ORNITOLOGIA NEOTROPICAL 19 (Suppl.): 269–278, 2008

AVAILABILITY OF CAVITIES FOR NESTING BIRDS IN THE ATLANTIC FOREST, ARGENTINA

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Resumen. – Disponibilidad de huecos para la nidificación de las aves en el bosque Atlántico, Argentina. – Examinamos la hipótesis que la tala selectiva de los árboles reduce el número de sitios disponibles para nidificación, y la densidad de nidos, para aves que anidan en huecos en el bosque Atlántico. Determinamos 1) si los huecos aptos son tan abundantes en bosque sujeto a la tala selectiva como en bosque primario, y 2) la proporción de estos huecos ocupados por nidos de aves. De Septiembre a Diciembre de 2006 (época de nidificación), contamos todos los huecos en ocho parcelas de 1 ha: cuatro en bosque primario y cuatro en bosque con tala selectiva, en el departamento de San Pedro, Misiones, Argentina. Medimos los huecos abajo de los 15 m. Instalamos 26 cajas nidos en 30 ha de bosque con tala selectiva en un sitio cercano, y medimos 25 nidos activos de 16 especies de aves. El bosque primario tenía significativamente más huecos que el bosque con tala selectiva. En las parcelas, sólo uno (5%) de los huecos aptos del sotobosque y estrato medio (el hueco más profundo y con pequeña entrada) y dos (8%) de los huecos potenciales en el estrato superior fueron ocupados por nidos de aves. Sin embargo, 13 de las 26 cajas nidos fueron ocupadas. Nueve (36%) de los 25 nidos activos tenían características similares a nuestras cajas nidos (profundidad $\geq$ 20 cm y diámetro de entrada $\leq$ 14 cm), aunque los huecos naturales con estas características fueron muy raros en las parcelas en el bosque primario (1.3 $\pm$ 1.0 huecos/ha), y aún más raros en el bosque con tala selectiva (0.5 $\pm$ 0.6 huecos/ha). Por lo tanto, aunque la baja tasa de ocupación de huecos podría sugerir que los huecos no son limitantes, los huecos de alta calidad podrían ser muy raros, especialmente en bosques con tala selectiva, y podrían limitar las poblaciones de algunas aves que anidan en huecos en el bosque Atlántico.

Abstract. – We test the hypothesis that selective logging reduces nest site availability and nest density for cavity-nesting birds in the Atlantic forest by determining 1) whether suitable cavities are as abundant in logged as in primary forest, and 2) the proportion of these cavities occupied by nesting birds. From September to December 2006 (breeding season), we counted all tree cavities in four 1-ha plots in each of primary and selectively logged forest in San Pedro Department, Misiones, Argentina. We measured all cavities below 15 m. We placed 26 nest boxes in 30 ha of logged forest at a nearby site, and measured 25 active cavity nests of 16 species of birds. Primary forest had significantly more cavities/ha than logged forest. In the plots, only one (5%) of the understory and midstory cavities (the deepest cavity, with a small entrance) and

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two (8%) of the canopy cavities were occupied by nesting birds. However, 13 of the 26 nest boxes were occupied. Natural cavities with characteristics similar to our nest boxes (≥ 20 cm deep and ≤ 14 cm entrance diameter) accounted for nine (36%) of the 25 active natural nests; however, cavities conforming to these characteristics were rare in plots in primary forest (1.3 ± 1.0 cavities/ha) and rarer still in logged forest (0.5 ±0 .6 cavities/ha). Thus, although low occupancy might suggest that cavities are not limiting, high quality cavities may indeed be rare, especially in logged forest, and may limit populations of some cavity-nesting birds in the Atlantic forest. *Accepted 21 October 2007.*

Key words: Cavity nest, cavity abundance, cavity quality, excavator, nest site limitation, parrot, secondary cavity nester, selective logging, subtropical forest, woodpecker.

INTRODUCTION

Cavity-nesting birds and mammals depend on a key resource, tree holes, for reproduction. Their populations may thus be limited by the availability of nest sites (Newton 1994). Most tests of nest site limitation have been conducted in managed temperate forest (e.g., Brawn & Balda 1988). Indirect evidence suggests that cavities are abundant, and unlikely to be limiting, in primary temperate forest of Europe (Wesołowski 2007; however, direct and indirect evidence suggests that even in primary forest, cavities may be limiting for some species in Australia and North America (Heinsohn *et al.* 2003, Aitken 2007). In South America, very little is known about cavity availability, nest site requirements of cavity nesters, or facilitation and competition for nest sites, either in primary forest or in managed landscapes (Cornelius *et al.* 2008).

The Atlantic forest of South America is one of the five most important global biodiversity hotspots, threatened by one of the highest rates of deforestation among tropical and subtropical forests (Balmford & Long 1994, Myers *et al.* 2000). This forest is estimated to have covered 1.2 million km^2 in south-eastern Brazil, eastern Paraguay, and the province of Misiones in Argentina (Harris & Pimm 2004), and supported a rich community of cavity-nesting birds and mammals. However, agriculture, cattle-ranching, and industry have replaced more than 90% of the original forest during the last 500 years of European colonization (Morellato & Haddad 2000). The loss of Atlantic forest has been correlated with declining populations (BirdLife International 2004) and local extirpations (Ribon *et al.* 2003) of many bird species, including cavity-nesters, raising grave concerns about the future of biodiversity in this region (Brooks & Balmford 1996).

In remaining Atlantic forest, high-grade (selective) logging of the largest trees may further threaten communities of birds and mammals that nest in tree cavities. Nearly all remaining Atlantic forest has been logged using high-grade methods, which, by removing the oldest and largest trees, may reduce the number of cavities. Guix *et al.* (1999) suggest that parrots in the Atlantic forest may depend heavily on woodpeckers for excavating their nest cavities, and may be limited by both the density of woodpecker populations and the density of standing dead trees (snags) for nesting. We ask whether cavities are a limiting resource for cavity-nesting birds in primary Atlantic forest, and whether and how much this resource is reduced in logged forest. To address these questions, we compare the abundance and characteristics of tree cavities, and the proportion of these cavities occupied by nesting birds, between logged and primary Atlantic forest.

STUDY AREA AND METHODS

Study area. The study took place in the Sierra Central, department of San Pedro, Misiones, Argentina, in subtropical semi-deciduous Atlantic forest classified by Cabrera (1976) as mixed forest with laurel (Lauraceae), guatambú (*Balfourodendron riedelianum*), and araucaria (*Araucaria angustifolia*). This forest supports over 60 species of obligate cavity-nesting birds (A. Bodrati in prep.). We evaluated cavity availability in eight, randomly located, 1-ha (100 m x 100 m) plots on deep red soil with negligible slope, classified as Red Latisol (Ríos 2006).

Four plots were in primary forest at Parque Provincial (PP) Cruce Caballero (26°31'S 53°59'W; 600 m a.s.l.), two were in logged forest at PP Cruce Caballero, and two were in logged forest at Tobuna (26°27'S 53°54'W; 600 m a.s.l.). In the primary forest at PP Cruce Caballero, no logging has ever been recorded. Although the area was used for commercial production of araucaria seeds for many years, and the structure of current vegetation suggests a few trees may have been removed from the forest at some time (Ríos 2006), we found no stumps or other signs of logging. In contrast, logged forest plots were placed in forest with a history of repeated selective logging which removed the largest trees over many years. Unlike primary forest, they had many cut stumps. Within logged forest, there were small clearings (tree removal gaps) dominated by bamboo and young trees.

Cavity availability and use. Plots were searched systematically in the breeding season (September to December 2006), using binoculars to locate all potential cavities (apparent entrance hole with a diameter $\geq$ 2 cm; interior depth unknown), and all active nests in such cavities. Potential cavities below 15 m were inspected using a pole-mounted video camera to determine whether they were deep enough for a nest chamber (cavities with a depth of > 8 cm were considered suitable cavities) and whether they were being used by nesting birds or other organisms (bees, mammals). A depth of 8 cm was chosen as a cut-off because all active cavity nests we found were at least 8 cm deep (see below). We identified many potential cavities above 15 m, but we could not determine whether these cavities were suitable (> 8 cm deep) because we could not reach them with the camera. However, we watched each of these high cavities once or twice for a total of at least 2 h to determine possible nesting activity. To compare the abundance of cavities between primary and logged forest, we used t-tests when data met normality assumptions, and a Mann-Whitney U test when they did not. For all statistical analyses, we used SAS Version 9.1.3 and $\alpha = 0.05$.

Cavity quality. To determine whether the cavities we found in the plots were representative of cavities used as nests, we compared several characteristics of unoccupied cavities in plots with those of active nest cavities found throughout the study area (approximately 50 ha) through extensive but non-systematic nest-searching from September to December 2006. Cavities were considered active nests if they contained eggs and/or chicks. From January to April 2007, for cavities below 15 m, we measured the following variables potentially important to birds: cavity making agent (avian excavator vs decay/damage), interior vertical depth of cavity, and cavity entrance diameter (maximum width in narrowest direction, usually horizontal). Interior vertical depth of cavities was measured using an infrared reflectometer mounted on a 15-m telescoping pole. To measure cavity entrance diameter, we used a Criterion RD 1000 electronic dendrometer. We present characteristics of used and unused cavities, but we did not test statistical hypotheses regarding used vs unused cavities because 1) all unused cavities were in our eight, 1-ha plots, while most used cavities were outside of plots, and 2) active nests belonged to 16 different species of birds; their different body sizes and cavity requirements made it inappropriate to pool these species for statistical tests, yet no species was sufficiently abundant to test individually.

Nest boxes. To examine use of nest boxes by cavity-nesting birds and mammals, we installed 26 nest boxes in approximately 30 ha of heavily logged forest at PP de la Araucaria (26°38'S 54°7'W; 600 m a.s.l.). This site was 15 km from the nearest plots at PP Cruce Caballero, and had been subject to heavier logging than the plots. Nest boxes were not located randomly but were placed where appropriate trees were found (adequate height and diameter). Boxes were made of wood, had circular entrances 8–14 cm in diameter, and measured 22–45 m deep (bottom rim of entrance hole to floor). Floors were covered with 5 cm of sawdust. All boxes were nailed or tied to trees at a height of 5–7 m. Boxes were inspected using the same camera system employed for natural cavities.

RESULTS

Availability of cavities. Overall (including both low and high cavities), primary forest [16.8 ± 5.0 cavities/ha (mean ± SD), n = 4 plots] had more potential cavities than logged forest (7.5 ± 5.3 cavities/ha, n = 4, t = -2.5, df = 6, P = 0.04). Cavities below 15 m did not differ statistically in abundance between forest types, either when we considered only suitable cavities (overall mean for both forest types 4.6 ± 3.0 /ha; t = -1.08, P = 0.32) or when we included all potential cavities (overall mean for both forest types 8.8 ± 5.2 /ha; t = -1.3, P = 0.25). Potential cavities above 15 m, however, were significantly more abundant in primary forest (5.6 ± 1.5 /ha) than in logged forest (1.0 ± 1.4 /ha; Mann-Whitney U = 10.0, P = 0.03).

Occupancy of cavities and nest boxes. There were no active cavity nests in logged plots and only three active cavity nests in primary forest plots (0.8 ± 1.0 nests/ha). One nest [Maroon-bellied Parakeet (*Pyrrhura frontalis*)] was below 15 m, and two [Streaked Flycatcher (*Myiodynastes maculatus*) and White-eyed Parakeet (*Aratinga leucophthalma*)] were above 15 m. No mammals or bees were found in cavities in plots. In contrast, 13 (50%) of the 26 nest boxes were occupied by birds [Tropical Screech-Owl (*Megascops choliba*) n = 2; Barred Forest-Falcon (*Micrastur ruficollis*) n = 1; and Planalto Woodcreeper (*Dendrocolaptes platyrostris*) n = 7)] or mammals [(white-eared opossum (*Didelphis albiventris*) n = 3].

Quality of cavities. We found 25 active nests below 15 m high, belonging to 16 species of birds (Table 1). Of the 37 suitable but unoccupied cavities below 15 m in plots, eight (22%) were excavated by birds (woodpeckers and trogons); the remaining 29 (78%) were created by damage processes or decay organisms. While excavator species (woodpeckers, n = 5, and trogons, n = 1) used only excavated cavities, secondary cavity nesters (n = 19) used cavities (mostly outside of plots) in proportion to their availability (in plots), with five nests in excavated cavities (26%), 13 nests in cavities formed by decay or damage (68%), and one nest of undetermined origin (5%).

Cavities in plots were 8 to 50 cm deep (20 ± 10 cm) with entrance diameters of 2 to 28 cm (10 ± 6 cm). Cavities used by nesting birds were 8–100 cm deep (33 ± 28 cm) with entrances 3–66 cm in diameter (11 ± 13 cm). Although shallow cavities with small

TABLE 1. Active nests in tree cavities showing bird species, number of nests (n), cavity making agent (e = avian excavator, d = decay/damage), entrance diameter, and interior depth (mean ± SD). Nests in chimneys (broken-off tree trunks) are shown separately in parentheses.

Species	n	Agent of cavity formation	Entrance diameter (cm)	Depth (cm)
Psittacidae				
White-eyed Parakeet (*Aratinga leucophthalma*)	1	d	7	80
Maroon-bellied Parakeet (*Pyrrhura frontalis*)	6	d	5 ± 2	29 ± 15
Scaly-headed Parrot (*Pionus maximiliani*)	3	e, d	8 ± 2, (36)	38 ± 11, (95)
Vinaceous-breasted Parrot (*Amazona vinacea*)	2	e	11 ± 0	21 ± 4
Tytonidae				
Barn Owl (*Tyto alba*)	1	d	(66)	(100)
Strigidae				
Tropical Screech-Owl (*Megascops choliba*)	1	d	20	10
Ferruginous Pygmy-Owl (*Glaucidium brasilianum*)	1	d	5	17
Trogonidae				
Surucua Trogon (*Trogon surrucura*)	1	e	6	8
Ramphastidae				
Red-breasted Toucan (*Ramphastos dicolorus*)	1	e	8	19
Chestnut-eared Aracari (*Pteroglossus castanotis*)	1	d	10	20
Picidae				
White-spotted Woodpecker (*Veniliornis spilogaster*)	1	e	6	12
Green-barred Woodpecker (*Colaptes melanochloros*)	2	e	7 ± 2	54 ± 51
Lineated Woodpecker (*Dryocopus lineatus*)	1	e	7	23
Furnariidae				
Planalto Woodcreeper (*Dendrocolaptes platyrostris*)	1	d	3	18
Tyrannidae				
Streaked Flycatcher (*Myiodynastes maculatus*)	1	e	11	10
Incertae Sedis				
Black-crowned Tityra (*Tityra inquisitor*)	1	e	8	12
Total	25		11 ± 13	33 ± 28

entrances were available and unused in plots, deep cavities with small entrances were very rare (Fig. 1). In plots, only one cavity below 15 m was occupied; it was the deepest of all cavities in all plots (50 cm) and had a very narrow entrance (4 cm). Cavities with characteristics similar to our nest boxes (≥ 20 cm deep and with entrance diameter ≤ 14 cm) accounted for nine (36%) of the 25 natural nests measured; however, cavities conforming to these characteristics were rare in plots in primary forest (1.3 ± 1.0 cavities/ha) and rarer still in logged forest (0.5 ± 0.6 cavities/ha).

DISCUSSION

In such a complex community of cavity-nesters, it is difficult to determine the point (number and quality of cavities) at which cavities would not be a limiting resource for birds. In this study, only 5% of understory and midstory cavities were occupied by nesting birds in plots in primary forest, and no cavities were occupied in plots in logged forest. Brightsmith (2005) and Bai *et al.* (2003) report similar low rates of cavity occupancy by birds in mature tropical floodplain forest in Amazo-

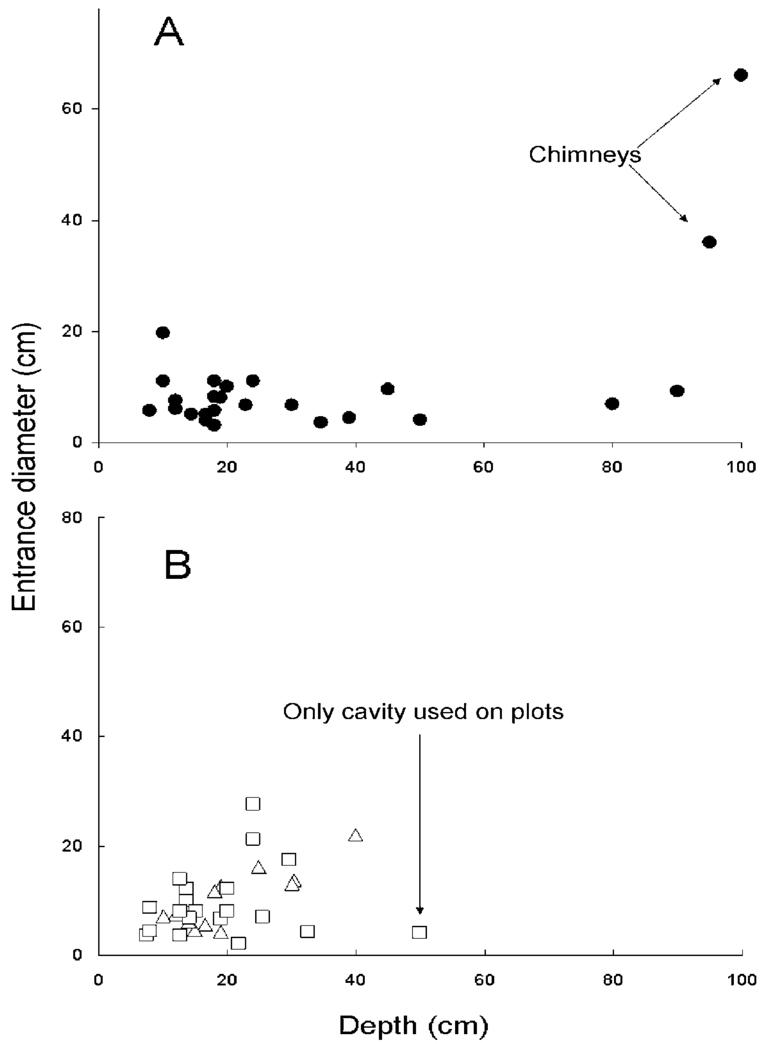

FIG. 1. Interior vertical depth vs entrance diameter for cavities below 15 m in Atlantic forest, Misiones province, Argentina. A) Active cavity nests; B) Cavities in eight 1-ha plots in primary forest (squares), and logged forest (triangles). "Chimney" indicates nests in broken-off tree trunks. Within plots, only one cavity below 15 m was used by nesting birds: it was the deepest cavity in all plots, and had a small entrance diameter.

nian Peru (2%) and Taiga forest in Mongolia (8%), respectively, and conclude that nest sites do not limit the breeding density of cavity-nesting birds in these systems. These results contrast with 35–44% occupancy of cavities in temperate mixed forest in the Cariboo-Chilcotin, Canada (Aitken & Martin 2004), where experimental cavity blocking also suggested that high quality cavities are a limiting resource for some species of birds (Aitken 2007).

Our results underscore the need to understand nest site requirements when evaluating cavity availability. Although we found many potentially suitable, but unused, cavities in our plots, in both primary and logged forest, we also found a relatively high occupancy of nest boxes and a paucity of deep cavities with small entrances that appear to be preferred by some birds. The high occupancy of nest boxes should be interpreted with caution, since nest boxes were spread over a much larger area (approx. 30 ha) than the plots (1 ha each), allowing more territorial birds of the same species to use the 26 nest boxes than to use the natural holes in any single plot. Nevertheless, the many active nests in deep cavities with small entrances, and in deep nest boxes with small entrances, and the relative paucity of such cavities in the plots, especially in logged forest, suggest that such cavities may indeed be limiting.

Even where cavities appear to be abundant, there may be a shortage of high quality cavities (Lohmus & Remm 2005). Cavity quality may be determined by a number of variables such as size, height, habitat, and origin (e.g., Wiebe & Swift 2001, Wesołowski 2002, Mahon & Martin 2006). In our study, only 21% of suitable cavities were excavated by birds, compared to 95% in the Cariboo-Chilcotin of Canada (Aitken & Martin 2007), and 88% in riverine forest in Estonia (Remm *et al.* 2006). While in Europe, secondary cavity nesters avoided cavities created by excavators (Wesołowski 2002, Remm *et al.* 2006), in the Cariboo-Chilcotin (Aitken & Martin 2007), they used excavated cavities in proportion to their availability. Our preliminary results also suggest that secondary cavity nesters used excavated cavities in proportion to their availability. In strong contrast to a study in the Brazilian Atlantic forest, where 36 of 37 (97%) parrot nests were in cavities excavated by woodpeckers (Guix *et al.* 1999), parrots in our study (including some of the same species) mostly used holes created by decay/damage. Thus cavity quality in the Atlantic forest may be determined by shape, size, or other factors, rather than the agent that formed the cavity, and these factors may change depending on habitat context (e.g., identity and foraging strategies of major predators). Deep cavities with small entrances were rare in our study, yet appeared to be chosen preferentially by some birds (e.g., parrots). In southeastern Australia, too, deeper hollows were more likely to be occupied by vertebrate fauna, and cavity depth was the most important predictor of use (Gibbons *et al.* 2002). By excluding large predators (Wesołowski 2002), cavities with small entrances (Wesołowski 2002, Remm *et al.* 2006) and large interior volume (Wiebe & Swift 2001) may offer the best protection from predation, the principal cause of nest failure among birds (Martin 1993), including cavity-nesters (Martin & Li 1992, Thorstrom 2000, Wesołowski & Tomialojc 2005, but see Deng & Gao 2005). Thus, although cavities may be abundant overall, cavities of high or even adequate quality may be very rare. Cavity quality may limit populations of some cavity-nesting birds in the Atlantic forest, especially if there are interspecific dominance hierarchies.

Important pieces are still missing from this puzzle. First, cavity attributes not reported in this study may strongly influence the quality of cavities, making fewer cavities suitable for nesting. For example, lianas may increase access by predators (Koenig *et al.* 2007), and upward pointing entrances may increase the risk of flooding (pers. observ.), both important causes of nest failure for cavity-nesting birds (Wesołowski *et al.* 2002). Thus, in this study, we probably over-estimated the density of suitable cavities below 15 m. Second, we do not know how many suitable cavities are present in the forest canopy, or whether higher cavities are preferred. Logged forest had significantly fewer potential cavities in the canopy than did primary forest, suggesting that logging reduces cavity availability for birds that nest in the canopy. Third, we need to consider bird species (or at least groups of species) individually to determine which cavities are indeed suitable as nest sites (Aitken & Martin 2004). In tropical forest of Guatemala, although cavities were not limiting for owls, they were probably limiting for falcons, which had more specialized nest site requirements (Gerhardt 2004). In the Atlantic forest, we predict that species with specialized requirements for deep cavities with small entrances will experience nest site limitation, particularly in logged forest. We are testing this hypothesis using a 3-year BACI nest box addition experiment. Finally, cavity availability needs to be understood in the context of the nest web, where some species facilitate, and other species compete for nest sites (Martin & Eadie 1999, Martin *et al.* 2004). Nest webs may include behaviorally dominant species that restrict access to nest holes by subordinate species. Thus, nest site limitation for any one species, and subordinate species in particular, may be strongly related to the abundance of other cavity-nesting species in the community.

ACKNOWLEDGMENTS

For assistance in the field, we thank N. Fariña, A. Bodrati, M. Debarba, M. Ruiz Blanco, R. Villalba, M. Welter, M. Nuñes, O. Villalba, C. Carrió, and many volunteers from the Carrera de Guardaparques Provinciales (Instituto Superior San Pedro). For permission to work at field sites and for participating in fieldwork, we are especially grateful to the families Debarba, González, Barreto, and Da Silva, the Instituto de Enseñanza Agropecuaria de Tobuna, and the Ministerio de Ecología de Misiones. Funding and/or equipment for this study were provided by the National Science and Engineering Research Council of Canada, the Rufford Foundation, Columbus Zoo, the British Ornithologists' Union, the Oregon Zoo Future for Wildlife Program, Cleveland Metroparks Zoo, Environment Canada (Pacific and Yukon Region), the Neotropical Ornithological Society, and the Area de Manejo Integral de la Reserva de la Biósfera Yabotí. We thank Daryl Cockle for designing and building the camera and reflectometer, and Alejandro Bodrati, Cintia Cornelius, and Natalia Politi for helpful discussions about the study and manuscript.

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