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9 authors, including:

Cintia Cornelius
Federal University of Amazonas

Kristina Cockle
IBS-CONICET

Igor Berkunsky
National University of the Center of the Buenos Aires Province

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CAVITY-NESTING BIRDS IN NEOTROPICAL FORESTS: CAVITIES AS A POTENTIALLY LIMITING RESOURCE

Cintia Cornelius[1,9], Kristina Cockle[2,3], Natalia Politi[4,5], Igor Berkunsky[6], Luis Sandoval[7], Valeria Ojeda[8] , Luis Rivera[5], Malcolm Hunter, Jr.[4], & Kathy Martin[2]

[1]Department of Biology, University of Missouri-St. Louis, One University Blvd., St. Louis, MO 63121, USA, & Fundación Senda Darwin, Casilla 81 - Correo 9, Santiago, Chile. *E-mail:* cintia.cornelius@gmail.com

[2]Department of Forest Sciences, University of British Columbia, 2424 Main Mall, Vancouver, British Columbia V6T 1Z4, Canada.

[3]Proyecto Selva de Pino Paraná, Fundación de Historia Natural Félix de Azara, Departamento de Ciencias Naturales y Antropología, CEBBAD, Universidad Maimónides, Valentín Virasoro 732, Buenos Aires, C1405BDB, Argentina.

[4]Department of Wildlife Ecology, University of Maine, 210 Nutting Hall, Orono, ME 04469, USA.

[5]Fundación CEBIO, Roca 44, S.S. de Jujuy, Jujuy, 4600, Argentina.

[6]Departamento de Ecología Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Pabellón II Ciudad Universitaria, Buenos Aires, C1428EHA, Argentina.

[7]Escuela de Biología, Universidad de Costa Rica, San Pedro, Montes de Oca, Costa Rica.

[8]Consejo Nacional de Investigaciones Científicas y Técnicas and Departamento de Ecología, Universidad Nacional del Comahue, Quintral 1250, (8400) Bariloche, Argentina.

Resumen. – Aves que anidan en huecos en bosques Neotropicales: los huecos como un recurso potencialmente limitante. – Frecuentemente se asume que las aves que nidifican en cavidades pueden estar limitadas por la presencia de sitios de nidificación. Sin embargo la mayoría de los estudios que apoyan la limitación de sitios de nidificación han sido realizados en paisajes modificados por actividades humanas de Norteamérica y Europa. Tanto en bosques maduros como en bosques degradados del Neotrópico, se sabe muy poco sobre la ecología y la disponibilidad de cavidades para este grupo de aves. Aquí revisamos artículos publicados y presentamos cinco estudios de casos que examinan la disponibilidad de cavidades, las limitaciones potenciales sobre las poblaciones, el reuso de cavidades y las relaciones entre especies de aves que nidifican en cavidades en cinco hábitats de tipo boscoso de América Central y América del Sur. No encontramos evidencia conclusiva de limitación de cavidades en bosques no perturbados sub-tropicales, en los cuales una gran cantidad de cavidades estaban disponibles, pero no fueron utilizadas. Sin embargo, las cavidades no utilizadas difirieron de las cavidades con nidos activos, mostrando que es importante considerar la calidad de las cavidades al determinar la disponibilidad y limitación de éstas. Además, uno de nuestros estudios de caso no mostró evidencia de competencia por interferencia por cavidades a

[9]*Current address:* Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão 321, Trv. 14, Cidade Universitária, São Paulo, 05508-900 SP, Brasil.

pesar de una alta tasa de reuso, como para sugerir limitación de cavidades. Sin embargo, en bosques subtropicales y templados degradados por tala selectiva y fragmentación, hubo evidencia de una menor densidad de cavidades y una potencial limitación de cavidades para las aves. Nuestros estudios de caso también sugieren que los adoptadores de cavidades o usuarios de cavidades secundarios (UCS) en bosques Neotropicales utilizan en su gran mayoría cavidades no excavadas. Sin embargo, algunos UCS prefirieron cavidades excavadas, por lo que, en algunos bosques, los pájaros carpinteros pueden ser agentes creadores de cavidades de gran importancia. Además, algunas especies de árboles fueron más importantes que otras como sustrato para cavidades. Se requiere de más investigación en esta región para entender la estructura de las "tramas de nidos" y determinar bajo que condiciones las cavidades son un recurso limitante.

Abstract. – Although cavity-nesting birds are often assumed to be limited by nest site availability, most evidence for nest site limitation has come from human-modified landscapes in North America and Europe. In the Neotropics, little is known about the ecology of cavity-nesting birds or the availability of nest sites for these species, either in mature or disturbed forests. We review published articles and present five case studies that examine cavity availability, potential limitations on populations, cavity reuse, and relationships among cavity-nesters in five forest-like habitats in Central and South America. We did not find conclusive evidence for cavity limitation in undisturbed subtropical forests, where many cavities were available but not used. However, unused cavities were measurably different from active nest cavities showing that it is important to consider cavity quality when assessing cavity availability and nest site limitation. In addition, one of our study cases showed no evidence of interference competition for cavities, despite a high rate of cavity reuse that might suggest cavity limitation. However, in subtropical and temperate forests degraded by logging and fragmentation, there was evidence for reduced density of cavities and potential nest site limitation for cavity-nesting birds. Our case studies suggested that secondary cavity nesters (SCN) in Neotropical forests use mostly non-excavated cavities; however, some SCN prefer excavated cavities, making woodpeckers important cavity-creating agents in some forests. In several Neotropical forests, some tree species were more important than others as substrates for cavities. More research is needed in this region to understand the structure of nest-webs and to determine the conditions under which cavities are limited. *Accepted 23 October 2007.*

Key words: Cavity nest, Central America, excavator, forest birds, nest site, resource limitation, secondary cavity-nester, South America, tree hole.

INTRODUCTION

Cavity-nesting birds form diverse, hierarchically structured communities, in which a key component of fitness depends on the acquisition of tree cavities for breeding and roosting (Martin & Eadie 1999). Whereas primary cavity-nesters (excavators) construct their own nest and roost cavities, secondary cavity-nesters (SCN) depend on existing cavities. Consequently, substrates suitable for cavity excavation can limit populations of excavators (Jackson & Jackson 2004), cavities often limit populations of SCN (Martin & Li 1992, Newton 1994), and both may constitute key resources around which communities are structured (Rudolph & Conner 1991, Aubry & Raley 2002, Martin *et al.* 2004). In some communities, SCN are strongly linked to excavator species such as woodpeckers, which create nearly all of the cavities (e.g., Martin *et al.* 2004), while in other communities, SCN depend primarily on non-excavated cavities (e.g., those produced by damage and/or decay; Gibbons & Lindenmayer 2002, Wesołowski 2007). Dependence on a limited number of cavities may influence interactions within (Murphy *et al.* 2003) and among species (Short 1979, Heinsohn *et al.* 2003, Martin *et al.* 2004, Aitken 2007), population dynamics (Holt & Martin 1997, Saab *et al.* 2004, Norris 2007), and even life-history strategies (Martin

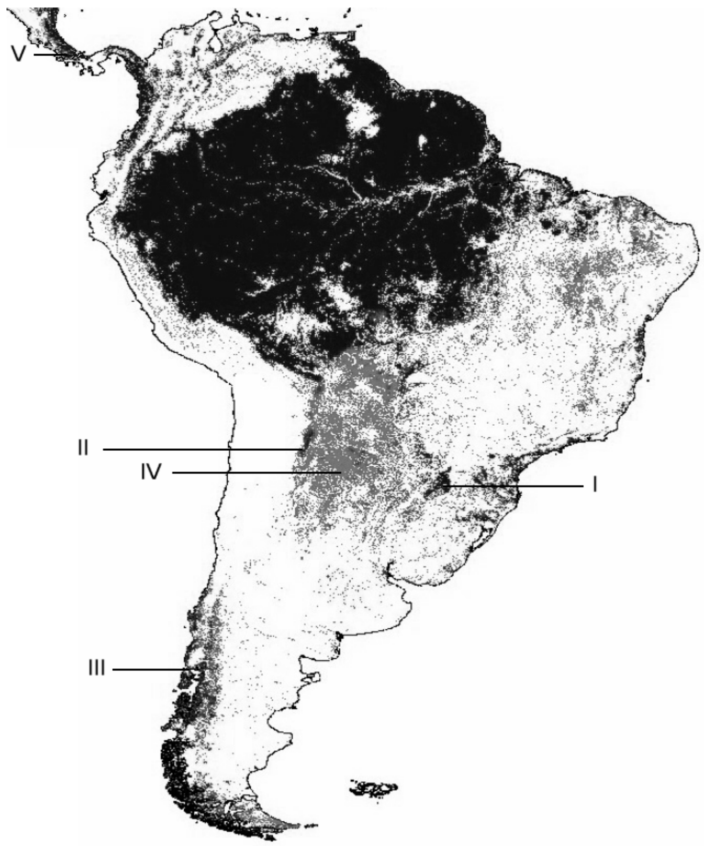

FIG. 1. Cover of humid forest (black) and dry forest (grey) in Central and South America showing locations of our five case studies: I- Atlantic forest in Argentina, II- Yungas in Argentina, III- South-temperate rainforest in Chile, IV- dry Chaco in Argentina, and V- tropical forests in Costa Rica (map modified from Eva *et al.* 2002).

& Li 1992, Eberhard 2002, Wiebe 2003, Wiebe *et al.* 2006).

Most evidence of cavity limitation has come from studies in human-modified landscapes of North America and Europe (Newton 1998). Furthermore, a growing body of evidence from northern forests suggests that cavities are not a limiting resource for most cavity-nesting birds in mature forest (see review in Wesołowski 2007). As a notable contrast, in Australia, where there are no woodpeckers, large-bodied obligate cavity-nesters appear to experience strong competition for cavities, even in mature forest (Gibbons & Lindenmayer 2002, Heinsohn *et al.* 2003). Nest site limitation may arise, not only as a result of human-induced habitat changes, but also because of processes related to forest type and age, composition and complexity of the cavity-nester community, or behavior and social dominance among cavity users.

In the Neotropics, in contrast to Australia, North America and Europe, almost nothing is known about nest site availability for cavity-nesting birds, either in mature or disturbed forests. Compared to forests in the Nearctic and Palearctic regions, many forest types in the Neotropics typically have greater structural complexity, higher species diversity, higher productivity, faster decay of standing dead trees (snags), more complex community structure, and greater diversity of nest types, all of which can affect the availability of cavities (Gibbs *et al.* 1993). Moreover, generally warmer climates and different forms of anthropogenic disturbance (e.g., widespread selective logging of the largest trees in tropical forests) may result in more or fewer available nest sites than in North America and Europe, and nest site limitation may have different effects on the ecology and conservation of cavity-nesting birds.

This synthesis article derives from the symposium "Cavity-nesting birds in Neotropical forests: are cavities a limiting resource?" which was organized for the VIII Neotropical Ornithological Congress in Maturín, Venezuela, in May 2007. Our purpose was to review current knowledge of the ecology of cavity-nesting birds in the Neotropics, and to assess the importance of cavities as a limiting resource in Neotropical forests. Specifically, our objectives were to: 1) examine the evidence for nest site limitation in cavity-nesting birds in Neotropical forests, and 2) identify priorities for future research and conservation. Here, we review published articles and present five case studies that examine cavity availability, cavity reuse, potential limitations on populations, and relationships among cavity nesters in five forest-like habitats in Central and South America (Fig. 1). These five forests were classified by Dinerstein *et al.* (1995) as regionally outstanding in their biological distinctiveness, and as either endangered or vulnerable in their level of threat, ranking them among the highest priorities for conservation in the Neotropics.

What do we know about the composition of cavity-nester communities in Neotropical forests? Few studies in the Neotropics have specifically examined communities of cavity-nesting birds. A recent review of the status of cavity-nesting birds in Mexico (Monterrubio-Rico & Escalante-Pliego 2006) revealed that 17% of Mexicos forest avifauna has some degree of tree-cavity requirement and 12% of birds are obligate cavity-nesters, a figure considerably higher than the 4–5% obligate cavity-nesters found in North America and Europe (Newton 1998), but similar to the 12% found in Australia (Saunders *et al.* 1982). The proportion of cavity-nesting bird species observed in tropical and humid cloud forests of Mexico correlated with the structural complexity of these forests, probably because more complex forests provide a high variety of cavities (Monterrubio-Rico & Escalante-Pliego 2006). Unfortunately, no analysis similar to that conducted in Mexico has been conducted for the entire avifauna of Central and South America, where the nesting habits of many species have yet to be described (Ojeda & Trejo 2002). An analysis of cavity-nesting birds in tropical and subtropical forests of Central America and Venezuela, however, revealed that these habitats supported up to 2.5 times as many species of cavity-nesting birds but a similar number of excavator species as in north temperate forests (Gibbs *et al.* 1993), suggesting a similar trend to that observed in México.

What do we know about cavity availability for birds in Neotropical forests? Few studies have attempted to assess cavity availability in Neotropical forests. However, in many other systems, availability of tree cavities is closely linked to the density of snags (e.g., Hutto 2006). Tropical and sub-tropical forests in Central America appear to have a lower density of snags compared to temperate North American forests (Gibbs *et al.* 1993), and also compared to tropical forests in Asia, because of differences in tree decay and spatial distribution of large trees (Gale 2000). A low density of snags in the Neotropics may result in few cavities for birds, especially for those that prefer snags for nesting [e.g., Hoffmanns Woodpecker (*Melanerpes hoffmannii*) in Costa Rica (Sandoval & Barrantes 2006)]. If Neotropical forests have few snags and a high diversity of cavity-nesting species, nest site limitation may be more severe in this region than in other tropical forests or northern temperate forests (Gibbs *et al.* 1993). However, snags may be of limited importance for many cavity-nesting birds (see Thorstrom 2001, Martin *et al.* 2004, Remm *et al.* 2006, Ojeda *et al.* 2007), and may be a poor surrogate for measuring cavity availability if live healthy trees, unhealthy trees with dead branches (e.g., Martin *et al.* 2004) or other substrates like termitaria (Brightsmith 2004) support many cavities and/or cavities with characteristics preferred by nesting birds.

Several studies have used indirect evidence to address questions about cavity availability and nest site limitation in mature Neotropical forests. Specifically, evidence of cavity limitation would include 1) a paucity of suitable, but unused, cavities, 2) a high rate of cavity reuse in successive breeding seasons, and 3) aggressive interactions around cavities (Wesołowski 2003). In mature Peruvian Amazon forest, only 2% of subcanopy cavities, apparently suitable for small to medium birds (< 200 g), were occupied by nesting birds, no aggressive interactions were observed among these species, and nest site selection appeared to be influenced more by nest predation than by competition for cavities, suggesting that nest sites are not limited for these birds in the subcanopy of undisturbed forest in this region (Brightsmith 2005). Similarly, in subtropical moist forest of Guatemala, cavities apparently suitable for the Mottled Owl (*Ciccaba virgata*) and the Vermiculated Screech-Owl (*Megascops guatemalae*) were abundant but unused, and Mottled Owls never reused their nest cavities, suggesting that cavities were not a key limiting factor for these owls (Gerhardt 2004). In contrast, at the same site, few cavities were available for falcons, which had specialized requirements for large cavities in large trees of particular species. Falcons reused cavities year after year, and were observed defending their nest sites from other cavity-nesters such as parrots, suggesting nest site limitation (Thorstrom 2001, Gerhardt 2004). Aggressive defense of nest cavities was also common among macaws in lowland forest (Brightsmith 2005) and a palm swamp (Renton 2004) in the Peruvian Amazon. Although there is some indirect evidence of cavity limitation for large birds in mature forest, this evidence is not conclusive and more studies, preferably experimental, are needed to evaluate cavity limitation in mature Neotropical forests.

Human activities that modify forests may reduce the number of cavities available to nesting birds. Declines of several cavity-nesting species have been reported in different regions of Central and South America, especially in areas where human activities have reduced forest cover and structural complexity [e.g., Moustached Woodcreeper (*Xiphocolaptes falcirostris*), BirdLife International (2004); Brazilian Merganser (*Mergus octosetaceus*), BirdLife International (2004); Vinaceous Parrot (*Amazona vinacée*), Cockle *et al.* (2007); Tucuman Parrot (*Amazona tucumana*), Rivera *et al.* (2007); White-browed Tit-Spinetail (*Leptasthenura xenothorax*), Engblom *et al.* (2002), BirdLife International (2004)]. Lack of cavities, however, is not necessarily the main cause of these declines, as deforestation affects food and predation for many species, pollution may affect waterbirds, and poaching (Wright *et al.* 2001) and persecution as crop pests (Bodrati *et al.* 2006) may contribute to declines of many parrots.

Secondary forests in tropical and temperate regions of Central and South America lack many structural components found in mature forests, such as large live trees, snags, and trees with dead limbs (DeWalt *et al.* 2003, Jaña-Prado *et al.* 2006). As a consequence, populations of cavity-nesting birds might be more limited in these types of forests than in mature forests, particularly populations of SCN that use large trees, snags, unhealthy trees, or specific tree species targeted by logging. Even for excavators, nest sites could be limited by the availability of suitable trees for excavation (e.g., Rudolph & Conner 1991), and interference competition from aggressive SCN (e.g., Ingold 1998). However, little is known about nest-tree selection by cavity excavators anywhere in the Neotropics (but see Sandoval & Barrantes 2006, Ojeda *et al.* 2007). In the temperate rainforest of southern Chile, nest-box-addition experiments have suggested nest site limitation for SCN in degraded second-growth forests (Tomasevic & Estades 2006). However, in tropical and subtropical forests of the Neotropics, no experimental studies on cavity limitation have yet been published.

The importance of cavity limitation in the Neotropical region may depend on forest type and age, composition and complexity of the cavity-nester community, and the degree of human disturbance. The goal of the following five case studies is to tackle the question of nest site availability and its relative role in limiting cavity-nester populations or communities in different forests of Central and South America (Fig. 1) under different ecological and human-disturbance settings.

I. Cavity availability in mature and logged Atlantic forest of Argentina. The Atlantic forest is a global biodiversity hotspot (Myers *et al.* 2000). It includes rainforest on the southeast coast of Brazil and semi-deciduous forest in the southern interior of Brazil, Paraguay, and Argentina (Morellato & Haddad 2000). Overall, the Atlantic forest has 200 endemic bird species (Stotz *et al.* 1996) and one of the highest rates of deforestation among tropical and subtropical forests (Balmford & Long 1994). Nearly all remaining Atlantic forest has been subject to selective logging of its large trees, which may affect cavity availability directly by removing potential nest sites, or indirectly by reducing the size of excavator populations, and thus the number of cavities created (see Guix *et al.* 1999).

Cockle *et al.* (2008) examined the availability of potential nest sites for cavity-nesting birds in mature and selectively logged stands in the Atlantic forest of Argentina. They found very low occupancy of cavities overall, but relatively high occupancy of deep cavities with small entrances. These characteristics may help birds avoid nest predation (Wiebe & Swift 2001, Wesołowski 2002). Logged forest had significantly fewer cavities than mature forest. Relatively few cavities (20–30%) were created by avian excavators; the rest were created by damage or decay processes, suggesting little potential for indirect effects if excavators decline. Although excavators may be less important than in North American systems (e.g., Martin *et al.* 2004, but see Guix *et al.* 1999), nest sites may be limiting for birds requiring deep cavities with small entrances, particularly in logged forest.

II. Cavity availability in mature and logged piedmont forest of the Yungas, Argentina. Yungas forests are subtropical montane forests in the central Andes, characterized by different forest types along an elevation gradient (Brown & Grau 1993). The piedmont forest, at the lowest elevations, harbors the greatest diversity of fauna and flora in the Yungas (Prado 2000). However, the piedmont forest is highly threatened by unsustainable selective logging, which reduces its ecological and economic value, driving the transformation of degraded forest remnants to other land uses (Brown & Malizia 2004). To ensure that logged piedmont forest remnants support a diverse community of native species, and to reduce the transformation of these remnants to other land uses, guidelines are needed to encourage sustainable forest management and biodiversity conservation (Lindenmayer & Franklin 2002).

To develop guidelines for sustainable forestry in the piedmont forests of the Argentine Yungas, Politi (2007) examined the nest site requirements of cavity-nesting birds and the effects of selective logging on cavity availability. They found 18 nests belonging to nine species of birds; 83% of the nests were in mature forest. Five of these nests were in cavities excavated by woodpeckers. Logistic regression showed that cavities were more likely to be used if they were, 1) in trees with a greater diameter at breast height (dbh), 2) higher above ground, 3) in *Calycophyllum multiflorum* trees, and 4) excavated by woodpeckers. This highlights the role of woodpeckers as a keystone group for the piedmont forest. The estimated density of all cavities was 6.75/ha in mature forest, compared to just 1.62/ha in logged forest. The estimated density of cavities suitable for nesting birds (with a roof, certain depth, etc.) was 2.51/ha in mature forest and 0.35/ha in logged forest. The difference in cavity density between mature and logged forest could not be explained entirely by the lower density of stems in the logged area, suggesting that the trees that harbor suitable cavities are also the trees chosen for harvesting. These data suggest that current methods of selective logging reduce the number of usable cavities for avian cavity-nesters, especially for those species dependent on large cavities (e.g., parrots, raptors, toucans, large owls).

III. Influence of selective logging and forest fragmentation on nest site limitation for a small-bodied SCN in the temperate rainforest of Chile. The temperate rainforest, located along the west coast of South America in southern Chile and part of Argentina, exhibits a high proportion of endemic species, and high heterogeneity of forest types and disturbance regimes (Armesto *et al.* 1998). Human activities such as fire, agriculture, and logging have led to forest degradation and fragmentation, which is shown by accelerated loss of forest cover (Echeverria *et al.* 2006). This degradation has been very acute, and this ecoregion is recognized as a high priority for conservation (Dinerstein *et al.* 1995, Armesto *et al.* 1998).

Cornelius (2006) evaluated effects of selective logging and forest fragmentation on nest-tree selection and nest site limitation for a small endemic SCN bird: the Thorn-tailed Rayadito (*Aphrastura spinicauda*). Density of rayaditos was compared during the breeding season among large and connected mature-forest, large and connected logged-forest, and small and isolated logged-fragments. Density was higher in mature stands than in logged but connected stands, whereas density in logged-fragments was intermediate. To test for nest site limitation, a nest site supplementation experiment was carried out by placing nest boxes in logged but connected stands (to test for the effect of selective logging) and in logged-fragments (to test for the combined effects of selective logging and isolation). Density of rayaditos was estimated before and after adding nest boxes. Density increased after nest-box addition, supporting the hypothesis that nest sites were limited in logged forests. However, although density in both types of logged stands (isolated and connected) reached a level similar to that observed in mature connected stands, populations increased more in connected stands than in isolated stands, whereas the proportion of nest-boxes used was higher in isolated than in connected stands. These results indicated that it is important to consider the landscape context when examining cavity availability and nest site limitation processes.

In the same study area, nest-tree selection patterns by rayaditos were compared among the three forest types. A total of 73 active nest-cavities were found but few of these (10–15%) were created by avian excavators, despite the fact that all known excavator species were present in this study area. Landscape-level variation in nest-tree selection was related more to differences in stand isolation than to logging. Nests of rayaditos in logged-fragments were in smaller trees, in a greater variety of tree species, and their use was proportional to availability, in contrast to nest-tree use in large and connected stands (mature and logged). This differential nest-tree use, however, had no apparent consequences for nesting success. Overall, nests in snags were more successful than nests in live trees, but nesting success did not differ among the three stand types. In large and connected stands (mature and logged), snags were used in greater proportion than their availability, suggesting an adaptive nest site choice. This study showed evidence for nest site limitation in forests with selective logging, and an adaptive nest-tree preference by Thorn-tailed Rayaditos, but it also indicated that nest site choice is spatially variable in response to ecological gradients produced by human activities.

*IV. Cavity reuse by a large-bodied SCN, the Blue-fronted Parrot (*Amazona aestiva*), in the dry Chaco of Argentina.* The dry Chaco is a subtropical forest and savanna ecoregion that covers parts of Argentina, Paraguay, and Bolivia. In Argentina, dry Chaco forest is the main breeding habitat for the Blue-fronted Parrot (Beissinger & Bucher 1992), a large-bodied SCN. Although much of the dry Chaco is subject to logging and conversion to agriculture, several parks protect mature forest where cavity-nesting birds can be studied in their natural habitat.

Berkunsky & Reboreda (in prep.) studied patterns of cavity reuse for the Blue-fronted Parrot in Argentina, in a continuous mature dry Chaco forest dominated by quebrachos (*Aspidosperma quebracho-blanco* and *Schinopsis lorentzii*). Most of 98 nest-cavities were in mature live *A. quebracho-blanco* or *S. lorentzii*, with no differences in the characteristics of cavities between tree species, or between live and dead trees. Cavities used by Blue-fronted Parrots were reused in 70% of cases and, in 89% of those reuse cases, the cavities were occupied by Blue-fronted Parrots. Thirteen of 20 banded female Blue-fronted Parrots (65%) reused their cavity the following year, and female cavity fidelity was 100%. In 30% of the total cases, cavities were not reused. Available cavities may not have been reused because the female switched cavities between years, did not breed every year, emigrated from the population, or died. The cavities most often reused by Blue-fronted Parrots were deep, with thick walls and small entrance holes, and had been successful in the previous year.

Although competition for nest sites seems to be common among parrots (Heinsohn *et al.* 2003), and between parrots and other cavity-nesters (Snyder *et al.* 1987, Prestes *et al.* 1997), Berkunsky & Reboreda (in prep.) found no evidence of competition for cavities among Blue-fronted Parrots in the Chaco. Cavities were used by several other vertebrates in the Chaco, but many cavities occupied by these other species were still available for Blue-fronted Parrots, which shared their nest cavities with other taxa (e.g., parrots and mice were observed in the same cavity at the same time). Gray leaf-eared mouse (*Graomys griseoflavus*), 17% of total cavities, and lizards (*Tropidurus spinulosus* and *Phyllopezus pollicaris*), 15% of total cavities, were the most common neighbors. Other less abundant vertebrates (and usually not sharing the cavity) were snakes (9%) and bats (2%). Although rates of cavity reuse were high, competition for cavities did not appear to be important for Blue-

TABLE 1. Number of known cavity-nesting species at Neotropical forest sites in five case studies, and percentage of secondary cavity-nesters' (SCN) cavities that were created by excavators.

Climate	Case study	Number of species		% of SCN cavities that were
		All cavity nesters	Excavators only	created by excavators
Subtropical	I - Atlantic Forest	63	11	28
Subtropical	II - Yungas	51	9	30
Temperate	III - Chile	13	3	10[a]
Subtropical	IV - Chaco	36	8	0[b]
Tropical	V - Costa Rica	12-56	2-15	Unknown

[a]One small-bodied SCN species (Furnariidae).
[b]One large-bodied SCN species (Psittacidae).

fronted Parrots in mature dry Chaco forest (Berkunsky & Reboreda in prep.) or in Pantanal savannas (Fernandes Seixas & Mourao 2002). However, outside of protected areas, where Chaco forest is subject to logging and conversion to agriculture, rates of cavity loss are probably very high, mainly because of recent increases in selective logging and conversion of forest to agriculture. This may result in a shortage of cavities in the near future.

V. Relationship between species richness of SCN and excavator species in seven tropical forests in Costa Rica. The dependence of SCN on excavators has been studied in temperate forests (e.g., Martin *et al.* 2004), but in the Neotropics these relationships are poorly known. Sandoval & Barrantes (in prep.) studied the relationship between species richness of SCN and excavators in seven tropical Costa Rican forests. The authors reviewed published checklists of birds for dry forest (Guanacaste), lowland rainforests (La Selva Biological Station and Península de Osa), premontane forests (Estación Biológica Las Cruces and Central Valley), montane forest (Monteverde), and high montane forest (Villa Mills). They found 95 cavity-nesting species in the seven localities, representing 11% of Costa Rican avifauna. The species richness and composition of excavators and SCN varied greatly among the seven forest localities, from four excavators and eight SCN at Villa Mills to 13 excavators and 43 SCN at La Selva. As expected, community similarity was highest between nearby localities and between localities with similar forest types. The total richness of SCN was not correlated with the richness of excavators; however, there was a weak positive correlation between the richness of those SCN that nest mostly in cavities made by excavators, and the richness of excavators, probably caused by factors (such as altitude) that drive overall species richness of the bird community, rather than by nest site limitation *per se.* The lack of a strong correlation between richness of SCN and richness of excavators could be explained by a lack of nest site limitation in these forests, a high abundance of a few key excavators, or a high abundance of non-excavated cavities, which could release SCN populations from dependence on excavator species.

CAVITIES AS A POTENTIALLY LIMITING RESOURCE IN NEOTROPICAL FORESTS

Neotropical forests have high overall bird diversity and high proportions of SCN (Gibbs *et al.* 1993). In our case studies, the number of species of cavity-nesting birds ranged from 12 in the high montane forest at Villa Mills in Costa Rica to 63 in the Atlantic forest of Argentina (Table 1). Excavators made up 17–25% of cavity-nesting bird species in these forests, similar to the 25% reported by Gibbs *et al.* (1993) for five tropical and subtropical forests in South and Central America. Sandoval & Barrantes (in prep.) found little correlation between richness of excavator species and richness of SCN species in Costa Rican forests.

Our case studies suggest that few of the cavities used by SCN in Neotropical forests are excavated by birds (0–30%, Table 1), similar to forests in Europe (2–60% depending on species and forest, Wesołowski 2007) and Asia (24%, Bai *et al.* 2003), but contrasting with North America (90%, Aitken & Martin 2007). This highlights the potentially important role of other cavity-creating agents (e.g., fungi, beetles) in Neotropical forests. Even in systems where excavator species may provide a large supply of cavities, non-excavated holes may release SCN from the constraints of excavator nest site preferences (Ojeda 2006, Aitken 2007). Woodpecker holes may, however, be preferred by some SCN, making woodpeckers important cavity-creating agents in some forests [e.g., in some tropical forests of Costa Rica (Sandoval & Barrantes in prep.), and in montane Yungas forests of northwestern Argentina (Politi 2007)]. In these forests, they could be keystone excavators (see nest-web concept in Martin *et al.* 2004). In some forests, there is also some evidence of keystone tree species [e.g., *Calycophyllum* trees in piedmont forest of the Yungas (Politi 2007) and *Nothofagus* trees in the temperate rainforest (Cornelius 2006, Ojeda *et al.* 2007)], and structural attributes [e.g., snags for the Thorn-tailed Rayadito (Cornelius 2006) and trees with crown die-back for the Magellanic Woodpecker (Ojeda *et al.* 2007)] that provide cavities or substrates for excavators.

We did not find conclusive evidence for cavity limitation in undisturbed mature forests. In the Argentine Chaco, for example, parrots did not seem to compete for cavities, despite a high rate of reuse of nest sites (Berkunsky & Reboreda in prep.). In the Yungas (Politi 2007) and the Atlantic forest (Cockle *et al.* 2008), as in the Peruvian Amazon (Brightsmith 2005), many cavities were available but not used. However, both in the Yungas and in the Atlantic forest, unused cavities were measurably different from active nest cavities (Politi 2007, Cockle *et al.* 2008). Although cavities may be abundant, cavities of the right size and characteristics may be in short supply for many bird species, showing that it is important to consider cavity quality when assessing cavity availability and nest site limitation.

Three of the case studies showed evidence for reduced density of cavities and potential nest site limitation for cavity-nesting birds in degraded forests. Current selective logging practices reduced the quality of breeding habitat for cavity-nesters in subtropical montane Yungas forests (Politi 2007), south-temperate rainforest (Cornelius 2006), and possibly in subtropical Atlantic forest (Cockle *et al.* 2008). However, most forests degraded by selective logging are also highly fragmented, so individual and population responses to cavity limitation need to be examined in a spatially-explicit context. Moreover, other forms of habitat degradation may also influence density of cavity-nesting birds, making it difficult to separate nest site limitation from other forms of population limitation (e.g., food or predation). Experimental studies, however, can help isolate underlying mechanisms. For example, a nest-box addition experiment in the temperate rainforest of Chile revealed that landscape connectivity was an important factor in determining cavity use patterns and nest site limitation (Cornelius 2006). The spatial context of cavities available for nesting, however, should not be considered only at the landscape scale but also at the local or microhabitat scale. At the local scale, territorial behavior of birds and spatial distribution of cavities may also be important to understanding cavity availability.

PRIORITIES FOR FUTURE RESEARCH AND CONSERVATION

This symposium exposed many gaps in knowledge about cavity-nesting birds in the Neotropics, allowing us to identify several priorities for future research. First, more information is needed on breeding biology and natural history of many species for which nests have not been described, especially in poorly known areas such as the Amazon region. This is essential for the next step: an exhaustive list of cavity-nesting birds for each forest type, with correct classification of excavators, obligate SCN, and species that are more flexible in their nesting strategies.

Second, to evaluate cavity availability, we first need to understand nest site requirements of cavity-nesting birds so that characteristics of good cavities can be assessed. It is challenging to determine nest site preferences for several species in several systems, especially when it is difficult to measure nest success. We propose that cavities frequently reused by nesting birds can be considered good-quality cavities, and can be compared with unused cavities to determine optimal cavity characteristics. However, this may not always be feasible because in forests with many cavities available, reuse of successful nest cavities could be low [e.g., to avoid nest parasites (Stanback & Dervan 2001)]. Therefore, whenever possible, long-term nest monitoring programs should be established since these will provide the most useful data.

Third, it is important to determine the conditions under which cavities are limited. It is clear that anthropogenic disturbances such as selective logging can reduce cavity availability, with potentially important consequences for populations of cavity-nesting birds in the Neotropics. However, more research is needed to determine the structural elements of the forest that contribute to cavity availability (e.g., live trees, unhealthy trees or snags), the main agents of cavity formation, the rates of cavity turnover (i.e., number and state of cavities across time), the specific disturbances that cause abundance of cavities to decline, and the consequences of these processes on populations of cavity-nesting birds. For example, snags are thought to be rare in Central American forests (Gibbs *et al*. 1993); however, little is known about their importance as cavity substrates, relative to large live trees and other structures such as termitaria. Furthermore, although indirect evidence can be useful, nest site limitation can best be tested using experiments. Adding artificial cavities or blocking natural cavities may help expose mechanisms underlying cavity use patterns and nest site limitation. These types of experiments, however, have been rare in the Neotropical region, particularly in subtropical and tropical forests.

Finally, interactions and dynamics of cavity-nesting communities are largely unknown in the Neotropics. Cavity availability and its potential role in limiting populations should be studied in undisturbed forests to examine specific processes and relationships. What are the roles of competition and predation in driving nest site selection, population dynamics, and community structure? How dependent are SCN on excavators, taking into account differences in body size among species? How important are other vertebrates and insects as competitors or facilitators? More research on these topics will be essential for the future application of concepts such as nest-webs and keystone excavators that have been applied in well-studied North American forests (Martin *et al*. 2004).

Based on our case studies and other studies reviewed above, we conclude that many species of cavity-nesting birds might be highly sensitive to habitat disturbances caused by human activities. Specifically, conversion of native forest to tree plantations, crops, and pastures eliminates habitat for many cavity nesters, and selective logging of remaining forest may affect cavity availability and cavity formation agents, and potentially limit nest sites for these species (Cornelius 2006, Politi 2007, Cockle *et al.* 2008). Large-scale timber operations are under way in most forests within the Neotropics, and in some cases without the controls needed to promote long-term sustainability of the industry (Fimbel *et al.* 2001). Even harvesting systems that may be sustainable from a silvicultural point of view, may negatively affect cavity-dependent wildlife by overlooking the ecological importance of dead trees and those with heart rots, often abundant in pristine forests and selected by cavity-nesting wildlife (e.g., Jackson & Jackson 2004, Ojeda *et al.* 2007). Large-scale forest degradation can occur not only through commercial operations, but also through the additive effects of small-scale logging, gathering of fire-wood, grazing by livestock, and clearing for small-scale agriculture, which occur, in many cases, without any planning or management guidelines.

Since there have been very few tests of the effects of these disturbances on cavity-nesting communities in the Neotropics (Fimbel *et al.* 2001), it is important to encourage the maintenance of current and potential cavity-bearing trees at all stages of the decay process (from large healthy trees, through heart-rot infected trees, to snags), both in managed forests and in landscapes that are largely unregulated. In areas where few controls currently exist, important strategies include educational programs at the community level, and agricultural programs that promote the conservation of cavity-bearing trees on small farms. However, environmental scientists and NGOs should also aim to influence political decisions so that conservation measures proposed by the scientific community are actually implemented and enforced. The best strategies for maintaining cavity-bearing trees will depend on the type of forest, local threats, legal frameworks, and the needs of local human populations.

Finally, many populations of Neotropical cavity-nesting birds, including some globally threatened species, are probably limited by factors other than tree cavities (e.g., food, capture of chicks, or hunting of adults). Although maintaining potential nest trees is important for all cavity-nesting birds, it will not suffice to conserve species that are limited by factors other than nest sites. Such species will require conservation measures directed at other aspects of their ecology, such as reducing adult mortality. Unfortunately, so little is known about the ecology of most species of cavity-nesting birds in the Neotropics, that appropriate conservation measures can be difficult to determine (Fimbel *et al.* 2001). It is our hope that this review article will stimulate research on the breeding and general ecology of cavity dependent birds in the Neotropics, to inform decisions that ensure the conservation of this diverse and fascinating group of birds.

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