JOURNAL OF AVIAN BIOLOGY 36: 74–83, 2005

# Competition, predation and nest niche shifts among tropical cavity nesters: ecological evidence

**Donald J. Brightsmith**

Brightsmith, D. J. 2005. Competition, predation and nest niche shifts among tropical cavity nesters: ecological evidence. – J. Avian Biol. 36: 74–83.

I studied cavity-nesting birds in an undisturbed site in lowland Peru to determine the relative roles of competition and predation in favoring termitarium nesting over tree cavity nesting. Occupancy rates of both nest boxes and natural tree cavities near 2% suggest that competition for tree cavities is not favoring the use of termitaria. Artificial nests and bird nests in termitaria suffer significantly lower predation rates than similar nests in old tree cavities showing that predation is favoring the use of termitaria over old tree cavities. Bird nests in newly excavated tree cavities also show lower predation rates than older cavities suggesting that cavity age is more important than substrate (tree or termitaria) *per se*. This study suggests that nest predation has a greater influence than nest competition on life history evolution for many cavity-nesting birds.

*D. J. Brightsmith, Department of Biology, Duke University, Durham NC 27708-0338, E-mail: djb4@duke.edu*

Nest site selection greatly influences avian natural history. Traits like clutch size, nestling period, renesting probability, nest initiation date and nest predation rates all correlate with nesting niche (Lack 1968, Martin 1995, Robinson et al. 2000). For species that nest in potentially limiting microhabitats like old tree cavities or oceanic islands, the availability of nesting sites often limits the reproductive rates of populations (Duffy 1983, Newton 1994). Studies have also shown that nest predation favors the formation of avian communities assembled from species that differ in nesting niche (Martin 1998a, b). This suggests that a species' choice of nest site may directly influence where it can live and with which species it can coexist. Despite the importance of nesting niche in avian evolution and ecology, evolutionary changes in nesting niche and the ecological forces favoring such changes have received relatively little study. The companion paper presented in this volume analyzed transitions in nesting niche by cavity nesting parrots and trogons (Brightsmith 2005). That work showed that nesting in old tree cavities (secondary cavity nesting) is the ancestral trait for parrots and trogons and that there have been at least eight independent evolutionary transitions from nesting in tree cavities to nesting in arboreal termite mounds. These transitions correlated with an increase in nestling period suggesting that predation rates in termite mounds are significantly lower than in old tree cavities. This phylogeny-based study suggests that predation, not competition, has favored the shift from nesting in tree cavities to termite mounds. However ecological data supporting this contention are lacking. In this study I examine the actual levels of competition and predation for tree cavity and termitarium nesting species.

Termitarium nesting species provide an ideal system to test the relative roles of competition and predation in favoring major nest niche shifts: 1) most genera that nest in termitaria have independently evolved this behavior (Brightsmith 2005), 2) most termitarium nesting species still retain the ability to use tree cavities, so current ecological forces must still favor the use of termitaria (Hindwood 1959, Collar 1997, Juniper and Parr 1998, Brightsmith 1999), and 3) both competition and predation are known to affect nest site selection by cavity-nesting birds (Van Balen et al. 1982, Nilsson 1984, Alatalo et al. 1991).

This study was conducted in pristine forests in the Peruvian Amazon at a site where there has been no recent extinction, introduction, logging or hunting. The study site provides a system where tree cavity abundance, termitarium abundance, avian abundance and species diversity have not been changed by recent anthropogenic disturbance, a condition not met by other studies of cavity-nesting bird communities (Newton 1994, 1999). The absence of large-scale, human-induced disturbances at this site provides the opportunity to study avian species under conditions similar to those they may have faced over evolutionary time. I hypothesize that if competition for tree cavities favors the use of termitaria, I would witness frequent fights over cavities by secondary cavity-nesting birds and that most nest boxes and natural tree cavities would be occupied. If predation favors the use of termite mounds, I hypothesized that predation rates on nests in termitaria would be significantly lower than predation rates on nests in tree cavities.

# Methods

## Study area

This study took place in late successional and mature 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 in the Holdridge system (Holdridge 1967). The mature forests of this site are estimated to be over 200 years of age and have canopies 35–40 m high, with emergents reaching 60 m (Terborgh et al. 1984, Robinson et al. 1990, Terborgh and Petren 1991). In addition, the forests have been completely free of hunting for over 30 years and subjected to no logging. There have been no recent introductions, extinctions or anthropogenic changes in species diversity at this site. This suggests that tree, termite and bird populations occur in natural, possibly pre-Colombian, densities and age distributions. This condition has not been met by other studies of cavity-nesting bird communities despite the fact that the ecological forces operating in communities that have been heavily impacted by humans may bear little resemblance to those in natural communities (Newton 1994, Sasvari et al. 1995, Martin and Clobert 1996).

Over 560 bird species have been recorded in the 15 km$^2$ surrounding the station. 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). Nearly 100 species at this site are suspected to nest in cavities although the nests of some have not been described.

## Competition for cavities

The goal of this section of the study was to evaluate the level of competition for cavities among small ( $<200$ g) sub-canopy and understory cavity nesters. These parameters were chosen to correspond with the height range and habitats used by the two most common termitarium using species at the site, *Trogon melanurus* (122 g) and *Brotogeris cyanoptera* (67 g, Dunning 1992, Brightsmith 2000). Both species nest only in termitaria at the field site, but all other species of *Brotogeris* and most termitarium nesting trogons species also nest in tree cavities indicating that the choice of nest site is not fixed in these lineages (Forshaw 1989, Collar 1997, Brightsmith 2005). The goal was to determine if competition for tree cavities in the habitat and height range used by these two species was favoring the use of termite mounds over tree cavities.

In many areas where competition for cavities is intense, fights among rival pairs and cavity guarding are common (Snyder 1978, Van Balen et al. 1982, Snyder et al. 1987, Ingold 1989, Waltman and Beissinger 1992, Nycander et al. 1995). During nest searches at the site I observed the behavior of cavity-nesting birds in the vicinity of potential and actual nesting cavities to determine the prevalence of cavity guarding and fights among rival pairs.

Systematic searches were conducted to determine the occupancy rates of naturally occurring tree cavities because this measure correlates with intensity of competition for nest cavities (Van Balen et al. 1982, Nycander et al. 1995). In late Sep. – early Nov. 1996 and 1997 researchers searched for cavities by slowly walking trails and visually inspecting the lower 15 m of all trees. During Oct. and early Nov. of 1997, teams of three researchers conducted exhaustive cavity searches in 7, one ha plots up to a height of about 15 m using 10 × binoculars. They checked tree cavities for active nests using one of three methods: a 5 m ladder, tree climbing gear, or a black and white micro-video camera (Watec model WAT-704R, 1.5 cm diameter) mounted on a 9 m telescoping pole.

I considered a cavity suitable for nesting birds only if it had a vertical depth from the bottom rim of the hole to the floor of the cavity of 4 cm or more and a horizontal depth from the entrance to the back wall of the cavity greater than 7 cm or if the cavity was a horizontal tube 14 cm or more in depth. These values represent the minimum dimensions of occupied tree cavity nests found during this study (Brightsmith unpubl. data). I measured horizontal cavity depth, vertical cavity depth, hole width and height, height of the hole above the ground and angle of orientation for all accessible tree cavities. I calculated percent occupancy by dividing the total number of bird nests located during systematic searches by the total number of suitable cavities found during these same searches.

I set out 60 nest boxes in a 10 $km^2$ area in Nov. 1995 to test if scarcity of useable tree cavities limits bird reproduction. Nest boxes were 20 cm × 16 cm × 30 cm deep with a 13 cm internal shelf even with the bottom of the entrance that left a 7 cm space at the back of the box to allow passage to the floor of the box. This shelf was to prevent raptors and monkeys (known predators of tree cavity nests), from seeing the box floor and easily removing the contents. Forty of the boxes had 5 cm diameter entrance hole and was hung 6–11 m high to approximate the diameter and 3.6–23.8 m height range used by *B. cyanoptera* (Brightsmith 2000, 2004). The maximum of 11 m was set to facilitate rapid checking of the boxes. Twenty boxes had 8 cm diameter holes and were placed 4–9 m high, within the 3.8–9.1 m height range used by nesting *T. melanurus* (Brightsmith 2000, 2004). I checked the boxes 2 or 3 times each during the breeding seasons (late Sept.- early Nov.) of 1996 and 1997.

## Nest predation

To determine the differences in nest predation rates among tree cavities and termitaria I conducted artificial nest experiments in 1996 and 1997. Clutches of 2 eggs were placed in naturally occurring tree cavities suitable for birds (see above for definition of suitable cavities), and in holes I excavated in termite mounds. The experiment simulated secondary tree cavity nests and nests birds excavate in termitaria, respectively. The entrance diameter and internal diameters of the holes made in termitaria approximated those made by *T. melanurus* because they were large enough to admit human hands, a prerequisite for excavating the chambers and placing the eggs (Brightsmith 2004). I used clutches of two eggs to simulate clutches of *T. melanurus* and many other tropical species (Skutch 1985, Brightsmith 1999).

I conducted the first artificial nest experiment in early Nov. of 1996 using two eggs made from ivory-white modeling clay (Møller 1987, Haskell 1995b). I checked these artificial nests after seven days and differences between the two nest types were tested using a chi-square test. In Oct. and early November I repeated the experiment using one clay egg and one quail (*Cotournix* sp.) egg painted with whitewash. The quail eggs (31 × 24 mm) were slightly smaller than a measured egg of *T. melanurus* (37 × 27 mm) so effects of oversized eggs that have called into doubts the validity of many egg experiments were avoided (Roper 1992, Haskell 1995a, DeGraff and Maier 1996, Major and Kendal 1996). I painted the naturally brownish speckled quail eggs white to simulate the egg color of *T. melanurus* and most other cavity-nesting birds (Howell and Webb 1995). No attempt was made to mask human scent (Whelan et al. 1994). Nests were checked at 4, 8, 16, and 24 days to determine the pattern of egg loss with time. The 24-day monitoring period simulated the long incubation periods of *Brotogeris* parakeets (Forshaw 1989). It was slightly longer than the incubation period for most New World trogons (16 to 19 days), but shorter than the total nesting period for these species (34 to 41 days; Skutch 1942, 1948, 1962, 1972, 1983).

I scored artificial nests as preyed upon if one or both eggs showed bite marks or were removed from the nest. I did not consider them preyed upon if they showed surface scratches characteristic of chewing by Orthoptera. The *Nasutitermes* termites that made and inhabited the mounds ate or covered some clay eggs. When this happened the nest was eliminated from the analysis and not considered depredated because these termites never attacked real eggs in this study. Ants drilled a hole in a natural egg and ate the contents in one artificial nest in a tree cavity. The ant species in question is common in arboreal tree cavities and was never aggressive during nest checks. It is unknown if this species is capable of depredating natural nests. Given that my hypothesis was that predation rates would be higher in tree cavities I chose to be conservative and not consider this nest depredated.

The spatial distribution of the artificial nests was constrained by the fact that artificial nests had to be placed in suitable termitaria and tree cavities. Most were > 100 m from other artificial nests in the same substrate (70 of 92). The average density of artificial nests in this study was about 0.5 nests per ha in each substrate. This nest density was 10 to 40 times less than in studies that found density dependent effects of nest predation (Martin 1987, 1988b, Gibbs 1991, Hoi and Winkler 1994, Tellería and Díaz 1995).

To determine the relative rates of predation on natural bird nests in tree cavities and termitaria, I monitored 47 bird nests representing at least 13 bird species (Appendix). Twenty-three nests were in termitaria, 12 were in newly excavated tree cavities (primary cavity nests) and 13 were in old tree cavities (secondary cavity nests). Most bird nests were found by the calls of young or adults near the nests, or by seeing birds enter or leave cavities as researchers walked the trails. Some nests were also found during systematic searches described above. I checked nests every 7 to 9 days in Sept. to Nov. 1997, using ladders, micro-video, or by climbing. Many *Brotogeris* parakeet nests in termitaria were unreachable and were checked from the ground by morning and evening observations of adults entering and leaving. Observations in 1993 revealed that chick vocalizations are readily audible and are a good indication of occupancy for these parakeets.

A subset of nests located in 1993, 1995 and 1996 were revisited every 7 to 9 days or less and these were included in the predation analyses. Two sets of abandoned eggs, one in a tree cavity and one in a termitarium were included in the analysis of active nests. Whenever possible, nests were monitored for at least 24 days to cover a time period similar to the artificial nest experiments.

For each bird nest and artificial nest in termitaria, I measured height above the ground, entrance orientation, entrance diameter, and tunnel length. For bird nests and artificial nests in tree cavities I measured horizontal depth, vertical depth, entrance width, entrance height, entrance orientation, and height above the ground. I could not take all the measurements for nests that were inaccessible or in weak dead trees. I scored bird tree cavity nests as primary or secondary. Primary cavities were defined as being recently excavated by a bird (i.e. a hole with fresh wood chips on the ground, or recent signs of excavation on the inside roof and entrance). Secondary cavities were all those cavities that were not recently excavated by birds. I may have falsely classified some nests if a competitively superior secondary cavity nester displaced the excavating species (for examples see, Short 1979, Ingold 1989, Kerpez and Smith 1990). At all nests in tree cavities and termitaria I determined whether or not eggs were visible from outside the cavity. To do this I put my eye to the entrance of the cavity and determined if the eggs were visible without the aid of an artificial light source.

## Data analyses

I calculated survival functions for each nest type and tested for differences using survival analyses (LIFETEST procedure SAS Institute 1989). Significance values for the Wilcoxon statistic are presented as opposed to the log-rank test or the likelihood ratio test, because 1) the assumption of an underlying exponential distribution required for the likelihood ratio test was not met and 2) the log-rank test tends to give more weight to the long surviving nests and many of the data from the 1996 experiment were truncated after only 7 days. I tested each of the 10 possible pairwise comparisons of nest types using LIFETEST. Resulting P-values were corrected using a sequential Bonferroni analysis (Sokal and Rohlf 1995).

# Results

## Competition for nest sites

Not once in the course of four breeding seasons (10 months total) did I witness confrontations between pairs of small, subcanopy, secondary cavity-nesting species. I did witness fights over tree cavities between pairs of large, canopy nesting *Ara macao* (scarlet macaw). I also saw a confrontation between two pairs of *Capito niger* (black-spotted barbet, a 64 g primary cavity nester) in the vicinity of a snag, but no nest was ever discovered and it could have been a territorial dispute. I checked 94 natural tree cavities in the subcanopy and understory of which 83 were empty and available for use. Of these, only one was occupied by secondary cavity nesting birds, giving an occupancy rate of 1.2% (Table 1).

In the two years following nest box placement, I found evidence of bird use in only two boxes. I located feathers in one box in 1996 suggesting that an unidentified woodcreeper used the box for roosting or nesting. In 1997, one nest box contained a *Dendrexetastes rufigula* nest with two chicks. No other boxes contained nests, nesting material, eggshells or feathers. Mammals and insects used many more boxes than birds (Table 2). Vertebrates and social insects potentially capable of excluding nesting birds occupied 21% of the nest boxes over the two years of the study. Of the 47 and 42 boxes available for bird use in 1996 and 1997, respectively, one nest was suspected, and another confirmed suggesting occupancy rates of about 2%.

## Nest predation

I placed 17 clutches of clay eggs in tree cavities and 21 in termitaria in 1996. Predation on the clutches in termitaria was lower than in tree cavities, but this was only marginally significant ($N_{term} = 16$, $\text{Depredated}_{term} = 4$, $N_{tree} = 16$, $\text{Depredated}_{tree} = 9$, $\chi^2_1 = 3.24$, $P = 0.07$). In 1997, 23 of the 28 artificial nests in tree cavities were preyed upon (82%), three were excluded because termites or ants ate the eggs (see justification in Methods) and only two remained uneaten. Of 28 clutches placed in

Table 1. Occupancy rates of natural tree cavities by birds and their potential competitors in a lowland forest in southeastern Peru.

| Cavity occupant | 1996 | 1997 |
|---|---|---|
| 2° cavity nesting birds | 0 | 1.6% |
| 1° cavity nesting birds | 0 | 6% |
| Mammals | 0 | 5% |
| Bees or wasps | * | 5% |
| Empty | 100% | 84% |
| Total checked | 29 | 64 |

*Presence of bees and wasps not recorded in 1996.

Table 2. Nest box occupancy by nesting birds and their potential competitors. Ants and termites were included only when they closed the entrance to the box or filled the box with their nests, and made the box unusable by birds. The nest boxes were hung about 10 months before the onset of data collection and not moved between years.

| Taxon | 1996 | 1997 |
|---|---|---|
| 2° cavity nesting birds | 0% | 2% |
| Marsupial | 3% | 11% |
| Bees | 2% | 2% |
| Wasps | 2% | 0% |
| Ants | 5% | 4% |
| Termites | 3% | 0% |
| Bat spp. | 0% | 2% |
| Rodent spp. | 0% | 4% |
| Lizard spp. | 2% | 2% |
| Empty | 83% | 75% |
| Total (N) | 59 | 57 |

termitaria ten were preyed upon (36%), seven were excluded because termites ate or covered the eggs and eleven remained intact. Comparisons of survival curves shows that the predation rate of artificial nests in termitaria was significantly lower than in tree cavities (LIFETEST, Wilcoxon test, $\chi^2_1 = 23.31$, $P < 0.0001$).

I monitored 47 natural bird nests for predation: 23 termitarium nests, 12 primary cavity nests and 13 secondary cavity nests (Appendix). For the termitaria nests, ten were still active 24 days after discovery, five could not be monitored for the entire 24 days, four fledged, one was ripped open and depredated, and three either fledged or were preyed upon. The three that either fledged or were preyed upon were scored as preyed upon for the purpose of the survival analysis to be conservative since my hypothesis was that predation rates would be lower in termite mounds than tree cavities. These results indicate that 1 to 4 of 23 bird nests in termitaria were preyed upon (4%–17%). Of the 13 secondary cavity nests monitored, 10 were preyed upon (77%), one was monitored for less than 24 days and two still remained active 24 days after discovery. Of the 12 bird primary cavity nests, only three (25%) were preyed upon and the remainder, were still active 24 days after discovery.

The survival functions for the bird nests and artificial nests in tree cavities and termitaria differed significantly (data from all years and nest sites combined, LIFETEST, Wilcoxon test, $\chi^2_4 = 41.52$, $P < 0.0001$; Fig. 1). Artificial nests in tree cavities suffered significantly higher predation than artificial nests in termitaria, bird nests in primary tree cavities and bird nests in termitaria ($\chi^2_1 > 23.8$, Bonferroni corrected $P < 0.001$ for all three pairwise comparisons). Bird nests in secondary tree cavities suffered significantly higher predation than bird nests in termitaria ($\chi^2_1 = 11.2$, $P = 0.006$), bird nests in primary tree cavities ($\chi^2_1 = 8.6$, $P = 0.02$) and marginally significantly higher predation than artificial nests in termitaria ($\chi^2_1 = 5.4$, $P = 0.09$). Predation rates for bird nests and artificial nests in termitaria did not differ ($\chi^2_1 = 2.6$, $P = 0.34$), nor did predation rates for bird nests and artificial nests in secondary tree cavities ($\chi^2_1 = 2.5$, $P = 0.30$; Fig. 1).

Of the covariates measured (visibility of the eggs from outside the cavity, height above ground, minimum hole diameter, distance from the hole entrance to the back of the chamber, and year), none showed significant association with survival probability (all $P > 0.25$).

The natural and artificial nests did not differ in depth or visibility of the eggs. However artificial nests in termitaria were lower and had wider openings than natural nests in termitaria (t-tests unequal variance: $P < 0.001$ for both analyses). As neither the height nor the diameter of the opening varied significantly with predation rates these differences are not thought to have significantly influenced the results presented here.

Marks on clay eggs gave an indication of the nest predators for 36% of the recorded predation events ($N = 49$). Marks on eggs included 9 bird beak marks, 6 marsupial bites, 2 rodent bites, and one monkey hand print. The eggs from seven nests bore no identifying marks.

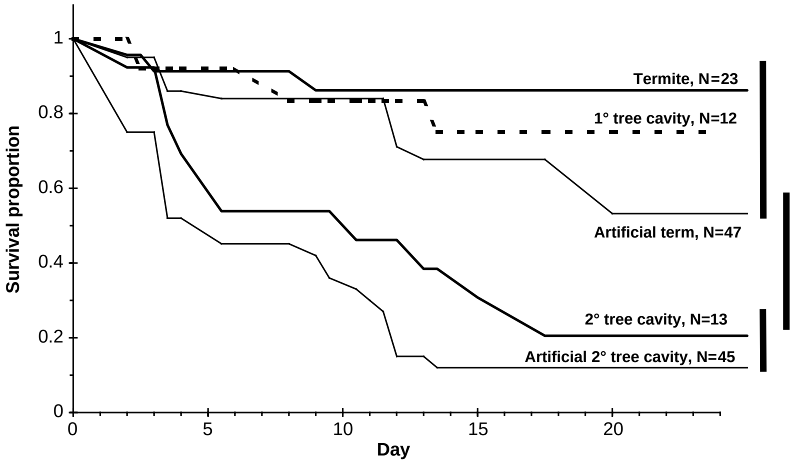

Fig. 1. Survival functions for nests in tree cavities and termitaria. Nest types include bird nests in termitaria (Termite), bird nests in recently excavated tree cavities (1° tree cavity), artificial nests placed in recently excavated holes in termitaria (Artificial term.), bird nests in previously existing tree cavities (2° tree cavity), and artificial nests placed in previously existing tree cavities (Artificial 2° tree cavity). The curves connected by thick black bars do not differ significantly. See text for details. Data analyzed using the survival analysis (LIFETEST, SAS Institute 1989).

## Discussion

### Competition for nest sites

There is apparently little competition for nest cavities among small ( <200 g), subcanopy, cavity-nesting birds at this site. Three lines of evidence support this contention: 1) lack of observed contests over tree cavities, 2) very low occupancy rates of nest boxes ( <2%), and 3) very low occupancy of natural tree cavities ( <2%). The goal of this work was not to determine if trogons and *Brotogeris* parakeets would use nest boxes, but instead to document the level of competition for tree cavities among the highly diverse community of cavity-nesting birds that inhabit the sub-canopy and understory at this site. By documenting the community-wide level of competition it provides an indication of what role competition for tree cavities may play in favoring the use of alternative nesting substrates like termite mounds. The cavity occupancy rates reported here are well below those recorded at sites where tree cavities were shown to limit bird reproduction (Van Balen et al. 1982, Brawn and Balda 1988, Gustafsson 1988, Waters et al. 1990, Nycander et al. 1995) suggesting that there is little competition. However, this finding must be interpreted with caution as all three measures of competition could be flawed. Proving the absence contests over tree cavities is difficult as they may have been inconspicuous or taken place at other times of year. Tree cavities found to be unoccupied may have been unsuitable to birds for reasons other than the characteristics measured. Additionally, nest boxes may not have been suitable for the majority of the species in the community. However, the fact that all three lines of evidence concur provides strong circumstantial evidence that competition for forest interior nest cavities below 10 meters is negligible.

My finding that tree cavities are plentiful contrasts with the findings of many studies from the temperate zone and heavily impacted tropical sites (Snyder 1978, Snyder et al. 1987, Martin 1993, 1995, Newton 1994, 1999), but joins the growing number of studies showing that tree cavities do not limit bird reproduction in old forests that have been relatively free from logging (Edington and Edington 1972, Higuchi 1978, McComb and Noble 1981, Brawn and Balda 1988, Waters et al. 1990, Carlson et al. 1998, Newton 1999). Large-scale forest clearing and forest management are relatively recent phenomena from an evolutionary perspective, indicating that most forest-dwelling cavity-nesting birds may have faced an abundance of tree cavities throughout most of their evolutionary history.

However, competition for tree cavities may be important under some circumstances. Species that live in open habitats may face greater competition for cavities due to the lower densities of trees (Beissinger and Waltman 1991, Beissinger 1996). Large cavity-nesting species like macaws (*Ara* spp.) may face chronic nest site shortages due to a scarcity of large, canopy-level cavities (Nycander et al. 1995, Brightsmith unpubl. data). Competition is also intense in areas like lake edges and islands cavities that are safe from non-volant predators (Robinson 1986, 1997). Birds that nest in the canopy, open habitats and predator free microhabitats may experience intense competition for cavities while many, if not most, tropical forest subcanopy cavity nesters may not face a shortage of nest sites.

### Nest predation

Marks left by predators on plasticine eggs suggest that birds and arboreal mammals are important nest predators at this site. However, data from plasticine eggs do not always reliably identify predators (Thompson and Burhans 2004) and large predators like toucans or monkeys were probably underrepresented in this study, as they are capable of removing or entirely consuming eggs. I did not find evidence of snake predation possibly because they do not attack clay eggs or leave them with identifiable marks. However, snakes may still be important predators of natural nests (Thompson and Burhans 2004).

My finding that nest height did not correlate with nest predation is difficult to interpret because of the small range of heights sampled in this study. Previous work in the temperate zone has found that higher cavities are safer (Van Balen et al. 1982). At my site in Peru, nests in the canopy may be safer but this was not tested. Egg visibility, minimum hole diameter and cavity depth did not significantly covary with predation rates. Some of these factors might become significant with larger sample size, but they are clearly less important than the effects associated with substrate (termitaria versus tree cavities) and cavity age (primary versus secondary).

### Validity of artificial nest studies

Artificial nest experiments have been widely criticized in the literature (Willebrand and Marcstrom 1988, Roper 1992, Haskell 1995a, Major and Kendal 1996, Wilson et al. 1998, Faaborg 2004). Most of the criticisms involve failure to compare success rates of real and artificial nests, failure to mimic nest type accurately, inappropriate egg size, egg color pattern and clutch size, and differences between bird nests and artificial nests in levels of concealment. The methodology employed here was designed to address these criticisms. The differences that did exist between bird nests and artificial nests (greater entrance diameter and lower height for artificial nests in termitaria) did not measurably influence predation rates. Nevertheless, certain differences between real and artificial nests are unavoidable viz., attending adult birds or nestlings and their associated odors. I have no reason to believe that lack of attending birds would cause systematic biases between nest substrates. The olfactory environment may have differed significantly between termite mounds and tree cavities (Brightsmith 2000), but this should have been true for both real and artificial nests. As a final caveat, it should be noted that combining data from a variety of different bird species undoubtedly hides species-specific patterns in nest predation. Some studies suggest that artificial nest studies should be avoided due to low correlation between predation rates in natural and artificial nests (Burke et al. 2004). However, given the difficulties of finding and monitoring natural nests, in termite mounds and tree cavities in primary tropical forest, supplementing the observations of natural nests with artificial nest experiments was warranted (Villard and Pärt 2004).

## Predation among nest types

Analysis of nest survivorship indicates that the five types of nests fall into two categories: 1) bird nests and artificial nests in old tree cavities, and 2) bird nests in new cavities, bird nests in termitaria and artificial nests in termitaria. Primary cavity nests and recently excavated nests in termitaria had similar predation rates. This was not expected and suggests that cavity age is more important than nesting substrate in predicting predation rate. The lower predation rates in newly excavated cavities is consistent with a review of 20 studies that found primary cavity nesters had significantly higher nesting success than secondary cavity nesters (Johnson and Kermott 1994). Similar conclusions were drawn from studies in northern Europe where birds that nested in newly located cavities suffered significantly lower predation rates (Nilsson et al. 1991, Sønerud 1993). The authors of the European studies concluded that the main predator, the pine martin *Martes martes*, remembered locations where it had found nests in previous seasons, and returned to check them in subsequent years (see also Miller 2002).

The nest predators recorded here are predominantly opportunistic generalists (Terborgh 1983, Hilty and Brown 1986, Emmons 1997). My observations indicate that large insects, especially Orthoptera (grasshoppers and their relatives), arachnids (spiders) and blatteria (roaches) occur in 29% (N = 61) of tree cavities suitable for nesting birds, providing predators added incentive to visit tree cavities. Some predatory marsupials and rodents also roost in cavities, providing another reason for these species to regularly visit tree cavities. In turn, these roosting mammals provide an additional food source for foraging *Cebus* monkeys (Terborgh pers. comm.). I thus surmise that opportunistic tropical forest predators remember and frequently revisit tree cavities. These visits are likely directed searches for insects or other cavity occupants or inspections of potential roost locations. If these suppositions hold, the high predation rates for secondary cavity nests may be a byproduct of these frequent visits to cavities. Researchers studying predation's effect on nest site selection must consider that alternative food sources may attract nest predators and maintain high predation rates in some nesting niches making them inherently bad places to nest.

Phylogenetic analyses of trogons and parrots show that secondary tree cavity nesting is the ancestral state for both of these groups and that there have been multiple transitions to both primary thee cavity nesting and termitarium nesting (Brightsmith 2005). These transitions have not been accompanied by an increase in clutch size as would be predicted if competition for old tree cavities was favoring the use of novel nesting niches (limited breeding opportunities hypothesis, Beissinger and Waltman 1991, Martin 1993, Beissinger 1996). However, these switches to new nesting niches were accompanied by an increase in nestling period (Brightsmith 2005). As increased nestling period correlates with reduced predation rates (Lack 1968, Bosque and Bosque 1995, Martin 1995), this suggests that lower predation rates have favored evolutionary transitions from secondary cavity nesting to primary cavity nesting and termitarium nesting. The present investigation shows that the mechanisms hypothesized to have favored the evolutionary transitions to novel nesting niches are apparently still operating today in a pristine site where anthropogenic impacts have been negligible.

Nest predation is thought to structure avian communities by favoring the coexistence of species that have differing nest niches (predation/diversity hypothesis Martin 1988a, b, Sieving and Willson 1998, but see Marini and Weale 1997). One premise of this theory is that species are rather fixed in their nesting niches, so this theory has only been applied to discussions of community assembly. The current study and companion phylogenetic analyses show that predation can favor major shifts in nesting niches (Brightsmith 1999, 2005). My findings, when combined with the original predation/diversity hypothesis, suggest that nest predation may act to increase the alpha diversity of avian communities by promoting shifts to novel nesting substrates and then allowing for the coexistence of species that differ in nest site. While this is highly speculative, this scenario could have produced modern avian diversity patterns, especially in tropical forests where the world's most diverse avian communities inhabit structurally diverse forests with high densities and diversities of nest predators (Richards 1952, Terborgh et al. 1990, Karr et al. 1990, Gibbs 1991, Robinson and Terborgh 1997).

Studies in northern Europe and North America have left the impression that secondary cavity-nesting birds are chronically limited by intense competition for tree cavities and this continues to dominate thinking about the life history evolution of cavity-nesting birds (Collias and Collias 1984, Beissinger and Waltman 1991, Martin 1993, Beissinger 1996, Mönkkönen and Orell 1997). This conclusion has not been reinforced by the present study. To the contrary, this work joins a growing number of studies from less disturbed areas suggesting that competition for tree cavities does not limit reproduction of secondary cavity-nesting birds (Edington and Edington 1972, Higuchi 1978, McComb and Noble 1981, Brawn and Balda 1988, Carlson et al. 1998, Waters et al. 1990). The present study, coupled with phylogenetic analyses suggest that predation is an important force molding the natural history of many tropical cavity-nesting birds (Brightsmith 2005).

*Acknowledgements* – I would like to thank the people that made this study possible especially my field assistants who collected the data: D. Huamán, D. Cossíos, J. I. Pareja, L. Pautrat, W. Tori, W. Shelsky, N. Gerhart, R. Bright and M. Higgens. Thanks also the Peruvian government (INRENA) for allowing me to work in Manu National Park. Earlier drafts of this document were improved by the comments of S. Robinson, S. Beissinger, J. Terborgh, D. Burdick, W. Morris, K. Smith, P. Klopfer, B. Hudgens and three anonymous reviewers. Thanks also to Patagonia Inc., The Explorer's Club, W. and L. Smith, West Hempstead Rotary Club, Duke University Graduate School, Raleigh-Durham Caged Bird Society, American Museum of Natural History (Chapman Fund), Greater Rochester Hookbill Association, Duke University Department of Biology, and the Duke-UNC Program in Latin American Studies for their funding. Thanks also to my family for their support. This work was supported by the National Science Foundation under Grant No. DEB-95-20800.

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(*Received 15 September 2003, revised 16 April 2004, accepted 23 May 2004.*)

Appendix. Natural nests used for the predation analyses presented in Fig. 1.

| Nest type Species | Year | Nests | Depredated |
|---|---|---|---|
| Termitarium nest | | | |
| *Brotogeris cyanoptera* | 1993 | 6 | 2 |
| ” | 1995 | 1 | 0 |
| ” | 1996 | 3 | 0 |
| ” | 1997 | 9 | 2 |
| *Brotogeris santithomae* | 1997 | 1 | 0 |
| *Trogon melanurus* | 1995 | 2 | 0 |
| ” | 1997 | 1 | 0 |
| 1° tree cavity | | | |
| *Xiphorynchus guttatus* | 1997 | 4 | 0 |
| *X. spixii* | 1997 | 2 | 0 |
| Woodcreeper sp. | 1995 | 1 | 1 |
| ” | 1996 | 1 | 0 |
| *Capito niger* | 1997 | 1 | 0 |
| *Trogon collaris* | 1995 | 1 | 1 |
| ” | 1996 | 1 | 0 |
| *Phylidor ruficaudatus* | 1997 | 1 | 0 |
| 2° tree cavity | | | |
| *Formicarius analis* | 1997 | 3 | 3 |
| *Pyrrhura picta* | 1997 | 1 | 0 |
| *Phylidor sp.* | 1997 | 1 | 1 |
| *Trogon collaris* | 1997 | 1 | 1 |
| *Phlegopsis nigromaculata* | 1996 | 1 | 1 |
| ” | 1997 | 1 | 0 |
| *Ramphotrygon ruficaudata* | 1997 | 1 | 1 |
| Unknown | 1996 | 3 | 3 |
| ” | 1997 | 1 | 1 |