not explain a significant proportion of the difference between occupied and unoccupied termitaria when the variables height, volume, and substrate type were included. The conflicting results reported here leave questions about the importance of termite activity in nest site choice and nest success unresolved.

Anecdotal information for other birds that excavate nest cavities in wasp and ant nests also does little to clarify the question. *Colaptes brachyurus,* a woodpecker from southeast Asia, is known to hollow out cavities in the nests of a stinging ant of the genus *Crematogaster.* Although this ant is a major food source for the woodpecker, the woodpecker apparently does not depopulate the host ant colony (Hindwood 1959), suggesting that it may be advantageous to leave the colony intact. In contrast, nesting pairs of *Trogon violaceus* invest great effort in exterminating the resident wasps before beginning to excavate nesting cavities in vesparies (Skutch 1972).

NICHE DIFFERENTIATION

Brotogeris cyanoptera and B. sanctithomae. Small sample sizes hindered attempts to distinguish statistically between the termitaria used by these two congeners. The most obvious difference between them was that *B. sanctithomae* used edges and early successional forests, whereas *B. cyanoptera* used late successional and mature forests and edges. The nesting habitat of these two overlapped only where mature forest bordered on a lake. Near a lake edge, both species independently investigated the same termitarium (pers. observ.). Observations and acoustic registrations at Cocha Cashu, Peru show a similar habitat division among these species: foraging *B. sanctithomae* use lake and river edge trees and young forest, whereas *B. cyanoptera* use older forest types (Terborgh et al. 1984; pers. observ.). *Brotogeris cyanoptera* are known to come to lake-edge fig trees and occasionally forage simultaneously with *B. sanctithomae* in such sites. In contrast, *B. sanctithomae* was never recorded foraging or perching in mature floodplain forest in over six months during which I could distinguish the two by their calls. These observations coincide with the published habitat descriptions for both species (Parker et al. 1982, Hilty and Brown 1986, Forshaw 1989). Reasons why *B. sanctithomae* are confined to waterside edge habitats are unknown. In the tropics, many congener pairs segregate along successional gradients as a result of interspecific aggression (Robinson and Terborgh 1995), but aggressive displacement by the larger *B. cyanoptera* was not witnessed during this study. In addition, the abundance and low occupancy rates of termitaria found in this study suggest that nest-site availability is not preventing *B. sanctithomae* from using forest interior habitats.

Brotogeris parakeets and Trogon melanurus. Nests of *Trogon melanurus* are in termitaria that are larger and lower than nests of *Brotogeris* parakeets. The height differences among these species may be due to the fact that *Brotogeris* feed, roost, rest, and travel in or above the canopy (Gilardi and Munn 1998, Brightsmith 1999b). Only once did I observe *B. cyanoptera* or *B. sanctithomae* foraging inside the forest below canopy level; otherwise, all sightings below the canopy were near termitaria. *Brotogeris* may choose to nest in high termitaria to reduce the distance they have to descend through the forest to arrive at the nest. The slow and deliberate way that these birds descend to the nest (pers. observ.) suggests that predation risk associated with this behavior may be high. In contrast, *T. melanurus* is a species that commonly forages in the subcanopy and lower forest strata (Terborgh et al. 1984, Hilty and Brown 1986). Therefore, the trogons gain little by placing nests closer to the canopy. In some systems nest predation rates are inversely proportional to nest height, but within the height range of termitarium nests I have examined, predation is apparently independent of height (van Balen et al. 1982; unpubl. data).

The use of larger termitaria by *T. melanurus* (body mass: 90 g) when compared to *Brotogeris* parakeets (63 and 67 g) at first glance appears to be a function of larger body size, but this is not likely the case because both species excavate nesting chambers of similar total volume (Brightsmith 1999a).

The canonical discriminant analysis suggests that *T. melanurus* nests are more likely to be on *Astrocaryum* or *Scheelia* palms than those of *Brotogeris* parakeets, but this is likely because termitaria on these palms occurred predominantly between 3 and 13 m high. When I control for height, the birds use termitaria on these palms in proportion to their availability. I predicted that birds would avoid termitaria on these palms because *Cebus* monkeys are known nest

predators and frequently visit these palms in search of insects, fruits, seed, inflorescences, and petiole pith (Terborgh 1983, Robinson 1997). Nesting birds may be able to use termitaria on these palms because monkey use of these resources peaks in the early dry season (64% of the total foraging time in May–July) and drops to 1% by October, when bird breeding peaks (Terborgh 1983).

BIRD NESTING AND *DOLICHODERUS* ANTS

Although inquilines (insects that live in the nests of other social insects) are commonly reported in studies of termites (Lee and Wood 1971, Redford 1984, Domingos and Gontijo 1994), this is the first documented case of birds choosing to nest in termitaria containing such species (but see the second-hand note on kookaburras using termitaria with ants in Hindwood 1959). Because birds choose to excavate nests in termitaria containing ants, this is an active association of the birds with the ants and not a case of the ants moving into termitaria with bird nests. Both birds and ants may select termitaria with similar characteristics, but this possibility cannot be addressed with the available data. Associations between ants and nesting birds have been known for decades. Most bird-ant associations are instances where birds choose to nest in trees inhabited by aggressive stinging ants (Maclaren 1950, Janzen 1969, Young et al. 1990) or colonies of stinging ants (Myers 1929, Hindwood 1959).

In many cases of birds nesting with ants, the ants are part of a mutualistic relationship with their host trees: the tree provides shelter and food sources and the ants provide protection from herbivorous insects and browsing vertebrates (Janzen 1966). The ants attack and quickly repel snakes, lizards, and other vertebrates that touch the tree. This reduces predation rates on bird nests (Janzen 1969, Grimes 1973). The nesting of *Colaptes brachyurus* in *Crematogaster* ant nests discussed above may also be due to the defensive advantages provided by the presence of these stinging ants. Unlike the *Pseudomyrmex* and other ants discussed here, the *Dolichoderus* ants I found in the termitaria are stingless. Although a small number of stinging ants can quickly repel vertebrates, the bites of the *Dolichoderus* ant are only mildly painful (pers. observ.), and their ability to repel nest predators remains untested.

My observations suggest a number of reasons why birds choose to nest in termitaria with *Dolichoderus* ants, but I have no experimental tests of the following hypotheses. Attempts to check bird nests in termitaria with large ant colonies always solicited strong defense responses from the ants. When investigators climb trees containing ant-infested termitaria, the ants swarm out covering the surface of the termitarium, tree, and adjacent branches for a distance of 1–2 m in all directions. Ants also fall or jump from the nest in large numbers, coating everything below the nest. Even the comparatively mild disturbance of checking the nest using a micro-video camera on a 9-m pole elicits a strong response and results in the observers being covered in ants. In less than 30 sec the ants can mount a full defense response. This rapid response indicates that the ants may effectively deter casually searching predators.

Although the bites of *Dolichoderus* ants may not be strong enough to dissuade all nest predators, these ants may protect the birds in another way. The characteristic odor exuded by this species is strong (Bolton 1994; pers. observ.). Nest-related smells such as feces and old eggs are known to attract nest predators in some instances (Henry 1969, Petit et al. 1989) but not all (Hammond and Forward 1956, Whelan et al. 1994). The scent trail left by researchers walking among nests can also attract predators. The latter effect can be effectively masked using artificial "deer scent" (Whelan et al. 1994). This suggests that reducing olfactory cues around nests can reduce predation. The strong smell of *Dolichoderus* ants may serve to mask the odors of the nesting birds that share their termitaria. If this is the case, then this "olfactory camouflage" could significantly reduce predation by nocturnal, olfactory predators such as marsupials and rodents (Roper and Goldstein 1997). Reduction of nocturnal predation may be particularly beneficial because both adult birds and young may fall victim to nocturnal nest predators. Of course, nesting in an area with a strong characteristic odor would be advantageous only as long as the percentage of such sites occupied by birds was low enough that predators would not learn to associate the masking odor with the presence of bird nests (M. S. Foster, pers. comm.).

Birds could also be choosing termitaria with *Dolichoderus* ants if the ants help sanitize the nests or deter avian ecto-parasites. My obser-

vations indicate that nests of trogons and *Brotogeris* parakeets in termitaria are relatively free of feces after the young fledged. I also know that the *Dolichoderus* ants regularly enter bird nest chambers. They also eat bird feces presented to them (pers. observ.). Although these observations are suggestive, the mechanism of feces removal remains unknown because the nest chambers contain other insect larvae capable of consuming feces (Myers 1929; pers. observ.). For now, the role of the ants in nest sanitation remains unknown. Similarly the ability of the ants to deter nest parasites is untested.

One other class of bird-ant association reported in the literature is that of birds nesting in association with *Azteca* sp. ants. *Cacicus cela* and *C. haemorrhous* are known to place nests near colonies of *Azteca* ants (Meyers 1929), whereas *T. violaceus* excavates nests in the arboreal nests of *Azteca* ants (Hindwood 1959, Hilty and Brown 1986, Skutch 1999). During the present study, pairs of *T. violaceus* were seen excavating cavities in *Azteca* sp. ant nests on two occasions, but neither of these resulted in a nest. *Azteca* and *Dolichoderus* are both stingless ants in the subfamily Dolichoderinae and both have similar nest defense strategies (pers. observ.). At this time it is impossible to know whether these two trogon-ant associations arose independently, but future observers should carefully document the presence or absence of ants at trogon nests to help clarify the evolution and ecology of these associations.

ACKNOWLEDGMENTS

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