NESTING ECOLOGY AND COMMUNITY STRUCTURE OF CAVITY-NESTING BIRDS IN THE NEOTROPICAL ATLANTIC FOREST

by

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A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

in

The Faculty of Graduate Studies

(Forestry)

THE UNIVERSITY OF BRITISH COLUMBIA
(Vancouver)

August 2010

ABSTRACT

Tree cavities are proposed to limit populations and structure communities of cavity-nesting birds, making these birds particularly vulnerable to anthropogenic activities that destroy potential nest trees. The greatest diversity of cavity-nesting birds is found in tropical rainforests, yet little is known about the ecology or conservation of these birds. I studied how the production, consumption and loss of tree cavities structure a cavity-nesting community in one of the five most important global biodiversity hotspots, the subtropical Atlantic forest of Argentina.

I found that the cavity-nesting community in the Atlantic forest is structured primarily around the production and persistence of high, deep, non-excavated cavities in large live trees. I show the first experimental evidence that the supply of tree cavities limits the breeding density of secondary cavity-nesting birds (species that do not excavate their own cavity) in a tropical forest. Conventional tropical logging strongly reduced cavity availability: logged forest had half the basal area of primary forest, but only one third the density of large trees, nine times fewer cavities suitable for nesting birds, and 17 times fewer active nests. My results suggest a severe impact of tropical logging on the abundance of cavity-nesting birds, and a need for management strategies that conserve large live cavity-bearing trees. In contrast to North America where vertebrate excavators create most of the nest cavities for secondary cavity nesters, but similar to sites outside of North America, 80% of nests of secondary cavity nesters in the Atlantic forest were in cavities created by natural decay processes. These non-excavated cavities were often in live stems or branches. The predominance of excavated cavities in North America and non-excavated cavities elsewhere can be explained partly by high rates of persistence of excavated cavities at a site in North America and low rates of persistence of excavated cavities at a site in Europe and my site in Argentina. To conserve cavity-nesting birds of the Atlantic forest, I recommend a combination of policies, economic assistance, environmental education, and technical support for forest managers and small-scale farmers, to maintain large healthy and unhealthy trees in commercial logging operations and on farms.

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ACKNOWLEDGEMENTS

I am especially grateful to my family, supervisors, and members of Proyecto Selva de Pino Paraná. My husband Alejandro Bodrati helped me run the field project under difficult conditions; my dad Daryl Cockle built the excellent camera systems that allowed me to check nest cavities; and my mom Rita Cockle and in-laws Regina and Atilio Bodrati looked after many details and provided a great deal of support so that Alejandro and I could work on this and other projects in San Pedro. My supervisors Kathy Martin and Karen Wiebe, and committee members Bob Elner, Peter Marshall and Darren Irwin, were five excellent mentors. Many of the ideas behind this research and ultimate management recommendations arose from discussions in the Proyecto Selva de Pino Paraná, especially with Alejandro Bodrati, Rodrigo Fariña, Marcos Debarba, Nestor Fariña, Gabriel Capuzzi, Nacho Areta, José Segovia, and Emilse Mérida.

Many farmers and property managers in Tobuna and Santa Rosa helped me find and study nests on their property, showed great support and enthusiasm for their birds, and shared their ideas and knowledge with me. They included the Debarba, Barreto, Da Silva, Prestes, Gonzalez, Barboza, Bortolini, Rodriguez, Nekel, Do Prado, and Dominico families; Víctor Lescano; and the sisters and I.E.A. of Tobuna.

I had an excellent group of field assistants: Nestor Fariña, José Segovia, Emo Jordan, Cecilia Ramón, Analia Fernández, Marcos Debarba, Mariana Welter, Mariel Ruiz Blanco, Emilio Correa, Ruso Carrió, and many others, especially volunteers from the Carrera de Guardaparques Provinciales de Misiones. They taught me to climb trees, cure meat over the campfire, and be a better listener. Alejandro, José and Nestor were especially instrumental in finding and monitoring cavities and leading volunteers.

My thesis also benefited from discussions and/or written comments from Andrea Norris, Mark Drever, Tomasz Wesołowski, Katie Aitken, Natalia Politi, Gerardo Robledo, Rosendo Fraga, Alejandro Pietrek, Jorge Tomasevic, Amy Koch, Cintia Cornelius, Amanda Edworthy, Martjan Lammertink; members of the Vertebrate Zoology Lab Group, Grupo FALCO, Grupo HARPIA, and NEOORN; and several anonymous reviewers. My external examiners David Lindenmayer, Charley Krebs and Suzanne Simard, and exam chair Diane Srivastava provided helpful feedback on the exam copy.

Funding was provided by Rufford Small Grants for Nature Conservation, Columbus Zoo and Aquarium Conservation Fund, Oregon Zoo Future for Wildlife Program, Charles A. and Anne Morrow Lindbergh Foundation, British Ornithologists' Union, Cleveland Zoo, Explorers' Club, Conservar La Argentina Grant from Aves Argentinas/BirdLife International, Neotropical Bird Club Conservation Award, Natural Sciences and Engineering Research Council of Canada (NSERC, Canada Graduate Scholarship, Discovery Grant to Kathy Martin), Killam Foundation Predoctoral Fellowship, and Donald S. McPhee Fellowship and Namkoong Family Fellowship in Forest Sciences from the University of British Columbia. The Area de Manejo Integral de la Reserva de la Biósfera Yaboty, Environment Canada, RF-Links and Idea Wild loaned or donated equipment. I thank the Ministerio de Ecología, RNR y Turismo of the Province of Misiones for authorizing my fieldwork, and many provincial park rangers, especially Cacho Maders, Diego Terra, Colo Baez, Paisa Di Santo, Marcos Debarba, Enrique Olivera, Nadia Clavero, Luna Ciccia, Natalia Sandoval, Vanessa Maciel and Ramón Villalba, for their help and company at PP Cruce Caballero, PP Caá Yarí and PP de la Araucaria. Institutional support throughout this project was provided by Fundación de Historia Natural Félix de Azara.

CO-AUTHORSHIP STATEMENT

My thesis is written in manuscript-based format. Chapters 2 through 5 represent independent chapters that have been or will be submitted in a similar format, except that I moved my descriptions of the study area to Chapter 1 and my management recommendations to Chapter 6. I took the lead in developing the research program, performing the research, data analysis and manuscript preparation for Chapters 2 to 4. However, these chapters greatly benefited from discussions with Kathy Martin, Karen Wiebe, Mark Drever and Gerardo Robledo, each of whom will be co-authors on one or more of the published manuscripts. Chapter 5 arose from discussions with my co-authors Kathy Martin and Tomasz Wesołowski who contributed data from their field sites in Canada and Poland; I contributed data from my field site in Argentina, performed all analyses, and prepared the manuscript with input from co-authors.

CHAPTER 1. GENERAL INTRODUCTION AND THESIS OVERVIEW

Resources that limit the size and distribution of animal populations can also determine the composition and structure of communities in ecological networks. For example, abundance of food often determines how bird species compete and coexist in communities (MacArthur 1958, Mac Nally & Timewell 2005). For shelter-using species such as crayfish, coral reef fish and cavity-nesting birds and mammals, population size and community structure may be determined by the availability of shelters (von Haartman 1957, Bovbjerg 1970, Newton 1998, Gibbons & Lindenmayer 2002, Forrester & Steele 2004, Aitken & Martin 2008).

Tree cavities and the ecology and conservation of cavity-nesting birds

Cavity-nesting birds depend on tree cavities for reproduction and sometimes roosting. Tree cavities may provide birds with a safe, dry environment to incubate eggs and raise a brood of nestlings, or to spend nights. Communities of cavity-nesting birds can be described as hierarchical 'nest webs' (Martin & Eadie 1999). Nest webs are interaction webs analogous to trophic webs, whereby tree cavities are the resource that flows from producers to consumers. Cavities are created by excavators (species of birds that excavate their own cavity) and natural decay processes. Secondary cavity nesters are species that cannot excavate their own cavity and instead may compete for existing cavities (Martin & Eadie 1999, Martin *et al.* 2004). Changes in abundance of one cavity-nesting species can affect the abundance and habitat selection of other species via facilitation and competition (Aitken & Martin 2008, Strubbe & Matthysen 2009, Norris & Martin in press). Thus, understanding how species interact in a nest web can be important for predicting the response of cavity-nesting communities to changes in the supply of resources or the abundance of one or more species (Blanc & Walters 2007).

The cavity-nesting habit may render organisms especially vulnerable to anthropogenic habitat change (Imbeau *et al.* 2001, Monterrubio-Rico & Escalante-Pliego 2006). Compared to mature forests, logged forests and agricultural areas often support fewer cavities (Newton 1994, Pattanavibool & Edge 1996) and cavity nesters (Haapanen 1965, Felton *et al.* 2008, Monterrubio-Rico *et al.* 2009). Hence logging and conversion of forest to agricultural lands are considered the key threats to many cavity-nesting birds and mammals (Lindenmayer *et al.* 1990, Wiley *et al.* 2004). Nevertheless, many populations of cavity-nesting birds can persist in logged forests and even agricultural landscapes when these habitats retain suitable foraging areas and nest sites (Manning *et al.* 2004, 2006; Mahon *et al.* 2008). Indeed, where logging operations left key nest tree species standing, Drever & Martin (2010) found higher densities of most woodpecker species on logged sites compared to unlogged sites, suggesting that logging could even increase the production of tree cavities in the short term if cavity production is correlated with woodpecker abundance.

Cavity-nesting communities in tropical and subtropical forests in the Neotropics

Worldwide, most birds nest in the tropics or subtropics, yet most knowledge of breeding birds comes from studies in the temperate zone of the northern hemisphere (Stutchbury & Morton 2001). The Neotropical region has more breeding landbird species than any other region, with 3,370 (36%) of the estimated 9,416 landbirds in the world (Newton 2003). Many of these birds are cavity nesters with key ecological roles in Neotropical forests. For example, many Neotropical cavity-nesting birds are dispersers of tree seeds (Howe 1981, Cardoso da Silva & Tabarelli 2000, Holbrook & Loiselle 2009). Where seed dispersers decline or disappear, for example in logged, hunted, and fragmented forests, lower rates of seed dispersal can depress tree regeneration, reducing the economic and biodiversity value of the forest (Metzger 2000, Cardoso da Silva & Tabarelli 2000, Holbrook & Loiselle 2009, Kirika *et al*. 2008, Sethi & Howe 2009). To conserve cavity-nesting birds and the services they provide in tropical rainforests, it is important to understand their nesting ecology and dependence on cavity resources. Nevertheless, little is known about cavity availability, nest-site requirements of cavity nesters, or cavity nester community structure, either in primary or disturbed forest in the Neotropics (Cornelius *et al.* 2008).

Gibbs *et al.* (1993) compared five tropical forests in Venezuela and Central America with temperate forests in North America. They found fewer dead trees (snags), similar species richness of cavity excavators, and much higher species richness of secondary cavity nesters at tropical forest sites compared with temperate forest sites. Consequently, they suggested that tropical forest may have a shortfall of cavities. Compared to temperate North America, forests of tropical Central and South America also have more species of arboreal mammals (Fleming 1973, Bakker & Kelt 2000) and bees (Guedes *et al.* 2000, Vega Rivera *et al.* 2003) that occupy the same cavities as birds (*e.g.*, Cáceres & Pichorim 2003, Valdivia-Hoeflich & Vega Rivera 2005).

However, alternative substrates such as termitaria (Brightsmith 2004, Sánchez Martínez & Renton 2009), dead and broken branches, and live trees with cavities may compensate for the scarcity of dead trees. Gibbs *et al*. (1993) recommended future studies to examine the availability of tree cavities in relation to forest type and age, causes of cavity development in tropical trees, importance of live versus dead trees as avian nest sites, the degree to which availability of nest sites constrains reproduction in tropical cavity-nesting birds, and the degree of dependence of secondary cavity nesters on cavity-excavating species.

Little is known about the nesting requirements of most cavity-nesting animals in tropical or subtropical forests of the Neotropics. Detailed nest descriptions are available for some species thanks in large part to the pioneering work of Alexander Skutch in Costa Rica (*e.g.* Skutch 1946, 1969, 1971). However, many species' nests have been described only in recent years (*e.g.*, Young & Zook 1999, Willis & Oniki 2001, Brightsmith 2005a, Pichorim 2006, Lebbin 2007, Camargo Guaraldo & Staggemeier 2009, Whittaker *et al*. 2010), and many others' nests have never been described, although they likely include cavities (Cornelius *et al*. 2008). Nevertheless, some species-level studies have examined nesting ecology in more detail, mainly in *Amazona* parrots (Seixas & Mourão 2002, Renton & Salinas-Melgoza 2004, Rodríguez Castillo & Eberhard 2006, White *et al.* 2006, Sanz 2008, Berkunsky & Reboreda 2009, Monterrubio-Rico *et al.* 2009, Salinas-Melgoza *et al.* 2009) but also in other parrots (Monterrubio-Rico *et al.* 2006, Guittar *et al*. 2009), raptors (Thorstrom *et al.* 2000), passerines (Auer *et al*. 2007) and a woodpecker (Sandoval & Barrantes 2006). Additionally, a few studies have looked at cavity requirements and interactions among two or more species of cavity nesters (Koenig 2001, Thorstrom 2001, Gerhardt 2004, Renton 2004, Brightsmith 2005a,b, Carrara *et al*. 2007, Pizo *et al*. 2008, Renton & Brightsmith 2009). Boyle *et al*. (2008) assessed potential cavity availability based on ground surveys, and Brightsmith (2005b) examined occupancy of artificial cavities in primary tropical forests in Costa Rica and Peru, respectively. However, to my knowledge, only Politi *et al*. (2009) have examined more than a small proportion of the cavity nester community. The research questions identified by Gibbs *et al*. (1993) remain largely unanswered. Overall, very little is known about cavity nesters as a community, or the importance of tree condition, excavators, and competitors in the acquisition of cavities by secondary cavity nesters in the Neotropics (Cornelius *et al*. 2008).

Cavity-nesting communities in the Atlantic forest

The Atlantic forest of South America, a tropical and subtropical moist forest, is one of the five most important global biodiversity hotspots (Myers *et al.* 2000). The Atlantic forest once covered an estimated 1.2 million km^2 in south-eastern Brazil, eastern Paraguay, and the province of Misiones in Argentina (Myers *et al.* 2000, Harris & Pimm 2004). The Atlantic forest is estimated to harbour 8,000 endemic plant species and 567 endemic vertebrates (Myers *et al.* 2000), but it is threatened by one of the highest rates of deforestation among tropical and subtropical forests (Balmford & Long 1994). Agriculture, cattle-ranching, and urbanization have replaced more than 90% of the original forest since Europeans began to colonize the region in the 1500s (Fonseca 1985, Morellato & Haddad 2000), and most of the remaining forest has been severely fragmented or selectively logged (Câmara 2003, Ribeiro *et al*. 2009). The loss of Atlantic forest and the advance of agriculture have been correlated with declining populations and local extirpations of many bird species, including cavity nesters, raising grave concerns about the future of avian and plant diversity in the region (Brooks & Balmford 1996, Metzger 2000, Cardoso da Silva & Tabarelli 2000, Ribon *et al.* 2003, Bodrati *et al*. 2006, BirdLife International 2009).

In the remaining Atlantic forest, widespread high-grade (selective) logging of the largest trees may further threaten communities of birds and mammals that nest in tree cavities (Cockle *et al*. 2007, 2008). Guix *et al.* (1999) suggest that parrot populations in the Atlantic forest may depend heavily on woodpeckers for excavating cavities, and may be limited by the densities of woodpeckers and dead trees. However, Siqueira Pereira *et al.* (2009) did not find strong correlations between the abundance of woodpeckers and that of secondary cavity-nesting woodcreepers in the Atlantic forest, in contrast to the results obtained by Martin & Eadie (1999) in Canada. Until now, there have been no community-wide studies of cavity-nesting birds in the Atlantic forest.

THESIS OBJECTIVES

My study addresses how a cavity-nesting community in the Atlantic forest is structured around the production, use, and loss of tree cavities. The objectives were to identify key relationships among cavity producers and consumers (Chapter 2); to determine the characteristics of trees and cavities important in nest-site selection (Chapter 3); to determine whether the supply of cavities limits the breeding density of birds (Chapter 4); to determine whether differences in the persistence of cavities excavated by woodpeckers could explain why so few woodpecker cavities are used by secondary cavity nesters in the Atlantic forest and elsewhere outside North America (Chapter 5); and, based on my results, to recommend strategies for conserving cavity-nesting birds in the Atlantic forest and other tropical forests (Chapter 6).

STUDY AREA

I studied cavity-nesting birds in the Sierra Central, Misiones province, Argentina (Fig. 1.1, Cockle *et al*. 2008). Given the general lack of knowledge about the bird species and habitat use and the difficulty of finding nests in tropical forest, I monitored nest cavities wherever possible in the general study area, and collected detailed information on eight 1-ha study plots. The study area was the mosaic landscape of forest, parks, and small farms from San Pedro (26°38’S, 54°07’W) to Parque Provincial (PP) Cruce Caballero (26°31’S, 53°59’W) and Tobuna (26°27’S, 53°54’W), Department of San Pedro, with two cavities monitored at PP Caá Yarí in the Yaboty Biosphere Reserve (26°52’S, 54°14’W; Guaraní department; Fig. 1.1; Bodrati & Cockle 2005, Bodrati *et al*. 2005a,b). The vegetation is classified as subtropical semi-deciduous Atlantic mixed forest with laurels (*Nectandra* and *Ocotea* spp.), guatambú (*Balfourodendron riedelianum*), and Paraná pine (*Araucaria angustifolia*; Cabrera 1976). Elevation is 520–700 m asl and annual rainfall 1200–2400 mm distributed evenly throughout the year.

Most field effort was spent in primary forest at PP Cruce Caballero, the only 400 ha of uncut laurel, guatambú and Paraná pine forest remaining in the western Atlantic forest region of Brazil, Paraguay and Argentina. Although PP Cruce Caballero is considered primary forest, Paraná pine seeds were harvested there for many years and the park is surrounded on three sides by a mosaic of farms with forest patches and corridors. On the fourth side of the park is a large tract of selectively logged forest in the valley of the Arroyo Alegría (Fig. 1.1; Bodrati *et al*. in press).

I also studied nests in logged forest and regenerating forest at PP Cruce Caballero, at PP Caá Yarí, at PP de la Araucaria (on the outskirts of the town of San Pedro), and on nearby farms. Farms are 10–100 ha, on land selectively logged beginning in the 1950s–1960s and partly cleared beginning in the 1970s. Farm labour is performed by family members using hand tools and oxen. Each farm produces a diversity of products including tobacco, trees, or cattle for sale; and manioc, beans, vegetables, corn, citrus, pigs, peanuts and dryland rice for subsistence. Farms retain patches and corridors of forest, from which farmers selectively harvest wood for sale and for their personal use in cooking and construction of buildings, furniture and tools. Forestry policy in the province of Misiones sets the minimum DBH (diameter at breast height) below which trees cannot be harvested. The exact minimum DBH depends on the tree species, but generally trees can be harvested legally when they are above ~60 cm DBH. The critically endangered Paraná pine was once the main source of income in the study area, but harvesting was so intense between 1950 and the early 1980s that the species was legally protected from harvesting in 1986. Harvest slowed but continues illegally and many new buildings are still constructed of Paraná pine. Both on farms and in parks, "logged forest" had a history of repeated conventional logging that removed the largest trees over many years leaving small clearings (tree removal gaps) dominated by bamboo (*Merostachys claussenii*, *Chusquea tenella* and *Guadua trinii*) and young trees of a variety of native species. Additionally, isolated trees on farms support nesting cavities. Although we did not actively search for nests in these isolated trees, we monitored nest cavities that were either discovered accidentally or shown to us by farmers.

Experimental plots

I evaluated cavity availability and performed a nest-box addition experiment (Chapter 4) in eight 1-ha (100 m x 100 m) plots randomly located within areas of deep red soil with negligible slope, classified as Red Latisol (Ríos 2006). Four plots were established in primary forest (PP Cruce Caballero) and four in logged forest (two at PP Cruce Caballero and two at Tobuna).

Cavity-nester community

The community of cavity-nesters in the study area includes 69 species of birds, 11 of which are rare or occasional (Table 1.1). Fourteen species in three avian orders are excavators or probable excavators (one puffbird in the Galbuliformes, ten woodpeckers in the Piciformes, two trogons in the Trogoniformes, and one xenops in the Passeriformes), and the rest are believed to be obligate or facultative secondary cavity nesters in seven orders (Cathartiformes, Falconiformes, Piciformes, Psittaciformes, Strigiformes, Apodiformes, Passeriformes). Twenty-one species are endemic to the Atlantic forest, and 15 are threatened or near-threatened according to national or international red-lists (Table 1.1). One additional species, the Blue-winged Macaw

(*Primolius maracana*) was common in the study area until the 1970s, but now appears to be extinct in Argentina (Bodrati *et al*. 2006).

GENERAL FIELD METHODS

I monitored all the cavity-nests I could find over four breeding seasons (August 2006 – January 2007; August 2007 – January 2008; September – December 2008; October – December 2009). Each year, my field assistants and I searched for nests mostly from pre-existing trails. We stopped frequently to observe the behaviour of adult birds and look for evidence of recent wear around cavity entrances. Also, we asked farmers to show us nests on their properties. We suspected the presence of a nest if we saw an adult bird repeatedly visit the same tree, fly out of a tree suddenly, disappear from view for long periods, cling to a cavity entrance, perch near a cavity, enter or exit a cavity. We searched for a cavity whenever we suspected the presence of a nest, and inspected cavities using 1.5–5 cm diameter home-made video cameras. For cavities below 15 m, a video camera was mounted on a 15 m telescoping fiberglass pole and inserted into the cavity. For cavities 15–26 m high, we carried a video camera up to the cavity using single-rope climbing techniques. We used a camera at the end of a 3-m hose for cavities in which the side walls obstructed our view of the nest chamber. When nests could not be accessed with a camera (*i.e.*, cavities above 15 m that did not have a sturdy fork above them), we observed the activities of adult birds from the ground for 20 minutes to 5 hours. Cavities were considered active nests if they contained eggs and/or chicks, or if the behaviour of adult birds indicated nesting (*e.g.*, adult carrying food into cavity; female parrot leaving cavity to be fed by male and returning immediately to cavity). Roosting was inferred when a diurnal bird entered an empty cavity at dusk and did not emerge before dark. Nocturnal owls were found roosting in cavities during the day, but always in cavities they used for nesting in the same breeding season, so I did not include these observations separately as roosts. Data on roosting are presented only in Chapter 2, in order to include two species that were found roosting but not nesting. Both species are globally threatened, their nests have not been described, and one of the species is believed to be threatened by nest-site competition (BirdLife International 2009), so I felt it was important to show their links in the nest web. Cavity formation process (excavated, decay) was determined by observing excavating activity by birds or by the shape of the cavity entrance and interior. Cavities with round or oval entrances and regular interiors were considered excavated cavities, and those with irregular entrances and interiors were considered formed by decay.

THESIS OVERVIEW

One of the overall goals of my research program is to compare the cavity-nesting community of a subtropical moist forest with well-studied, hierarchically-structured cavity-nesting communities in temperate North America (Martin & Eadie 1999, Martin *et al*. 2004, Blanc & Walters 2007). Thus I begin by investigating the key interactions among cavity producers and consumers in the Atlantic forest. In Chapter 2, I examine the role of vertebrate excavators and heart rot fungi in creating tree cavities, and the role of avian body mass in structuring cavity reuse among secondary cavity nesters.

To determine whether cavities are a limiting resource for communities of cavity-nesting birds, it is necessary to understand the characteristics that make a cavity suitable, assess the abundance of suitable cavities in different habitats, and determine the response of cavity-nesting birds to changes in cavity abundance. In Chapter 3, I determine the characteristics of cavities and trees selected by excavators and secondary cavity nesters. Chapter 4 tests the hypothesis that nest sites limit breeding density of secondary cavity-nesting birds and examines the effect of selective logging on the abundance of cavities and cavity nesters in the Atlantic forest. Experiments in temperate forests (reviewed by Newton 1994) have tested whether adding nest sites leads to increased nest density of cavity-nesting birds; I conduct the first such experiment in a tropical forest.

To understand global patterns in the ecology of cavity-nesting birds, in Chapter 5, I examine global variation in the proportion of cavities created by vertebrate excavators as opposed to natural decay processes. I then examine the extent to which differential persistence of excavated and non-excavated cavities can explain this pattern by comparing persistence of cavities between my study area in the Atlantic forest and sites in north temperate forest of Europe and North America.

My thesis has broad implications for the ecology and conservation of cavity-nesting birds. In Chapter 6 I present key implications for life history, community ecology, and conservation, discuss avenues for future research, and recommend strategies for conservation of cavity-nesting birds in the Atlantic forest.

Table 1.1. Cavity-nesting bird species, their mode of cavity acquisition (excavator or secondary cavity nester, SCN), conservation status, relative abundance in the study area (Bodrati *et al.* in press, A. Bodrati *in litt.*) and sample size of cavities (total number of different cavities used for nesting or roosting), nests (number of nesting attempts in any cavity), and roost cavities (number of different cavities used for roosting). Categories of relative abundance for each species are based on number of sight or auditory records/observer/unit time as follows: Abundant- >10 records/day every day; Common- 5–10 records/day every day; Frequent- 1–5 records/day most days; Uncommon- 1–2 records every 2–3 days; Rare- fewer than 1–2 records every 2–3 days; Occasional- 1–5 records in >300 days of field work, no known territory or nest. Atlantic forest endemism follows Brooks *et al.* (1999) with modifications based on a review of current systematics and species distributions. I follow BirdLife International (2009) and Aves Argentinas/SAyDS (2008) for international and national conservation status, respectively.

Species	Mode of cavity acquisition	Relative Abundance	Number of Cavities	Number of Nests	Number of Roosts	Endemism to Atlantic forest	Conservation Status	
							Global	Argentina
Black Vulture (*Coragyps atratus*)	SCN	Common						
King Vulture (*Sarcoramphus papa*)	SCN	Occasional						
Laughing Falcon (*Herpetotheres cachinnans*)	SCN	Rare						
Barred Forest-Falcon (*Micrastur ruficollis*)	SCN	Common						
Collared Forest-Falcon (*Micrastur semitorquatus*)	SCN	Uncommon						Vulnerable
American Kestrel (*Falco sparverius*)	SCN	Frequent	1	1				
Bat Falcon (*Falco rufigularis*)	SCN	Rare						
White-eyed Parakeet (*Aratinga leucophthalma*)	SCN	Abundant	5	8				
Maroon-bellied Parakeet (*Pyrrhura frontalis*)	SCN	Abundant	13	24				
Red-capped Parrot (*Pionopsitta pileata*)	SCN	Common	2	2		Endemic		

Species	Mode of cavity acquisition	Relative Abundance	Number of Cavities	Number of Nests	Number of Roosts	Endemism to Atlantic forest	Conservation Status	
							Global	Argentina
Scaly-headed Parrot (*Pionus maximiliani*)	SCN	Frequent	10	13				
Vinaceous Parrot (*Amazona vinacea*)	SCN	Uncommon	8	11		Endemic	Endangered	Critically Endangered
Barn Owl (*Tyto alba*)	SCN	Frequent	1	1				
Tropical Screech-Owl (*Megascops choliba*)	SCN	Frequent	2	2				
Black-capped Screech-Owl (*Megascops atricapilla*)	SCN	Rare				Endemic		Vulnerable
Long-tufted Screech-Owl (*Megascops sanctaecatarinae*)	SCN	Rare						Threatened
Tawny-browed Owl (*Pulsatrix koeniswaldiana*)	SCN	Uncommon				Endemic		Vulnerable
Rusty-barred Owl (*Strix hylophila*)	SCN	Uncommon				Endemic	Near-threatened	Vulnerable
Mottled Owl (*Ciccaba virgata*)	SCN	Rare						Threatened
Black-banded Owl (*Ciccaba huhula*)	SCN	Rare						Threatened
Ferruginous Pygmy-Owl (*Glaucidium brasilianum*)	SCN	Common	3	5				
Buff-fronted Owl (*Aegolius harrisii*)	SCN	Rare						
Gray-rumped Swift (*Chaetura cinereiventris*)	SCN	Common						
Sick's Swift (*Chaetura meridionalis*)	SCN	Common						
Surucua Trogon (*Trogon surrucura*)	Excavator	Abundant	5	6				
Black-throated Trogon (*Trogon rufus*)	Excavator	Frequent						
Buff-bellied Puffbird (*Notharchus swainsoni*)	Excavator	Rare				Endemic		Vulnerable

Species	Mode of cavity acquisition	Relative Abundance	Number of Cavities	Number of Nests	Number of Roosts	Endemism to Atlantic forest	Conservation Status	
							Global	Argentina
Toco Toucan (*Ramphastos toco*)	SCN	Rare						
Red-breasted Toucan (*Ramphastos dicolorus*)	SCN	Common	9	15	1	Endemic		
Spot-billed Toucanet (*Selenidera maculirostris*)	SCN	Uncommon				Endemic		Threatened
Chestnut-eared Aracari (*Pteroglossus castanotis*)	SCN	Common	3	6				
Saffron Toucanet (*Pteroglossus bailloni*)	SCN	Uncommon	1		1	Endemic	Near-threatened	Threatened
Ochre-collared Piculet (*Picumnus temminckii*)	Excavator	Common				Endemic		
White Woodpecker (*Melanerpes candidus*)	Excavator	Uncommon						
Yellow-fronted Woodpecker (*Melanerpes flavifrons*)	Excavator	Common	2	2		Endemic		
White-spotted Woodpecker (*Veniliornis spilogaster*)	Excavator	Abundant	2	2		Endemic		
White-browed Woodpecker (*Piculus aurulentus*)	Excavator	Uncommon				Endemic	Near-threatened	Vulnerable
Green-barred Woodpecker (*Colaptes melanochloros*)	Excavator	Common	8	9				
Campo Flicker (*Colaptes campestris*)	Excavator	Common	4	4				
Helmeted Woodpecker (*Dryocopus galeatus*)	Excavator	Uncommon	1		1	Endemic	Vulnerable	Endangered
Lineated Woodpecker (*Dryocopus lineatus*)	Excavator	Common	4	3	2			
Robust Woodpecker (*Campephilus robustus*)	Excavator	Frequent	2	2		Endemic		
Buff-browed Foliage-gleaner (*Syndactyla rufosuperciliata*)	SCN	Abundant	1	2				

Species	Mode of cavity acquisition	Relative Abundance	Number of Cavities	Number of Nests	Number of Roosts	Endemism to Atlantic forest	Conservation Status	
							Global	Argentina
Sharp-billed Treehunter (*Heliobletus contaminatus*)	SCN	Rare				Endemic		Vulnerable
Streaked Xenops (*Xenops rutilans*)	Excavator	Frequent						
Plain-brown Woodcreeper (*Dendrocincla turdina*)	SCN	Occasional				Endemic		
Olivaceous Woodcreeper (*Sittasomus griseicapillus*)	SCN	Abundant	1	1				
White-throated Woodcreeper (*Xiphocolaptes albicollis*)	SCN	Common	3	5				
Planalto Woodcreeper (*Dendrocolaptes platyrostris*)	SCN	Abundant	5	6				
Lesser Woodcreeper (*Xiphorhynchus fuscus*)	SCN	Frequent				Endemic		
Scalloped Woodcreeper (*Lepidocolaptes falcinellus*)	SCN	Common				Endemic		
Black-billed Scythebill (*Campylorhamphus falcularius*)	SCN	Uncommon				Endemic		
Short-tailed Antthrush (*Chamaeza campanisona*)	SCN	Common						
Rufous-tailed Antthrush (*Chamaeza ruficauda*)	SCN	Rare				Endemic		Vulnerable
Euler's Flycatcher (*Lathrotriccus euleri*)	SCN	Abundant						
Long-tailed Tyrant (*Colonia colonus*)	SCN	Frequent	1	1				
Cattle Tyrant (*Machetornis rixosa*)	SCN	Frequent						
Three-striped Flycatcher (*Conopias trivirgatus*)	SCN	Uncommon						

Species	Mode of cavity acquisition	Relative Abundance	Number of Cavities	Number of Nests	Number of Roosts	Endemism to Atlantic forest	Conservation Status	
							Global	Argentina
Streaked Flycatcher (*Myiodynastes maculatus*)	SCN	Common	1	1				
Sirystes (*Sirystes sibilator*)	SCN	Common						
Swainson's Flycatcher (*Myiarchus swainsoni*)	SCN	Common	4	4				
Short-crested Flycatcher (*Myiarchus ferox*)	SCN	Rare						
Large-headed Flatbill (*Ramphotrigon megacephalum*)	SCN	Common						
Black-crowned Tityra (*Tityra inquisitor*)	SCN	Frequent	2	3				
Black-tailed Tityra (*Tityra cayana*)	SCN	Common	4	4				
Brown-chested Martin (*Progne tapera*)	SCN	Rare						
Gray-breasted Martin (*Progne chalybea*)	SCN	Rare						
House Wren (*Troglodytes aedon*)	SCN	Frequent	1	1				
Chopi Blackbird (*Gnorimopsar chopi*)	SCN	Common	2	3				

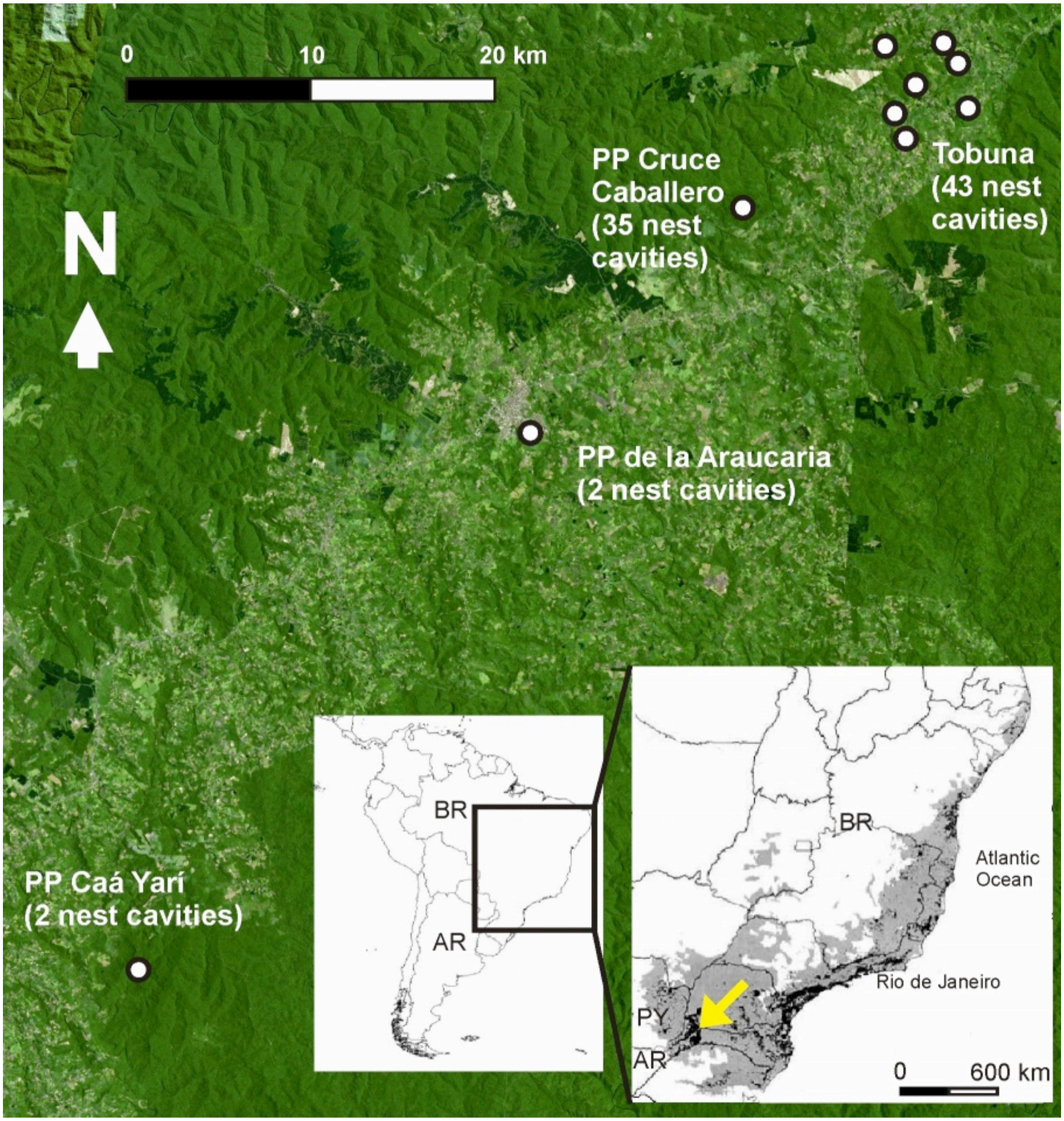

Figure 1.1. Satellite image of the study area in the Atlantic forest of Argentina showing mature tree plantations (dark green), native forest (medium green), and farmland and urban areas (light green, beige and pink; courtesy CONAE). White dots indicate where nests were studied. Inset maps: South America with original extent of the Atlantic forest (grey) and remaining forest (black), adapted from Harris & Pimm (2004); AR- Argentina, BR- Brazil, PY- Paraguay. Yellow arrow indicates the study area and the province of Misiones.

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CHAPTER 2. TREE CAVITIES IN THE ATLANTIC FOREST: PRODUCTION AND USE BY CAVITY-NESTING BIRDS

Communities of cavity-nesting birds and mammals interact around a key structuring resource: cavities. Secondary cavity nesters, species that cannot make their own cavity, may compete for existing cavities created by vertebrate excavators or natural decay (Short 1979, Martin & Eadie 1999). They may modify or expand existing cavities, but they do not initiate excavation. Woodpeckers (Picidae) are the strongest vertebrate excavators (Martin & Eadie 1999), with morphological adaptations in their bills, skulls, neck musculature, ribs and legs that allow them to chisel out cavities in hard tree substrates (Burt 1930, Spring 1965, Kirby 1980). Weaker avian excavators have fewer adaptations for excavation. They include barbets (Capitonidae), trogons (Trogonidae) and several passerines such as nuthatches and chickadees (Martin & Norris 2007) that excavate cavities in soft substrates. Natural decay processes that produce cavities include abiotic factors such as fire, wind and rain, and biotic factors such as fungi, termites, and other insects (Gibbons & Lindenmayer 2002).

Usually, the formation of cavities begins with parasitic heart rot fungi, mainly polypores (Basidiomycota; but see Conner & Locke 1982). The activity of these fungi modifies the chemical and physical properties of wood cells, softening the heartwood (Robledo & Urcelay 2009). Heartwood is the older, dead xylem tissue at the centre of a tree, surrounded by the living sapwood. The combination of decayed heartwood with firm and healthy sapwood appears ideal for cavity-nesting birds because the firm sapwood helps exclude predators from nest cavities (Conner *et al.* 1976, Tozer *et al.* 2009). A cavity may form when avian excavators penetrate the sapwood and remove the softened heartwood (Conner & Locke 1982, Jackson & Jackson 2004). Alternatively, the softened heartwood may be exposed by physical or insect damage that breaches the sapwood (Gibbons & Lindenmayer 2002). The decayed material inside the tree then collapses, drains away, or is removed by insects, fire, or vertebrates (Gibbons & Lindenmayer 2002). Although many vertebrates may be involved in removing decayed material from inside a natural cavity, these species are not considered to be excavators because they do not initiate cavities.

Martin & Eadie (1999) proposed using hierarchical interaction webs called ‘nest webs’ to study facilitation of cavity formation by excavators and decay, and competition for cavities among secondary cavity nesters. Nest web interactions are important determinants of population size and resource use in cavity-nesting communities. For example, Red-breasted Nuthatches (*Sitta canadensis*) sometimes excavate new cavities and sometimes reuse old cavities, often those excavated by Downy Woodpeckers (*Picoides pubescens*). In a recent study, the density of Red-breasted Nuthatches increased at the site-level following increases the previous year in density of Downy Woodpeckers (Norris & Martin in press). In a nest box experiment in Sicily, competition from dormice (*Muscardinus avellanarius*) reduced the breeding density of blue tits (*Parus caeruleus*; Sarà *et al.* 2005). In Canada and Belgium, competition from exotic secondary-cavity nesters has apparently led to shifts in cavity- and nest-patch selection by less competitive native birds (Aitken & Martin 2008, Strubbe & Matthysen 2009). Thus population size and habitat use of cavity-nesting birds can be regulated through direct and indirect interactions with other cavity-nesting species.

Wood decaying fungi vary widely in their ability to colonize and break down different substrates, including live and dead trees of different sizes and species (Gilbert & Sousa 2002, Urcelay & Robledo 2004). Consequently, some heart rot fungi may be more likely than others to create the conditions under which cavities form in trees. In temperate forests, heart rot fungi reported in nest and roost trees often belong to the genus *Phellinus* (Family *Hymenochaetaceae*; Kilham 1971, Conner *et al.* 1976, Hart & Hart 2001, Losin *et al.* 2006); however, *Fomes*, *Spongipellis*, *Armillaria*, and other genera are also important at some sites (Conner & Locke 1982, Runde & Capen 1987, Parsons *et al.* 2003). Studies of cavity-nesting birds in temperate forests have shown that some woodpeckers preferentially select trees with fruiting bodies of heart rot fungi (Hart & Hart 2001, Pasinelli 2007). However, to my knowledge there have been no studies of the fungi associated with nest trees in tropical forests, where warm temperatures and moist conditions promote fungal activity, and where the species diversity of wood-decaying fungi is exceptionally high (Gilbert *et al*. 2002).

Interaction webs are not only structured vertically (resources flow from producers to consumers), but may also be structured or compartmentalized horizontally according to key resources or habitats (Krause *et al.* 2003, Woodward *et al*. 2005) such as grass versus trees (Pringle & Fox-Dobbs 2008). In mixed temperate forest in British Columbia, the nest web is structured primarily around the production of cavities by two key excavator species in one tree species (Martin *et al.* 2004). However, smaller excavators create smaller holes and interact with other small-bodied species (Norris & Martin in press). By using a cavity with an entrance just large enough for the adult to squeeze through, birds may reduce their risk of nest predation (Martin *et al*. 2004, Paclík *et al*. 2009). In a Longleaf Pine (*Pinus palustris*) forest in Florida, the nest web is compartmentalized according to nest tree species and condition, whereby some species of cavity-nesting birds depend primarily on dead hardwood trees, and others on living or dead pines (Blanc & Walters 2008).

Although communities of cavity-nesting birds reach peak species diversity in tropical rainforests (Gibbs *et al.* 1993), nearly all research on interactions among cavity nesters has been conducted in temperate forests (Gibbons & Lindenmayer 2002, Martin *et al.* 2004, Wesołowski 2007, Bai & Mühlenberg 2008, Blanc & Walters 2008). Studies of cavity-nesting communities in tropical forests are limited to a few species from much larger communities; nevertheless, there is evidence of substructuring in these communities. In the lowland Amazon rainforest of Peru, 15 species of parrots depend primarily on two plant species for nesting cavities: *Dipteryx micrantha* trees (Fabaceae) and *Mauritia flexuosa* palms (Arecaceae; Brightsmith 2005). These parrots partitioned the cavity resource temporally according to body size, with smaller species nesting earlier than larger species (Brightsmith 2005). In the same region, small Blue-and-yellow Macaws (*Ara ararauna*) primarily nested in palms, larger Red-and-green Macaws (*Ara chloropterus*) primarily used *Dipteryx* trees, and medium-sized Scarlet Macaws (*Ara macao*) used a wide range of trees, frequently entering into conflict with Red-and-green Macaws (Renton & Brightsmith 2009). Thus, key resources and size-specific nest-site competition may substructure tropical communities of cavity nesters. Given that nest webs can be useful tools for predicting the response of cavity-nesting communities to perturbation (Blanc and Walters 2007), understanding nest web interactions is important for the conservation of cavity-nesting birds in tropical rainforests experiencing habitat loss and other threats from anthropogenic activities.

In this chapter, my goal was to determine how tree cavities are produced and used by a cavity-nesting avian community in the Atlantic forest, one of the most threatened tropical rainforests in the world. The first objective was to determine the main producers of cavities used by secondary cavity-nesting birds in the Atlantic forest. The second objective was to identify potential competitors for nest cavities by determining the extent to which the Atlantic forest nest web is structured according to avian body size. I predicted that the depth and diameter of cavities used by birds would be correlated with their body mass as reported by Martin *et al*. (2004), and that sequential interspecific use of tree cavities would occur most often among species with similar body mass. If small birds can use cavities of all depths and entrance diameters, but large birds are constrained to deep cavities with large entrance diameters, I predicted a negative relationship between body mass and the variance of depth and entrance diameter. On the other hand, if birds reduce their risk of predation by selecting deeper cavities with entrances just narrow enough to accommodate their body size, I predicted that variance of cavity depth and diameter would be constant among species of different body mass, and the probability of nest predation would increase with increasing cavity entrance diameter and decreasing depth. However, if larger species are released from predation pressure because they are better able to defend their cavities, or if they are as large as their nest predators, variance of cavity diameter should increase with body mass. If larger species are released from predation pressure, the probability of nest predation should decrease with body mass of the nesting species.

METHODS

Study Area and Field Methods

I studied nests of cavity-nesting birds over four breeding seasons (2006 to 2009) in the Sierra Central of Misiones (study area and methods described in Chapter 1). I included all nests and roosts in natural cavities, both within plots and outside of plots. I used a diameter tape to measure the diameter at breast height (DBH in cm) of all nest trees. I used a measuring tape to determine the vertical and horizontal depth of each cavity and the vertical and horizontal diameter of each cavity entrance in cm. Cavity depth was considered the maximum depth of the cavity, whether this was horizontal or vertical. For entrance diameter, I used the minimum distance across the largest entrance to the cavity, as this distance would determine the maximum body size of an animal that could enter the cavity. Where I could not climb to cavities I measured entrance diameter using a Criterion RD 1000 electronic dendrometer. Where I could not climb to the cavities but could access them with the pole mounted camera, (cavities 8–15 m high in dead trees) I estimated the horizontal depth of the cavity by determining how far the camera could be inserted, and the vertical depth by comparing the camera view of the cavity chamber to the view of cavities of known depth. Whenever possible, active nests were inspected every 1–10 days to determine their fate. Nests containing eggs or dead chicks, unattended by parents, were considered to have been abandoned. Nests where all chicks or eggs vanished before the expected fledging date were considered to have been predated.

To determine the species of wood-decaying fungi present in the nest trees, I visited all extant nest trees in October 2009 and collected samples of fruiting bodies of all polypore fungi inside cavities or on the same stem as the cavity. G. Robledo (Universidad Nacional de Córdoba, Argentina) attempted to isolate and culture the heart rot fungi from small pieces of wood taken from the cavity walls (with selective malt agar culture medium), but he was unsuccessful. All samples of fruiting bodies were identified by G. Robledo and deposited in the Herbarium (CORD), Museo Botánico, Universidad Nacional de Córdoba, Argentina.

Analyses

I used nest web diagrams to depict relationships among cavity-nesting birds and resources (Martin & Eadie 1999). Previous nest webs used line thickness to indicate the proportion of a species' nests produced by a given source (Martin *et al.* 2004, Bai 2005, Blanc & Walters 2008); in contrast, in my nest webs, line thickness indicates the absolute number of nests, because the small sample size of nests for many of my species renders proportions misleading.

I used R version 2.9.2 (R Development Core Team 2009) for all statistical analyses and I used published data to determine average body mass for adult female birds as a proxy for body size (*e.g.*, girth). I used general linear models to test whether mean body mass was a good predictor of mean cavity depth, mean entrance diameter, variance of log-transformed cavity depth, and variance of log-transformed entrance diameter. Variables were log-transformed before calculating variance in order to avoid the natural increase in variance associated with increases in the mean. A hollow stub or 'chimney' used by the large-bodied Barn Owl (*Tyto alba*) was excluded from the analysis as an outlier because Barn Owls will use a wide variety of structures for nesting (not just tree cavities) and the hollow stub was much larger than any other cavity used by any cavity-nesting bird in the study. The analyses for mean cavity depth and diameter were conducted twice, but gave similar results. In the first analysis, I calculated means by treating each nesting attempt as a different observation, even when the same species nested more than once in the same cavity in different years, because I wanted to weight cavities used multiple times by a species more heavily than cavities used only once. In the second analysis, I calculated means based only on nests in different cavities. Because results were very similar for these two analyses, I report only the results of the first analysis. To calculate the variance of log-transformed cavity diameter and depth I included only nesting attempts in different cavities for six species of secondary cavity nesters for which I had at least five nest cavities: Planalto Woodcreeper (*Dendrocolaptes platyrostris*; n = 5), Maroon-bellied Parakeet (*Pyrrhura frontalis*; n =13), White-eyed Parakeet (*Aratinga leucophthalma*; n = 5), Scaly-headed Parrot (*Pionus maximiliani*; n = 9), Vinaceous Parrot (*Amazona vinacea*; n = 8), Red-breasted Toucan (*Ramphastos dicolorus*; n = 9).

I used a randomization test with 2000 iterations to test whether pairs of species that occupied the same nest cavity sequentially were more similar in body mass than expected by chance. (1) I calculated the difference in body mass between birds of different species that occupied the same nest cavity sequentially (n = 31 interspecific pairs), and took the mean of those differences as the observed mean difference in body mass. (2) I created simulated data by drawing without replacement from the individuals that used the cavities in the second year, and randomly assigning them to share cavities with the individuals that used the cavities in the first year. (3) I calculated the difference in body mass for each simulated species pair, and took the mean of those differences as the simulated mean difference in body mass. (4) I repeated steps 2 and 3, 2000 times. (5) I calculated the proportion of the 2000 simulated cases in which the mean difference in body mass was as small as my observed mean difference in body mass (*i.e.*, the probability of observing a difference in body mass as small as the difference I observed, if the second species using the cavity had been random with respect to the first species).

I used a generalized linear model with binomial error structure (logistic regression model) to determine whether the probability of a secondary cavity nester's nest being predated could be predicted by the body mass of the nesting species. Nest outcome was either 'predated' or 'fledged'; abandoned nests were excluded from the analysis. The data set comprised 39 nests of secondary cavity nesters found with eggs and considered to be either predated or successful. I then built a suite of five generalized linear models with binomial error structure (logistic regression models) to predict the probability of nest predation based on cavity size for the same 39 nests. Model 1 included cavity entrance diameter; Model 2 included cavity depth; Model 3 included entrance diameter and depth; Model 4 included entrance diameter, depth, and an interaction between entrance diameter and depth; and Model 5 was the null intercept-only model. An information theoretic approach was used to compare these five models based on their Akaike's Information Criterion corrected for small sample size (ΔAICc) and Akaike weight (w; Burnham & Anderson 2002). Models with ΔAICc < 2 and $w > 0.8$ were considered to be well supported by the data. Parameters with $|z| > 1.96$ were considered to be significant at $\alpha = 0.05$. This last analysis was repeated using a second suite of models, mixed models with binomial error structure, that included the same variables to predict the probability of predation, but included species as a random effect. Within the second suite, models were again compared based on their ΔAICc and Akaike weights.

RESULTS

I studied 147 nesting attempts ("nests") and 5 roosts of 29 species of cavity-nesting birds in 79 tree cavities and 3 arboreal termitaria. Termitaria were only used by Surucua Trogon (*Trogon surrucura*, $n = 3$ nests in 2 cavities). Eighty percent of nests and roosts of secondary cavity nesters were in cavities created by decay processes and 20% were in cavities created by woodpeckers (Fig. 2.1). No secondary cavity nesters used the four cavities created by trogons. Woodpecker cavities ($n = 33$) occurred almost exclusively (97%) in dead substrates (sections of trees where the sapwood was dead and there were no live branches beyond the cavity), but non-excavated cavities ($n = 46$) occurred in both live (78%) and dead (22%) substrates (Fig. 2.1). Trees with excavated cavities were smaller in DBH than trees with non-excavated cavities (mean±SE $\mathrm{DBH}_{\mathrm{Excavated}} = 53.9 \pm 4.27$ cm, $\mathrm{DBH}_{\mathrm{Non\text{-}excavated}} = 75.2 \pm 4.15$ cm; $t = -3.58$, $P = 0.0006$). Of the 121 nests and roosts I found for secondary cavity-nesting birds, 105 (87%) were in live trees and 85 (70%) were in live substrate (*i.e.* a live branch or the live trunk of a tree).

Of the 73 nest trees I checked, 20 had fruiting bodies of wood-decaying fungi, 19 of which were polypores and could be identified to genus (Fig. 2.2). These included at least six species of *Phellinus* (*Hymenochaetaceae*; in six trees; one tree contained two species) and five other genera of polypores in the family *Polyporaceae* (5 species on 12 trees with 13 cavities; Fig. 2). The seven *Phellinus* occurred in six living trees with non-excavated cavities. Five of these six cavities were in a living section and one was in a dead section of the tree. Polypores in the family *Polyporaceae* occurred in eight living trees and four dead trees. These trees contained eight excavated cavities (all in dead sections of trees) and five non-excavated cavities (two in living sections and three in dead sections of trees). Thus 6 of 11 non-excavated cavities but none of eight excavated cavities were associated with *Phellinus* (Fisher's Exact Test, $p = 0.018$; Fig. 2.2).

There were 82 instances in which a cavity used by a secondary cavity nester was still available and checked the following year; 30 (37%) were reused by the same species, 16 (20%)

were reused by a different bird species, 3 (4%) contained bees or wasps, 2 (2%) contained standing water, and 31 (38%) were unoccupied. Excavators also reused old cavities, including one cavity created by natural decay processes (Fig. 2.1). I found one case of simultaneous cavity-sharing, in which a female Helmeted Woodpecker (*Dryocopus galeatus*) roosted inside the nest cavity where a pair of White-eyed Parakeets were incubating an egg (Cockle in press).

As expected, both mean cavity depth (general linear model: $b = 0.13$, SE = 0.05, $P = 0.013$, $R^2 = 0.21$, $n = 28$ species) and mean cavity entrance diameter (general linear model: $b = 0.013$, SE = 0.0051, $P = 0.017$, $R^2 = 0.19$, $n = 30$ species) increased with increasing mean body mass of species; however, these relationships were not strong (Fig. 2.3). One of the largest species, the Red-breasted Toucan, used cavities as small as 5 cm in diameter, similar to the 6 cm entrance diameter of the cavity used by the smallest species, the House Wren (*Troglodytes aedon*). Most interspecific interactions among birds were among species of similar body mass (Fig. 2.4). On average, pairs of species that sequentially occupied the same cavity differed in body mass by 91.7 ± 14.5 g (mean ± SE, $n = 31$ interspecific pairs), significantly less than expected by chance (randomization test, $P = 0.0025$). However, occasionally pairs of species as different in body mass as the 370 g Vinaceous Parrot and the 43 g Black-crowned Tityra (*Tityra inquisitor*) sequentially occupied the same cavity (Fig. 2.4).

Body mass did not predict the log-transformed variance of cavity entrance diameter (general linear model: $b = 0.000133$, SE = 0.000228, $P = 0.59$, $n = 6$ species) or depth ($b = 0.000564$, SE = 0.000877, $P = 0.56$, $n = 6$ species). Body mass was not a significant predictor of nest predation across 15 species of secondary cavity nesters (logistic regression model: $b = 0.0012$, SE = 0.0021, $P = 0.617$, $n = 39$ nests). Neither cavity entrance diameter nor cavity depth were significant predictors of the probability of nest predation (logistic regression; $w_{\text{Null}} = \Delta\text{AICc} < 2$ and $w < 0.3$ for all models, $\Delta\text{AICc}_{\text{Null}} = 0.12$, $|z| < 1.96$ and $P > 0.05$ for all parameters in all models, $n = 39$ nests) even when I controlled for species differences (mixed model logistic regression with species as a random effect; $\Delta\text{AICc} < 2$ and $w < 0.3$ for all models, $\Delta\text{AICc}_{\text{Null}} = 0.29$, $|z| < 1.96$ and $P > 0.05$ for all parameters in all models, $n = 39$ nests).

DISCUSSION

Cavity formation

Most cavities used by secondary cavity nesters were created by natural decay processes in live trees rather than by excavators in dead trees. Twelve species of secondary cavity nesters used excavated holes at least once, but only a few passerines such as tityras (*Tityra* spp.) used excavated holes predominantly. My finding that natural decay processes produced most nest cavities contrasts strongly with findings from North America where excavators produce up to 99% of the cavities used by secondary cavity nesters (Martin *et al.* 2004, Aitken & Martin 2007, Blanc & Walters 2008, Chapter 5). Gibbs *et al.* (1993) proposed that nest cavities may be a more limited resource in tropical forests than temperate forests because tropical forests have (1) a higher ratio of secondary cavity-nesting species to excavating species, and (2) fewer standing dead trees. In contrast, my results suggest that the species richness of excavators and the abundance of snags may be relatively unimportant in determining cavity availability in the Atlantic forest. Indeed, several studies in the Neotropics suggest that a variety of secondary cavity-nesting birds rely primarily on cavities produced by natural decay processes in living trees (Gerhardt 2004, Brightsmith 2005, Berkunsky & Reboreda 2009). Based on this finding, I hypothesize that populations of secondary cavity nesters in the Atlantic forest are only weakly linked to those of cavity excavators. If so, perturbations that affect populations of excavators are unlikely to have strong effects on populations of secondary cavity nesters. These weak functional links between vertebrate producers and consumers of cavities may explain why other studies in the Neotropics have not found correlations in the abundance or richness of excavators and secondary cavity nesters (Sandoval & Barrantes 2009, Siqueira Pereira *et al.* 2009).

Wood-decaying fungi were associated with both excavated and non-excavated cavities. There were eleven species of wood-decaying fungi fruiting in trees with nest cavities. Wood-decaying fungi may persist in a tree for many years without fruiting, and trees without fruiting bodies likely also had heart rot fungi. The fungi identified may not be the ones responsible for the formation of the cavities, but they are known producers of heart rot. The presence and abundance of the fruiting bodies of any fungal species do not necessarily directly correlate to the biomass and activity of the vegetative mycelia; however, identification of fruiting bodies is considered a reliable method of assessing polypore species abundance in natural communities (Niemelä *et al.* 1995, Urcelay & Robledo 2004, Robledo & Renison 2009). The present study suggests that a wide variety of wood-decaying fungi may perform the wood-softening function required for cavities to form in the Atlantic forest. *Phellinus* was found in several cavity trees in the present study, similar to studies in North America (Kilham 1971, Conner *et al.* 1976, Conner & Locke 1982, Runde & Capen 1987, Hart & Hart 2001, Parsons *et al.* 2003, Losin *et al.* 2006). However, in contrast to these North American studies, *Phellinus* fruiting bodies were not found on trees excavated by woodpeckers in my study. *Phellinus* is an important parasite on living trees in South America (Gilbert *et al*. 2002, Robledo *et al.* 2006). My sample consists of only 19 trees bearing polypore fruiting bodies, but I surmise that *Phellinus* may be important in creating the conditions for non-excavated cavities in live sections of trees in the Atlantic forest because *Phellinus* comprised five of the seven fruiting bodies associated with cavities in living sections of trees. Other genera of fungi may be more important in creating conditions for woodpecker excavations in dead wood.

Although natural decay processes provided most nest-sites for cavity-nesting birds in the Atlantic forest, excavators should not be overlooked as cavity producers. Excavators may play a key role for some species of secondary cavity nesters, or under certain forest conditions. For example, I found Tityras (*Tityra* spp.) mostly in excavated cavities as reported by Skutch (1946). Additionally, excavated cavities occurred in smaller trees than non-excavated cavities, suggesting that where large trees are limited (*e.g.*, anthropogenic landscapes), excavators may be the primary cavity-producing agents.

Reuse of cavities

I found an annual reuse rate of 57% for cavities used by secondary cavity nesters, with most cases of reuse involving the same species that used the cavity the previous year. Since individuals were not marked, I do not know whether these were the same individuals. Similarly, community-wide studies in British Columbia, Canada (Aitken *et al.* 2002), Colorado, USA (Sedgwick 1997) and Mongolia (Bai & Mühlenberg 2008) showed 48%, 53% and 48% reuse of cavities used by secondary cavity nesters, respectively, most often by the same species (possibly the same individuals) that had previously occupied the cavity. In British Columbia, cavities were more likely to be reused if they were large, deep, in trembling aspen (*Populus tremuloides*), and close to forest edges (Aitken *et al.* 2002). In Mongolia, cavities were more likely to be reused if they were in a live substrate (*i.e.*, a live branch or live tree trunk; Bai & Mühlenberg 2008).

Further research may reveal that the frequency of cavity reuse in the Atlantic forest may also vary with cavity and site characteristics; for example, reuse may be higher in cavities of a size appropriate for more species, or in landscapes where anthropogenic activities have reduced cavity supply.

Long-term reuse of cavities by the same species or individuals may be especially prevalent in parrots. Parrots are long-lived and often show high nest-site fidelity (Snyder *et al.* 1987, Waltman & Beissinger 1992, Heinsohn *et al*. 2007, but see Salinas Melgoza *et al*. 2009). In the South American Chaco, Berkunsky and Reboreda (2009) showed that 12 of 19 banded female Blue-fronted Parrots reused their nest cavity from one year to the next; none of the females in their study were found in a different cavity. In my Atlantic forest study, although individuals were not marked, local farmers reported Vinaceous Parrots using the same cavities for 20 years. Similarly, in lowland tropical Amazonia, Brightsmith (2005) speculated that cavities in *Dipteryx micrantha* trees may be useable by macaws for decades or even centuries. Parrots accounted for 39% of my nests, and their nest-site fidelity could partly explain the high levels of intra-specific cavity reuse in my study.

Body size and nest web structure

Interspecific reuse of cavities in the Atlantic forest was structured according to body size. For example, a group of species 65–120 g, especially Ferruginous Pygmy-Owl (*Glaucidium brasilianum*), Planalto Woodcreeper, Maroon-bellied Parakeet and Chestnut-eared Aracari (*Pteroglossus castanotis*) often used the same cavities. Likewise, cavities were frequently reused between the 370 g Vinaceous Parrot and 400 g Red-breasted Toucan. If competition for cavities is intense, changes in the abundance or habitat use of a given bird species would seem most likely to affect the abundance of bird species that have similar body size. In Canada, blocking cavities of the dominant European Starling (*Sturnus vulgaris*) led to increases in the density of Mountain Bluebirds (*Sialia corrucoides*), a similar-sized but subordinate secondary cavity nester (Aitken & Martin 2008). In the farming landscape around Tobuna, globally endangered Vinaceous Parrots rarely fledged chicks; instead, their cavities were usually usurped by toucans or other competitors part way through the breeding season (K. Cockle & J. Segovia obs. pers. and reports from farmers, cited in BirdLife International 2009). Future studies should test the hypothesis that the toucan is a dominant nest-site competitor and predator that prevents Vinaceous Parrots from nesting successfully in cavity-poor anthropogenic habitat. If so, adding cavities might allow the two species to co-exist. Where cavities are limiting (see Chapter 4), I predict negative correlations in species abundance between dominant and subordinate secondary cavity nesters of similar body size, but not between species of very different body size. I predict that the level of competition experienced by a given species will increase with the abundance of birds similar in body size, and decrease with the availability of appropriately-sized cavities.

As expected, larger species used larger cavities as shown by increases in mean cavity diameter and depth with increasing body mass. The same pattern was found by Martin *et al.* (2004) for tree cavity nesting birds in temperate forest in Canada, but not by Mello Beisiegel (2006) for ground-level shelter-using birds and mammals in the Atlantic forest in Brazil. The variance of cavity diameter and depth did not change with body mass, suggesting that large and small species were equally constrained by cavity size. Large species were as likely as small species to suffer nest predation. Indeed, the probability of predation was not influenced by cavity diameter or cavity depth, even when controlling for species, suggesting that cavity dimensions may play only a minor role in protecting a nest from predators. My field assistants and I witnessed only two incidents of nest predation: a Red-breasted Toucan depredated a Black-tailed Tityra (*Tityra cayana*) nest, and a Chestnut-eared Aracari depredated a Green-barred Woodpecker (*Colaptes melanochloros*) nest. Other important nest predators likely include possums and snakes, which may be able to enter very narrow cavities. Large birds may exclude smaller birds from the largest cavities.

CONCLUSION

In this chapter, I showed evidence that secondary cavity-nesting birds in the Atlantic forest use both woodpecker and non-excavated cavities, but rely mostly on cavities produced by natural decay processes in live sections of trees. Although the Atlantic forest nest web may be robust to changes in populations of excavators, it appears vulnerable to disturbances that affect the rates of production and loss of cavities by natural decay processes. Future research should determine how much time is required for non-excavated cavities to form in tropical trees and whether this process can be accelerated by management techniques. I showed that cavities are often reused among cavity-nesting birds, primarily by species similar in body size, suggesting that high quality cavities may be limiting; however, it is not known what cavity characteristics are important for nesting birds in the Atlantic forest, or what tree species or characteristics are associated with cavity formation. In Chapter 3 I will determine the characteristics of cavities suitable for cavity-nesting birds, and the characteristics of the trees that develop these cavities through excavation and natural decay processes.

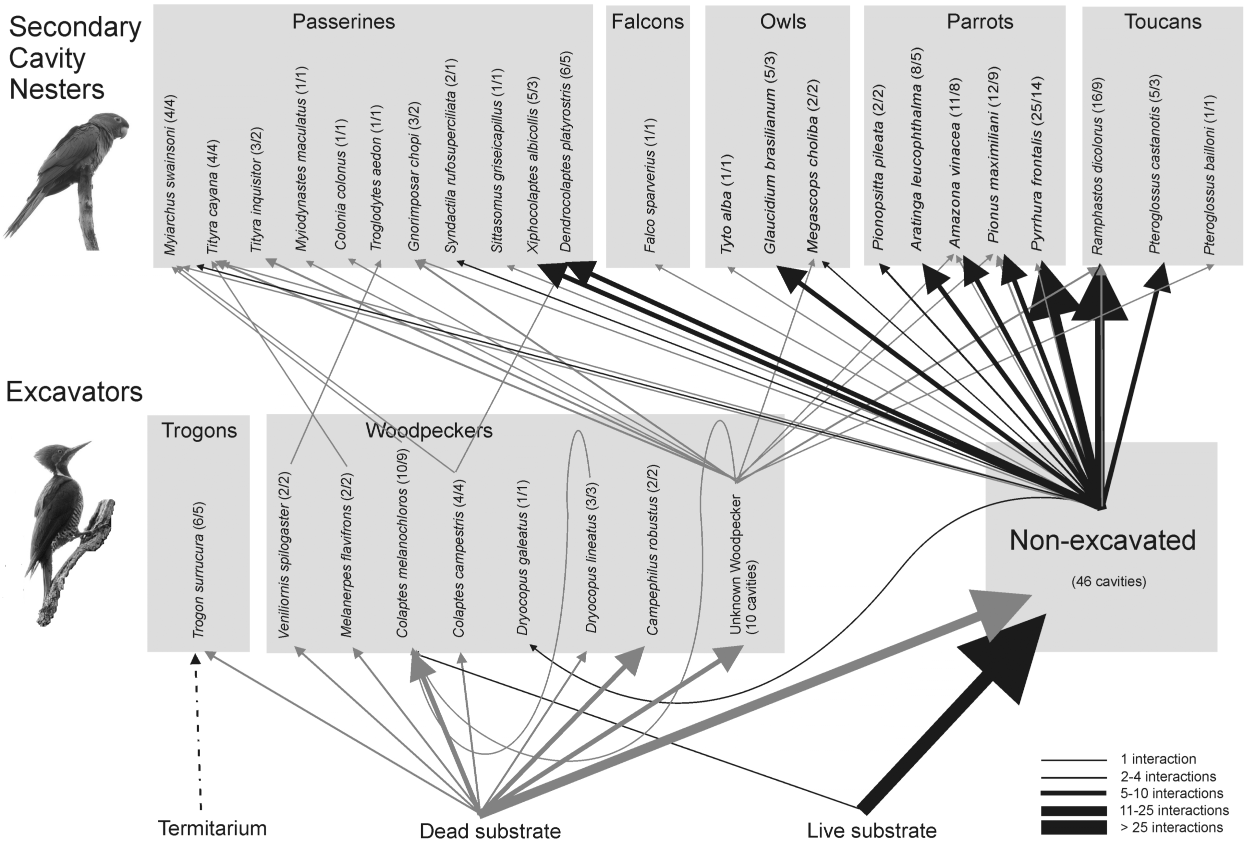

Figure 2.1. Nest web for cavity-nesting bird community of the Atlantic forest. This nest web shows connections between substrates (broken line- termitaria; solid light grey lines- dead trees or dead sections of trees; or solid black lines- live sections of trees), cavity producers (excavators or natural decay processes) and cavity consumers (secondary cavity nesters). Arrows point in the direction of resource flow (from producers to consumers of cavities). Line thickness indicates the number of times a particular interaction occurred. Numbers in parentheses denote sample size of nests/cavities.

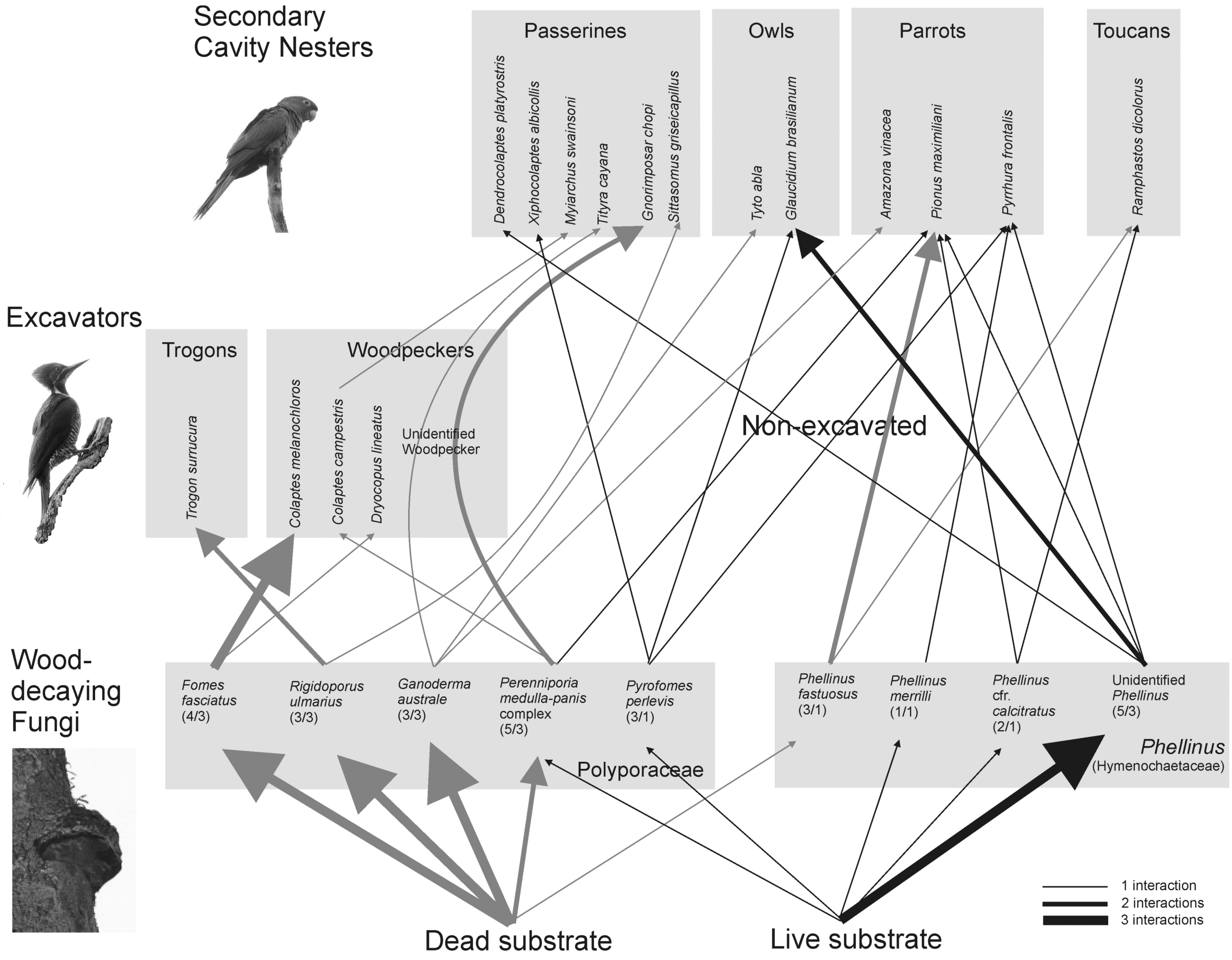

Figure 2.2. Nest web for cavity-nesting birds and wood-decaying fungi in the Atlantic forest of Argentina. This nest web shows connections between wood substrates (light grey- dead tree or dead section of tree; or black- live section of tree), wood-decaying fungi, excavators, and cavity consumers (secondary cavity nesters). Arrows point in the direction of resource flow (from producers to consumers of cavities). Line thickness indicates the number of times a particular interaction occurred. Numbers in parentheses denote sample size of nests and cavities.

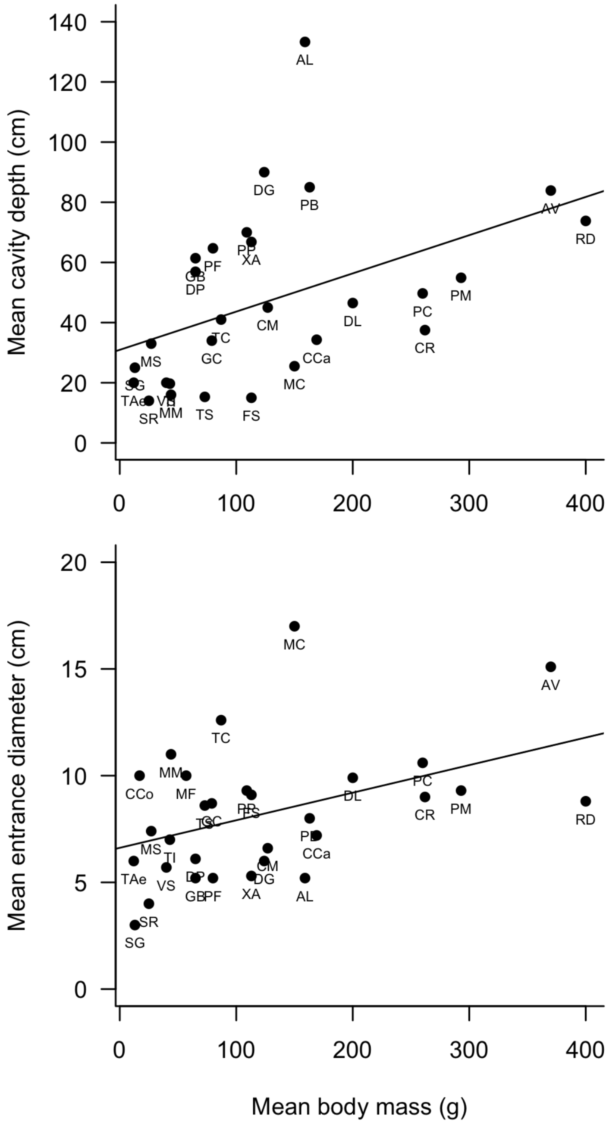

Figure 2.3. Mean cavity depth (general linear model: $b = 0.13$, SE = 0.05, $P = 0.013$, $R^2 = 0.21$) and mean cavity entrance diameter (general linear model: $b = 0.013$, SE = 0.0051, $P = 0.017$, $R^2 = 0.19$) as a function of mean adult female body mass for 28 and 30 species of cavity-nesting birds, respectively, in the Atlantic forest of Argentina. Mean cavity sizes were calculated from 1–25 nests/species. Species are coded by first letter of the genus name and first letter of the species name except House Wren (*Troglodytes aedon* – TAe) and Campo Flicker (*Colaptes campestris* – CCa). Full species names and sample sizes are given in Table 1.1.

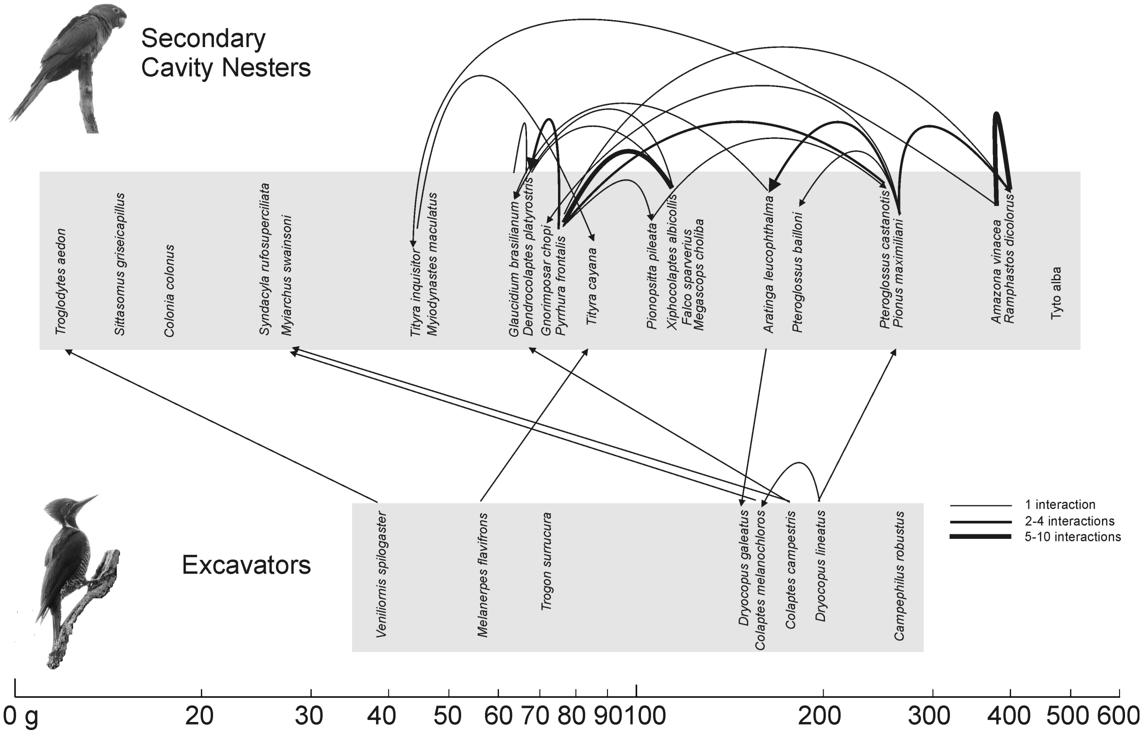

Figure 2.4. Nest web and body mass for cavity-nesting birds in the Atlantic forest of Argentina. This nest web shows connections between individual birds using the same cavities. Arrows point from the first to the second user of the cavity. Line thickness indicates the number of times a particular interaction occurred. Birds are arranged according to their mean body mass (logarithmic scale along bottom of figure) from the smallest (House Wren *Troglodytes aedon*) on the left to the largest (Barn Owl *Tyto alba*) on the right.

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CHAPTER 3. SELECTION OF NEST TREES BY CAVITY-NESTING BIRDS IN THE ATLANTIC FOREST[1]

Logging and clearing for agriculture remove some of the largest trees in tropical forests, possibly the same trees required by cavity-nesting birds (*e.g.*, Brightsmith 2005). However, managers might conserve the diverse assemblage of cavity-nesting birds if they could choose logging and agricultural methods that retain a sufficient supply of trees currently suitable for nesting and trees that will become suitable in the future. Several studies in the tropics and subtropics have shown that even agricultural areas can provide important habitat for native forest wildlife (Terborgh & Weske 1969, Manning *et al.* 2006, Ranganathan *et al.* 2008), including breeding habitat for cavity-nesting birds (Seixas & Mourão 2002, Cockle *et al.* 2005). To conserve cavity-nesting birds, such landscapes must support foraging habitat and suitable cavities over the long term. However, little is known about which trees provide suitable cavities.

When selecting a nest tree or cavity, birds need to balance several requirements and risks. Minimally, a cavity must be sufficiently large to contain a brood of nearly-fledged nestlings (Martin *et al.* 2004). Risks to nests of cavity-nesting birds include flooding (Wesołowski *et al.* 2002), usurpation (Deng & Gao 2005), predation (Wesołowski 2002), and blow-down (Vaughan *et al.* 2003). If nest-site selection is adaptive, birds should choose nest sites to balance space for nestlings, ease of acquisition, thermal properties, risk of flooding or tree collapse, and risk from terrestrial, scansorial, and volant predators and competitors. Birds might choose cavities high above the ground to avoid terrestrial predators such as snakes and rodents (Nilsson 1984, Fisher & Wiebe 2006), and in stands where the crowns of trees are isolated from other trees to avoid scansorial predators such as possums, monkeys and arboreal snakes (Snow 1976, Brightsmith 2005). Birds might choose cavities with good visibility, to observe the approach of predators and competitors in time to defend or leave their cavity (White *et al.* 2006). Entrance orientation may affect exposure to weather and thus risk of flooding (Wesołowski *et al.* 2002, Radford & Du Plessis 2003, White *et al.* 2006). Cavities pointing north toward the equator may be warmer, and those in live wood may be better insulated (Wiebe 2001). Those in dead branches or dead trees may be more likely to collapse during the breeding season (Vaughan *et al.* 2003) and more susceptible to predation because their walls can be torn open more easily (Wesołowski 2002, Paclík *et al.* 2009).

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[1] A version of this chapter has been accepted for publication. Cockle, K., K. Martin and K. Wiebe. 2010. Selection of nest trees by cavity-nesting birds in the Neotropical Atlantic forest. Biotropica.

Management strategies for cavity-nesting fauna require information about which trees are likely to contain suitable cavities. In some regions, characteristics associated with the formation of cavities suitable for fauna included the size, age, decay class, species, growth rate, and crown class of trees (Carey 1983, Lindenmayer *et al*. 1993, Whitford 2002, Whitford & Williams 2002, Wormington *et al.* 2003, Martin *et al.* 2004, Bai *et al.* 2005, Eyre 2005, Holloway *et al.* 2007, Koch *et al.* 2008b, Fox *et al.* 2009). In the Neotropics, cavities made by the Hoffmann's Woodpecker (*Melanerpes hoffmannii*) were more likely to occur in larger diameter snags with less canopy cover (Sandoval & Barrantes 2006), and cavities made by the Magellanic Woodpecker (*Campephilus magellanicus*) were more likely to occur in trees with crown die-back (Ojeda *et al*. 2007). However, secondary cavity nesters in the Atlantic forest use mostly non-excavated cavities in live trees (Chapter 2); to my knowledge, no studies have examined the characteristics associated with the formation of non-excavated cavities anywhere in the Neotropics.

The present study had three objectives. The first was to determine the characteristics of Atlantic forest trees associated with their selection for nesting by excavators. The second was to determine the characteristics of trees and cavities associated with their selection for nesting by secondary cavity nesters. The third was to determine the characteristics of trees associated with the formation of suitable nest cavities by natural decay processes (non-excavated cavities).

METHODS

Field methods

I studied cavity-nesting birds in the Sierra Central of Misiones, Argentina, outside of the experimental plots (Chapter 1). Cavities within experimental plots are not included in the analyses presented in this chapter. I used a stratified case-control design to compare nest trees and non-nest trees. The case-control design allowed me to ensure that my sample contained enough nest trees (Keating & Cherry 2004). Over three breeding seasons from 2006 to 2008 I found and monitored as many active cavity-nests as possible (Chapter 1).

I measured (1) trees with cavities used by excavators; (2) trees with cavities used by secondary cavity nesters; (3) trees with cavities not known to be used during the study (birds never seen entering or leaving the cavity); and (4) trees without cavities. For each tree used by an excavator (1), I selected a tree without a cavity (4) at a random distance (10–50 m), in a random direction, in the same habitat type (primary forest, logged forest, or open farmland). For each cavity used by a secondary cavity nester (2), I found the nearest unused cavity (3) that was in a different tree and in the same habitat type. To determine the tree characteristics associated with the formation of suitable cavities through decay in live trees, I compared each live tree that contained a non-excavated cavity used by a secondary cavity nester (2) with two live trees without cavities (4) at random distances (6–30 m), in random directions, in the same habitat type. For each tree, I recorded the following variables: tree species, height of tree, diameter at breast height (DBH), decay class (1 = live healthy tree, 2 = live unhealthy tree, 3 = recently dead tree with branches intact, 4 = long-dead tree with only stubs of large branches or no branches remaining), crown class (dominant, co-dominant, or intermediate/understory) and proportion of crown touching another tree. For each cavity, I measured cavity height, branch order (main stem or branch), diameter of branch at cavity height, distance to next branch, distance to any vegetation, cavity formation process (excavated or decay/damage), number of entrances to cavity, compass direction of lowest cavity entrance (degrees, measured from center of tree), vertical and horizontal diameter of each entrance to cavity, vertical and horizontal depth of cavity, angle of each cavity entrance (upward, downward, or side), and distance from the lowest cavity entrance to a major visual obstruction (*e.g.*, foliage) in each of four 45° sectors that formed a 180° angle in front of the cavity entrance.

I measured tree height (m) using a Bushnell Yardage Pro Sport 450 laser rangefinder. I used a 10 m ladder or single-rope climbing to obtain measurements of cavities. I measured DBH and diameter of the branch at cavity height using a diameter tape, and I estimated the proportion of the crown touching other trees. As in Chapter 2, cavity depth was considered the maximum depth of the cavity, whether this was horizontal or vertical, and entrance diameter was the minimum distance across the largest entrance to the cavity. Cavity height was measured using a 50 m measuring tape from the forest floor to the lower lip of the cavity's lowest entrance. Compass direction of the cavity entrance was measured using a compass. I measured the distance to visual obstructions from the lowest cavity entrance using the laser rangefinder and compass, then took the mean distance to obstructions over the four 45° sectors in front of the cavity as a measure of visibility from the cavity.

Where I could not climb to the cavities but could access them with the pole mounted camera, (cavities 8–15 m high in dead trees) I measured the diameter of the branch and the cavity entrances using a Criterion RD 1000 electronic dendrometer and cavity height using the telescoping pole. In these cases, I estimated the horizontal and vertical depth of the cavity using the camera and a calibration on the ground, and I measured or estimated the distance from the cavity to visual obstructions by standing on the ladder below the cavity, climbing to a similar height on a safe tree, or standing on the ground.

Analyses

I determined the characteristics of nest trees selected by excavators using univariate analyses, and trees and cavities selected by secondary cavity nesters using both univariate analyses and an information theoretic approach. All analyses were performed separately for excavators and secondary cavity nesters using R version 2.9.2 (R Development Core Team 2009), except one univariate analysis (paired Hotelling test for compass direction of the cavity) that was calculated by hand following Zar (1999). Individual cavities used by both excavators and secondary cavity nesters were included in both analyses, but within a given analysis, each cavity was included only once, even if it was used multiple times.

First, for univariate analyses, I constructed simple correlation matrices to determine which independent variables were correlated with one another. I compared variables for used versus unused trees for excavators and used versus unused cavities for secondary cavity nesters using McNemar's Chi-square tests for frequency data, paired *t*-tests for normally distributed continuous variables, paired Wilcoxon signed rank tests for non-normally distributed continuous variables, and the paired Hotelling test for compass direction of the cavity.

Second, I compared conditional logistic regression models within two sets to determine which variables increased the odds that (1) a cavity-bearing tree would be used by a secondary cavity nester; and (2) a non-excavated (decay) cavity would occur in a live tree. Case-control studies should be analyzed using conditional logistic regression because the ratio of controls to cases in the sample is not the same as the ratio of controls to cases in the population (Keating & Cherry 2004). I did not compare models for excavators because models including decay stage failed to converge, presumably because of my small sample size and the nearly complete separation of the data by this highly influential class variable (14 excavator nest trees but only 2 unused trees were dead, and no matched pairs included a dead nest tree and a live unused tree;

McNemar's test, $P = 0.001$). I used the clogit command in the survival package in R (Therneau & Lumley 2009) to build two sets of competing models that represented different biological hypotheses to be compared within each set using an information theoretic approach (Table 3.1; Burnham & Anderson 2002). All candidate models were matched case-control conditional logistic regression models in which cases were nest trees and controls were (1) trees with unused cavities (for nest site selection by secondary cavity nesters; 1:1 matching) or (2) non-cavity trees (for occurrence of non-excavated cavities in live trees; 1:2 matching). Clogit uses Cox proportional hazard regression to estimate a logistic regression model by maximizing the exact conditional maximum likelihood (R Development Core Team 2009). The estimated parameter for each predictor variable is the natural logarithm of its associated odds ratio. Each conditional logistic regression model included a different set of continuous and discrete explanatory variables. I standardized cavity entrance diameter and depth to each have a mean of 0 so that their interaction term could be interpreted.

I used the ROCR package (Sing *et al.* 2005) to calculate the area under the curve of the receiver operating characteristic (AUC), a measure of binary classifier performance (proportion of true positives and false positives) independent of cutoff values. An AUC value of 1 indicates perfect classifier performance (all cases correctly classified); values above 0.8 indicate good classifier performance, and a value of 0.5 indicates a classifier performance similar to random.

For each model I calculated Akaike's Information Criterion corrected for small sample sizes (AICc) and Akaike weight (*w*; Burnham & Anderson 2002). To evaluate the strength of support for each model, I compared the models within a set based on ΔAICc (difference between the AICc of a given model and the lowest AICc model in the set) and Akaike weight (a measure of the support for a given model relative to the other models in the set; Burnham & Anderson 2002). I considered a model to be well supported by the data if it had a $\Delta\text{AICc} < 2$ and Akaike weight > 0.8. I used a z-test for each parameter in the top model to determine whether its 95% confidence interval included zero (R Development Core Team 2009). Variables in the top models were considered to be important in nest-site selection or cavity occurrence if (1) the 95% confidence intervals on their parameters did not include zero, and (2) the 95% confidence intervals on their odds ratios did not include one.

RESULTS

I documented 120 nesting attempts of 7 species of excavators and 22 species of secondary cavity nesters in 78 cavities (Table 3.2).

Excavators

Excavators made nests in live or dead trees that ranged 16–94 cm DBH. Univariate analyses suggested that decay class and the percent of the crown touching other trees differed between used and unused trees (Table 3.3). Used trees were more likely to be dead, and had less of their crown touching other trees. However, decay class was negatively correlated with DBH ($r = -0.32$), tree height ($r = -0.41$), and the percent of the crown touching other trees ($r = -0.58$). Dead trees had often lost their tops and bark, so they were shorter, had smaller diameters, and were more isolated from other trees.

Secondary Cavity Nesters

Secondary cavity nesters selected nesting cavities 2.5–27 m (min-max range) high in live or dead trees 21–163 cm DBH. Their cavities were 12–346 cm deep with entrance diameters 3–49 cm. Univariate analyses suggested that the following variables differed between used and unused cavities: cavity depth (used cavities were 38 cm deeper), cavity height (used cavities were 5.7 m higher), percent of crown touching other trees (used cavities: 21%, unused cavities: 53%), tree DBH (trees with used cavities were 15 cm larger in DBH), tree height (trees with used cavities were 4 m taller) and visibility (used cavities had more than three times the visibility; Table 3.3). Cavity height was positively correlated with both DBH ($r = 0.47$) and tree height ($r = 0.70$).

The model that best explained selection of nest sites by secondary cavity nesters was Model 5 (cavity depth, entrance diameter, and height on tree; $w_5 = 0.84$), with limited support for Model 7 (cavity depth, entrance diameter, visibility, and percentage of crown touching other trees; $\Delta AICc < 4$, $w_7 = 0.16$; Table 3.1). A cavity was 1.1 times as likely to be used by a secondary cavity nester if it was 1 cm deeper (odds ratio = 1.11, 95% confidence interval for odds ratio = 1.02–1.21) and 1.6 times as likely to be used if it was 1 m higher on the tree (odds ratio = 1.63, 95% confidence interval for odds ratio = 1.13–2.35; Table 3.4).

Formation of non-excavated cavities

Thirty-six of 38 (95%) non-excavated nest cavities were in live trees. Twenty-two (61%) of these were in healthy trees and 14 (39%) in unhealthy trees. Thirty-two (80%) were in a living section of the tree. They occurred in the trunk and in 1st, 2nd and 3rd order branches 21–83 cm in diameter at the height of the cavity. The occurrence of non-excavated cavities was best explained by Model 5 (tree DBH, tree height, decay class, tree species, and crown class; $w_5 = 0.89$; Table 3.1). Based on the 95% confidence intervals on odds ratios and parameter estimates, cavities were more likely in grapia trees (*Apuleia leiocarpa*), trees with larger DBH, and trees in the lower crown classes (not dominant); however, the confidence intervals on the odds ratios of the categorical explanatory variables were large (Table 3.4). Although 11 nest cavities (31%) were in grapias, these made up only three (4%) of the non-cavity trees measured. The mean DBH of live trees bearing used decay cavities was 77 cm, with 86% of these cavities occurring in trees >50 cm DBH (range: 30–163 cm DBH).

DISCUSSION

Excavators selected dead and unhealthy trees to make their nest holes, similar to excavators in temperate (Li & Martin 1991, Martin *et al.* 2004, Remm *et al.* 2006, Mahon *et al.* 2007) and tropical forest (Sandoval & Barrantes 2006). As in a study of the Magellanic Woodpecker in temperate Patagonian forest (Ojeda *et al.* 2007), tree DBH was a poor predictor of tree use by excavators in my study.

Secondary cavity nesters selected cavities that were deeper and higher, were in more isolated trees, and had better visibility than the unused cavities, perhaps reducing their risk of predation. Although cavity height was positively correlated with both DBH and tree height, cavity height seems more likely to be the characteristic that birds are selecting directly. Similarly, deeper cavities were selected and reused more often by a wide variety of cavity nesters in temperate and subtropical forests (Gibbons *et al.* 2002, Aitken & Martin 2004, Berkunsky & Reboreda 2008, Koch *et al.* 2008a, Cockle & Bodrati 2009, Politi *et al.* 2009). Higher cavities were also selected preferentially by secondary cavity nesters in subtropical forest in the Andes (Politi *et al.* 2009) and Australia (Cameron 2006), and temperate forest in Europe (Wesołowski & Rowiński 2004) but not in Canada (Aitken & Martin 2004). Several studies have shown that nest success is greater in cavities higher above the ground, with larger internal volume (Nilsson 1984, Li & Martin 1991, Wiebe & Swift 2001, Mahon & Martin 2006, Sanz 2008). I did not find an effect of cavity depth on predation rate (Chapter 2), but that might have been because birds simply avoided using cavities that were too shallow. In Puerto Rico, snakes (*Epicrates inornatus*) preferentially used trees with crowns that touched neighbouring trees, and in Jamaica, Black-billed Parrots (*Amazona agilis*) suffered higher nest predation at the chick stage when nesting in such trees (Koenig *et al.* 2007). As observed in Canada (Aitken & Martin 2007), secondary cavity nesters in the Atlantic forest used cavities excavated by woodpeckers in proportion to their availability. In contrast, birds in Europe (Remm *et al.* 2006, Wesołowski 2007) and Asia (Bai *et al.* 2005) avoided cavities excavated by woodpeckers.

The density of standing dead trees in my Atlantic forest study area is 57 snags/ha (Ríos 2006), higher than the densities reported by Gibbs *et al.* (1993) for tropical and subtropical forests (3.5–21 snags/ha) and even temperate forests (23–49 snags/ha). These dead trees were selected preferentially by excavators, but not by secondary cavity nesters. The critical resource for secondary cavity nesters was large live trees with non-excavated (decay) cavities. In Canadian temperate forest, Martin *et al.* (2004) found most nests of secondary cavity nesters in live trees, 10% of them healthy and 45% unhealthy with visible signs of decay. However, in the Atlantic forest many of my nest-trees had no visible signs of decay other than the presence of a cavity. Indeed, live branches were the substrate for more than 2/3 of the nests of large-bodied secondary cavity nesters, the group most likely to be nest-site limited. Thus, although snags were important for excavators, I caution against focusing on snags for the conservation of secondary cavity nesters in humid tropical and subtropical forests.

Four caveats should be considered when interpreting my results. First, I pooled data from several years and several habitats: other studies have shown variation in nest-site selection over time and across habitats (Rudolph & Conner 1991, Cornelius 2008, Koch *et al.* 2008a, Norris & Martin 2008). Unfortunately, my small sample size meant that I could not model nest-tree selection by habitat. Secondly, potentially important variables were not measured in this study. Cavity-nesting birds select their nest trees based not only on cavity- and tree-level variables, but also on plot-level variables and larger scale context, such as surrounding vegetation and distance to edge (Aitken & Martin 2004, Mahon *et al.* 2007, Cornelius 2008, Koch *et al.* 2008a, Politi *et al.* 2009). Thirdly, used cavities may vary widely in quality. Future studies should examine which cavity characteristics affect nesting success. Finally, my main results reflect the breadth of many cavity-nesting species (about half the species present) – a breadth that is necessary to accommodate the needs of cavity-nesting communities. However, different species selected cavities and trees with different characteristics, as reported in other studies (Nilsson 1984, Lindenmayer *et al.* 1990, Aitken & Martin 2004). Some nest-tree characteristics might be very important to one or two species, but would not have been identified in my community-level study. Species-specific studies of nest-site selection are a research priority, especially for endangered species like the Vinaceous Parrot (*Amazona vinacea*; Cockle *et al.* 2007).

CONCLUSION

In this chapter I showed that secondary cavity-nesting birds in the Atlantic forest selected cavities based on their height and depth, using cavities at least 2.5 m high and 12 cm deep. These cavities form mostly through natural decay processes in large live trees. A management priority should be to conserve large live trees for secondary cavity nesters and dead and unhealthy trees for excavators where nesting substrates are limiting. However, little is known about the conditions under which nesting substrates limit populations of cavity-nesting birds in tropical forests. In Chapter 4, I will determine whether cavity supply limits nesting density of secondary cavity-nesting birds in primary and logged Atlantic forest.

Table 3.1. Ranking of conditional logistic regression models to compare (A) cavities used by secondary cavity nesters to cavities not used by any birds; and (B) live trees with non-excavated (decay) cavities (used by secondary cavity nesters) to live trees without any cavities. Within each set, models are arranged according to fit, from highest to lowest weighted, with top models in bold. k = number of parameters, AICc = Akaike's Information Criterion corrected for small sample size, ΔAICc = difference in AICc between this model and the minimum AICc model, *w* = Akaike weight, AUC = Area under the curve of the receiver operating characteristic. Sample size: (A) 45 used cavities (cases) and 45 unused cavities (controls); (B) 36 cavity trees (cases) and 72 non-cavity trees (controls).

Model	Variables included	k	AICc	ΔAICc	*w*	AUC
A. Selection of cavities by secondary cavity nesters						
5	**Depth, entrance diameter, cavity height**	**3**	**21.5**	**0.0**	**0.84**	**0.98**
7	Depth, entrance diameter, visibility, percentage of crown touching other trees	4	24.8	3.3	0.16	0.98
2	Tree height, decay stage (live healthy, live unhealthy, or dead)[a], DBH, percentage of crown touching other trees	5	36.3	14.8	0.00	0.96
6	Depth, entrance diameter, visibility	3	36.4	14.9	0.00	0.93
4	Branch diameter, entrance diameter, depth, any upward entrance	4	37.4	15.9	0.00	0.95
1	Branch diameter, depth, entrance diameter, depth x entrance diameter	4	37.6	16.1	0.00	0.95
3	Depth, entrance diameter, tree height, DBH	4	39.1	17.6	0.00	0.94

Model	Variables included	k	AICc	ΔAICc	*w*	AUC
B. Occurrence of non-excavated (decay) cavities in live trees						
5	**DBH, height, decay class (healthy vs unhealthy), species (grapia *Apuleia leiocarpa* vs all other species), crown class (dominant, co-dominant, or intermediate/understory)**	**6**	**38.8**	**0.0**	**0.89**	**0.96**
3	DBH, species (grapia vs all other species)	2	44.9	6.1	0.04	0.91
2	DBH, decay class (healthy vs unhealthy)	2	45.7	6.8	0.03	0.91
1	DBH, height	2	46.5	7.7	0.02	0.90
4	DBH, crown class (dominant, co-dominant, or intermediate/understory)	3	46.7	7.9	0.02	0.92

[a] Decay classes 3 and 4 combined. [b] Local farmers suggested that grapias contained many cavities used by birds. I was restricted by my small sample size to examine only grapia vs all other trees.

Table 3.2. Characteristics of trees and cavities used for nesting by 29 bird species in the Atlantic forest, Misiones province, Argentina. Means are reported for (1) excavators; (2) small secondary cavity nesters (13–60 g); and (3) large secondary cavity nesters (61–500 g), counting each cavity only once in each of these three groups, even if it was used by more than one species of bird within the group.

Species	*N* Nests	*N* Cavities	Habitat [a]	DBH (cm)[b]	Decay class[c]	Percent crown touching other trees[b]	Percent in live substrate	Depth (cm)[b]	Entrance diameter (cm)[b]	Cavity height (m)[b]
1. Excavators	**25**	**23**		**57 ± 7**	**4**	**12 ± 5**	**4**	**35 ± 4**	**8 ± 0.4**	**10 ± 1**
Surucua Trogon (*Trogon surrucura*)	6	5	PF, LF, Cl	93 ± 18	1	35 ± 9	0	15 ± 1	9 ± 0.6	14± 2
White-spotted Woodpecker (*Veniliornis spilogaster*)	2	2	PF, LF	43 ± 6	2,3	1 ± 1	0	20	6 ± 0.3	14 ± 5
Yellow-fronted Woodpecker (*Melanerpes flavifrons*)	1	1	PF	57	3	20	0		10	21
Green-barred Woodpecker (*Colaptes melanochloros*)	8	7	PF, LF, Cl	43 ± 10	4	21 ± 13	14	46 ± 10	7 ± 0.5	7 ± 1
Campo Flicker (*Colaptes campestris*)	4	4	Cl	30 ± 7	4	0 ± 0	0	34 ± 7	7 ± 0.2	2 ± 0.7
Lineated Woodpecker (*Dryocopus lineatus*)	2	2	PF	77 ± 17	2,4	20 ± 20	0	47 ± 17	10 ± 3.2	10 ± 0.7
Robust Woodpecker (*Campephilus robustus*)	2	2	PF, Cl	58 ± 18	4	0 ± 0	0	38 ± 4	9 ± 0.7	15 ± 8
2. Small secondary cavity nesters	**13**	**11**		**52 ± 6**	**2**	**20 ± 9**	**18**	**25 ± 3**	**7 ± 0.9**	**10 ± 2**
Buff-browed Foliage-gleaner (*Syndactyla rufosuperciliata*)	2	1	LF	70	1	40	100	14	4	16
Olivaceous Woodcreeper (*Sittasomus griseicapillus*)	1	1	LF	62	2	80	0	25	3	16

Species	*N* Nests	*N* Cavi-ties	Habitat[a]	DBH (cm)[b]	Decay class[c]	Percent crown touching other trees[b]	Percent in live substrate	Depth (cm)[b]	Entrance diameter (cm)[b]	Cavity height (m)[b]
Long-tailed Tyrant (*Colonia colonus*)	1	1	PF edge	65	2	0	0		10	20
Streaked Flycatcher (*Myiodynastes maculatus*)	1	1	LF	55	2	0	0	16	11	12
Swainson's Flycatcher (*Myiarchus swainsoni*)	4	4	Cl	48 ± 14	2	25 ± 17	25	33 ± 3	7 ± 1.1	4 ± 2
Black-crowned Tityra (*Tityra inquisitor*)	3	2	Cl	47 ± 17	3	0 ± 0	0	24 ± 12	8 ± 3.0	9 ± 1
House Wren (*Troglodytes aedon*)	1	1	Cl	36	3	0	0	20	6	9
3. Large secondary cavity nesters	**82**	**50**		**76 ± 4**	**1**	**27 ± 4**	**68**	**68 ± 8**	**10 ± 1**	**13 ± 1**
American Kestrel (*Falco sparverius*)	1	1	Cl	64	4	0.0	0	15	9	10
White-eyed Parakeet (*Aratinga leucophthalma*)	5	5	PF	84 ± 13	1	29 ± 11	100	118 ± 58	5 ± 0.2	15 ± 2
Maroon-bellied Parakeet (*Pyrrhura frontalis*)	21	14	PF, LF, Cl	77 ± 11	1	44 ± 9	93	61 ± 7	6 ± 0.9	12 ± 2
Red-capped Parrot (*Pionopsitta pileata*)	2	2	PF, LF	68 ± 18	1	28 ± 23	100	70 ± 19	9 ± 1.8	18 ± 2
Scaly-headed Parrot (*Pionus maximiliani*)	12	9	PF, LF, Cl	67 ± 11	2	26 ± 6	56	57 ± 7	9 ± 1.0	14 ± 2
Vinaceous Parrot (*Amazona vinacea*)	10	8	LF, Cl	79 ± 7	2	22 ± 9	63	84 ± 31	16 ± 1.9	16 ± 2
Barn Owl (*Tyto alba*)	1	1	Cl	104	2	10	0	110	49	8
Tropical Screech-Owl (*Megascops choliba*)	2	2	LF, Cl	74 ± 30	1,4	0±0	50	26 ± 5	17 ± 7.0	12 ± 2
Ferruginous Pygmy-Owl (*Glaucidium brasilianum*)	2	1	PF	60	1	0	100	32	5	9
Red-breasted Toucan (*Ramphastos dicolorus*)	11	7	PF, LF, Cl	61 ± 7	3	29 ± 5	71	91 ± 30	9 ± 1.5	13 ± 2
Chestnut-eared Aracari (*Pteroglossus castanotis*)	4	3	PF, LF, Cl	100 ± 33	1	17 ± 9	100	50 ± 1	9 ± 2.9	19 ± 4

Species	*N* Nests	*N* Cavi-ties	Habitat [a]	DBH (cm)[b]	Decay class[c]	Percent crown touching other trees[b]	Percent in live substrate	Depth (cm)[b]	Entrance diameter (cm)[b]	Cavity height (m)[b]
White-throated Woodcreeper (*Xiphocolaptes albicollis*)	3	2	PF, LF	49 ± 19	1,2	55 ± 15	100	75 ± 29	7 ± 1.6	11 ± 6
Planalto Woodcreeper (*Dendrocolaptes platyrostris*)	3	3	PF, LF, Cl	48 ± 16	2	33 ± 20	67	61 ± 15	6 ± 0.7	8 ± 4
Black-tailed Tityra (*Tityra cayana*)	4	4	PF, Cl	78 ± 10	3	8 ± 5	0	41 ± 4	13 ± 2.5	17 ± 2
Chopi Blackbird (*Gnorimopsar chopi*)	1	1	Cl	83	2	0	0	21	9	10

[a] Habitat where nest was found: PF = Primary Forest, LF = Logged Forest, Cl = cleared area, pasture, annual crop. [b] Mean ± standard error. [c] Mode.

Table 3.3. Univariate analyses for variables compared between (A) trees used and not used by excavators (n = 22 matched pairs); and (B) cavities used and not used by secondary cavity nesters (n = 45 matched pairs). Significant variables are shown in bold. For variables that differed significantly between used and unused trees, the characteristics selected by birds are shown in square parentheses.

Variable	Test	Test Statistic	P
A. Excavators			
Decay class (live healthy, live unhealthy, or dead) [dead]	**McNemar's**	$\chi^2 = 16$	**0.001**
Percent crown touching other trees [less]	**Paired *t*-test**	$t = 2.98$	**0.007**
Diameter at breast height (DBH)	Paired *t*-test	$t = -1.34$	0.20
Tree height	Paired *t*-test	$t = 1.11$	0.28
B. Secondary cavity nesters			
Depth [deeper]	**Paired Wilcoxon**	**V = 71**	**<0.001**
Cavity Height [higher]	**Paired *t*-test**	$t = -6.20$	**<0.001**
Percent crown touching other trees [less]	**Paired *t*-test**	$t = 5.76$	**<0.001**
DBH [larger]	**Paired *t*-test**	$t = -3.54$	**<0.001**
Tree height [taller]	**Paired *t*-test**	$t = -2.99$	**0.005**
Visibility [more visibility]	**Paired Wilcoxon**	**V = 318.5**	**0.025**
Substrate	McNemar's	$\chi^2 = 0.94$	0.33
Branch order (trunk or branch)	McNemar's	$\chi^2 = 0.76$	0.38
Any upward entrance	McNemar's	$\chi^2 = 0.70$	0.40
Number of entrances	Paired Wilcoxon	V = 89	0.55
Branch diameter	Paired Wilcoxon	V = 569	0.57
Compass direction of entrance (0–360°)	Paired Hotelling	$F = 0.395$	>0.25
Decay class (live healthy, live unhealthy, or dead)	McNemar's	$\chi^2 = 1.07$	0.78
Branch distance	Paired Wilcoxon	V = 502	0.94
Cavity formation process (excavated or non-excavated)	McNemar's	$\chi^2 = 0$	1
Entrance diameter	Paired Wilcoxon	V = 496	1
Tree species (grapia *Apuleia leiocarpa*, Paraná pine *Araucaria angustifolia*, or other)	7 nest trees in grapia, 2 in Paraná pine, no random cavities in either of these tree species		

Table 3.4. Parameter estimates (natural logarithms of odds ratios) and odds ratios for top conditional logistic regression models to compare (A) cavities used by secondary cavity nesters to cavities not used by any birds; and (B) live trees with non-excavated (decay) cavities (used by secondary cavity nesters) to live trees without any cavities, in the Atlantic forest, Argentina. z = parameter estimate/SE. Parameters where $|z| > 1.96$ have 95% confidence intervals that do not include 0 (in bold). An odds ratio of 1.63 for cavity height indicates that if a cavity is 1 m higher than another, it is 1.63 times as likely to be used by a secondary cavity-nesting bird, given all other variables are held constant.

Parameter	Estimate	SE	*z*	Odds ratio (95%CI)
A. Selection of cavities by secondary cavity nesters				
Cavity height (m)	**0.489**	**0.186**	**2.63**	**1.63 (1.13–2.35)**
Cavity depth (cm)	**0.106**	**0.0442**	**2.39**	**1.11 (1.02–1.2)**
Cavity entrance diameter (cm)	-0.206	0.118	-1.76	0.81 (0.65–1.02)
B. Occurrence of non-excavated (decay) cavities in live trees				
DBH (cm)	**0.15**	**0.05**	**2.86**	**1.17 (1.05–1.30)**
Grapia *Apuleia leiocarpa*	**4.85**	**1.94**	**2.50**	**128 (2.9–5736)**
Crown class (dominant)	**-4.61**	**2.26**	**-2.04**	**0.010 (0.0001–0.84)**
Decay class (unhealthy)	2.03	1.08	1.89	7.62 (0.93–62.8)
Tree height (m)	-0.18	0.11	-1.61	0.83 (0.67–1.04)
Crown class (codominant)	1.94	1.35	1.44	7.00 (0.49–99.4)

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CHAPTER 4. NEST-SITE LIMITATION AND EFFECTS OF HIGHGRADE LOGGING ON CAVITY-NESTING BIRDS IN THE ATLANTIC FOREST[2]

Tropical and subtropical moist- and wet forests (hereafter tropical rainforests) harbour most of the world's biodiversity, but forest loss and degradation have left these forests facing a conservation crisis (Bradshaw *et al.* 2009). Some tropical species can be conserved in protected areas, but many species depend on the vast areas of tropical rainforest currently exposed to selective logging, one of the few widespread economic activities that retain native tropical forest cover (Putz *et al.* 2001, Kareiva *et al.* 2007, Asner *et al.* 2009). However, current policies for conventional selective logging may be inadequate to conserve secondary cavity-nesting birds (Cornelius *et al.* 2008). As a limited but necessary resource, tree cavities can limit populations (Newton 1994) and structure communities of secondary cavity nesters (Martin *et al.* 2004, Aitken and Martin 2008). Although cavities may be abundant in structurally complex primary tropical rainforests (Boyle *et al.* 2008, Zheng *et al.* 2009), selective logging may reduce cavity supply below a critical threshold for cavity-nesting birds (Cornelius *et al.* 2008). Here, I present the results of the first controlled experiment to test whether cavity supply limits the breeding density of cavity-nesting birds in primary and logged tropical rainforest.

While several studies have examined the effects of logging on tropical rainforest fauna, they have focused primarily on patterns of diversity and abundance without examining the ecological mechanisms behind population and community responses to habitat change (Gardner *et al.* 2009). To conserve cavity-nesting birds, we need to understand how their population size and community structure respond to cavity supply in production landscapes. There is evidence that cavity supply limits populations in managed temperate forests where nest-box addition experiments have led to increases in breeding density and population size of cavity-nesting birds (Brawn & Balda 1988, Newton 1994, Holt & Martin 1997, Cornelius 2006). In contrast, there is controversy about whether cavities are limiting in mature temperate forests (Brawn & Balda 1988, Waters *et al.* 1990, Aitken 2007, Wesołowski 2007, Aitken & Martin 2008) and only conflicting circumstantial evidence from tropical forests (Marsden & Pilgrim 2003, Gerhardt 2004, Brightsmith 2005, Heinsohn *et al.* 2005).

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[2] A version of this chapter has been accepted for publication. Cockle, K. L., K. Martin and M.C. Drever. Supply of tree-holes limits nest density of cavity-nesting birds in primary and logged subtropical Atlantic forest. Biological Conservation.

Little is known about the supply of tree cavities in tropical forests (Cornelius *et al.* 2008). In primary tropical rainforest in the Amazon, birds occupied only 2% of cavities, leading Brightsmith (2005) to conclude that nest sites may not be limiting under natural conditions. However, cavity-nesting birds of two subtropical forests in Argentina relied for nest sites on the same trees targeted by logging operations (Chapter 3, Politi *et al.* 2009), suggesting that these birds may be particularly threatened by a reduction in cavity supply through conventional tropical logging. Felton *et al*. (2008) speculated that low densities of Barred Forest-Falcon (*Micrastur ruficollis*) in logged subtropical forest in Bolivia could be explained by a paucity of suitable nest cavities. Marsden & Pilgrim (2003) found fewer potential nest cavities for parrots and hornbills in logged than primary tropical rainforest in Papua New Guinea, and a high ratio of 10–20 birds per nest-hole, but similar abundance of birds in primary and logged forest. To my knowledge, there have been no experimental tests of nest-site limitation in either primary or logged tropical rainforest.

The present study had two objectives: to determine (1) how conventional logging affects cavity availability in the Atlantic forest, and (2) whether nest sites limit the breeding density of secondary cavity-nesting birds in primary or logged Atlantic forest. First, I predicted that logged forest would contain fewer cavities than primary forest. Secondly, I hypothesized that if nest-site limitation was induced only by removal of cavity trees through logging, adding nest boxes would lead to increases in breeding density in logged forest but not primary forest. In contrast, if cavity nest sites are generally limiting, I predicted that nesting density would increase in both logged and primary forest, with a greater increase in the more cavity-limited forest type. From 2006 to 2009 I determined the availability and occupancy of naturally occurring tree cavities (hereafter 'cavities'), and used experimental nest box addition to determine how adding nest sites affected nest density in primary and logged forest.

METHODS

Field methods

I studied cavity availability, cavity occupancy, and the response of nest density to resource supplementation, in eight randomly located 1-ha plots, four in primary forest and four in logged forest, within the Sierra Central, Misiones, Argentina. All eight plots were on deep red latisol with negligible slope (Chapter 1).

Cavity availability.— I measured the DBH of each tree in each plot and calculated the basal area of trees ≥35 cm DBH (hereafter basal area), and the density of large trees (≥60 cm DBH). Since conventional logging removes the largest trees, I expected lower basal area and density of large trees in logged forest plots than in primary forest plots.

To determine cavity availability, field assistants and I used binoculars to locate all potential cavities (apparent entrance hole with a diameter ≥2 cm; interior depth unknown) and a 10-m ladder or single rope climbing techniques to access these cavities. Since cavity internal depth and height above ground were the two characteristics most important for nest-site selection by secondary cavity nesters outside of the plots (Chapter 3), I measured the height and depth of each cavity as described in Chapters 2 and 3. I considered a cavity to be suitable for secondary cavity nesters if it was ≥12 cm deep and ≥2.5 m high. These represent the shallowest and lowest of 45 cavities used by secondary cavity-nesting birds outside the plots (Chapter 3).

Cavity occupancy. — I inspected all natural cavities ≥8 cm deep, regardless of their height. I inspected cavities using pin-hole video cameras mounted on a 15-m pole or carried up the tree, every three weeks from 15 September to 15 December in 2006, 2007, and 2008. Cavities were considered to contain a nest if I saw eggs or chicks. All cavities with any sign of avian use (nest or prospecting) from 2006 to 2008 were also monitored during a reduced field season throughout October and November 2009. Some potential cavities were above 15 m on trees unsafe to climb, and thus could not be accessed with video cameras. I watched these potential cavities once or twice each breeding season for a total of 2–6 hours to determine evidence of nesting (adults seen feeding chicks or spending sufficient time in the cavity to be incubating eggs). Field assistants and I searched for new cavities during five person-hours in each plot at the beginning of each breeding season, then monitored new cavities along with the old cavities.

Resource supplementation.— I added nest boxes in a before-after-control-impact design to examine how increasing cavity supply affected the nest density of cavity-nesting birds. All eight plots were monitored without nest boxes throughout the first breeding season in 2006. In June 2007, three months before the second breeding season, two plots in primary forest and two plots in logged forest were selected at random for nest box addition. To each of these treatment plots, field assistants and I added 15 wooden nest boxes 20 m apart in a 3 x 5 grid. The boxes were 10 x 12 cm in entrance diameter, 60 cm deep from the entrance to the floor, and were placed 8 m high on the southeast side of live trees where they would be in the shade during the hottest part of the day. Box size was chosen to match the size of natural cavities used by Vinaceous Parrots (*Amazona vinacea*) in my study area (Cockle *et al*. 2007) and box depth selected by Planalto Woodcreepers in a pilot study (Cockle & Bodrati 2009). We placed 5 cm of sawdust in the bottom of each box to simulate the conditions of natural cavities. All boxes were monitored using pole-mounted video cameras every three weeks through the breeding seasons of 2007, 2008 and 2009, in the same way that natural cavities were monitored.

Analyses

All analyses were conducted using R version 2.9.2 (R Development Core Team 2009).

Cavity availability. —I used univariate *t* tests or Wilcoxon rank sum tests (where data were not normally distributed) to compare the basal area, density of large trees ($\geq$60 cm DBH), and density of cavities between primary and logged forest. I used the glm package in R to build a generalized linear model (GLM) with a Poisson error structure and a log link function to determine how the availability of natural nest sites (response variable) was related to basal area (explanatory variable). Poisson models are appropriate when the response variable is a count. To determine how well each of these models fit the data, I calculated the log-likelihood ratio R^2 analog where

$$R^2 = 1 - \frac{\text{Log} - \text{Likelihood}_{\text{Model}}}{\text{Log} - \text{Likelihood}_{\text{Null}}} \qquad (1)$$

and $\text{Log-Likelihood}_{\text{Null}}$ is the log-likelihood of the intercept-only model.

Resource supplementation.—To determine how adding nest-boxes affected the breeding density of cavity nesting birds I used the lmer package to build four candidate general linear mixed effects models (GLMM), to be compared using an information theoretic approach (Burnham & Anderson 2002). I specified a Poisson error structure and a log link for all models. Each candidate model included number of nests as the response variable and plot as a random effect. Fixed effects were the number of natural cavities and the treatment (box treatment or control). Including plot as a random effect accounted for the repeated observations made over time at the same locations. To improve the fit of other parameters I excluded year from the models to be compared, because preliminary analyses showed that (1) including year as a random effect did not improve model fit, and (2) the number of nests did not change over the study period at control sites (b_{year} = -0.08, SE = 0.30, P = 0.78; GLMM including year [AICc = 19.03] did not perform better than the intercept-only model [AICc = 16.03]). For each model in the suite of four, I calculated Akaike's Information Criterion corrected for small sample sizes (AICc), Akaike weight (*w*; Burnham & Anderson 2002), and the log-likelihood ratio R^2 analog. To evaluate the strength of support for each model, I compared the models based on ΔAICc and Akaike weights (Burnham & Anderson 2002). I used model averaging to calculate the average parameter estimates based on all models in which the parameter appeared, weighted by their Akaike weights. I used a *z* test for each parameter to determine whether its 95% confidence interval included zero.

RESULTS

Cavity availability

Initially I identified and monitored 97 potential cavities. On inspection and measurement, 18 of these (19%) were suitable for cavity-nesting birds (≥12 cm deep and ≥2.5 m high); 68 (70%) were unsuitable; and 11 (11%) could not be inspected and were not used by birds.

Primary forest had twice the basal area of logged forest and three times the density of trees ≥60 cm DBH (Table 1). Only 6% of trees ≥60 cm DBH contained a suitable cavity, while 30% of trees ≥100 cm DBH contained a suitable cavity. The abundance of cavities suitable for birds increased with increasing basal area (log-likelihood ratio $R^2 = 0.41$; $b_{\mathrm{BasalArea}} = 0.13$, SE = 0.04, $z = 3.14$; Fig. 4.1), with at least nine times as many suitable cavities/ha in primary forest than in logged forest (Table 4.1).

Cavity occupancy

Each year, nesting birds occupied 25% of the natural cavities I considered suitable, but 63% of the suitable cavities in trees ≥60 cm DBH. There were ten cavities I considered suitable in trees <60 cm DBH, but none were used. Only one natural cavity was occupied in logged forest, and only in one of the four years; in contrast, five cavities were used for a total of 17 nests in primary forest, giving an occupancy rate of 17/20 or 85% for the five used cavities in primary forest. The natural cavities used were among the deepest in the plots, with a mean depth of 66 ± 13 cm ($n = 5$), compared to 34 ± 7 cm ($n = 14$) for cavities considered suitable but unused. Four of the five cavities 51–100 cm deep were occupied (all in primary forest), while only one of the 12 cavities 13–50 cm deep was occupied (in logged forest), and only in 2007, by the smallest bird (the Olivaceous Woodcreeper; *Sittasomus griseicapillus*). Eight species were found nesting in natural cavities in primary forest plots: Streaked Flycatcher (*Myiodynastes maculatus*), Ferruginous Pygmy-Owl (*Glaucidium brasilianum*), Maroon-bellied Parakeet (*Pyrrhura frontalis*), Red-capped Parrot (*Pionopsitta pileata*), White-throated Woodcreeper (*Xiphocolaptes albicollis*), White-eyed Parakeet (*Aratinga leucophthalma*), Scaly-headed Parrot (*Pionus maximiliani*), and Chestnut-eared Aracari (*Pteroglossus castanotis*). Only the Olivaceous Woodcreeper nested in a natural cavity in the logged forest plots.

Resource supplementation

Each year, cavity-nesting birds occupied 1 or 2 of the 15 nest boxes in each treatment plot. Nest density for cavity-nesting birds was best predicted by models that included both the number of natural cavities and the experimental treatment (nest-box addition) as fixed effects (Table 4.2). Nest density increased with the number of natural cavities and the experimental provision of nest boxes (Table 4.3, Fig 4.2). The model that included an interaction between the number of natural cavities and the experimental treatment (box addition) had a comparable Akaike weight to the top model and the interaction term did not have a significant slope (Table 4.3). Therefore I conclude there was a similar positive effect of adding nest boxes on breeding densities regardless of the number of natural cavities in the plot. Nest boxes in both primary and logged forest were occupied by White-throated Woodcreeper and Planalto Woodcreeper (*Dendrocolaptes platyrostris*), but not parrots, owls or toucans. Other nest boxes were used by snakes, small marsupials, wasps and bees, while many remained unoccupied. On average, there were 1 nests/ha in primary forest plots without nest boxes, 2.3 nests/ha in primary forest plots with nest boxes, 0 nests/ha in logged forest plots without nest boxes, and 1.2 nests/ha on logged forest plots with nest boxes.

DISCUSSION

Of the potential cavities I identified from the ground, 70–80% were unsuitable for nesting birds. Koch (2008) suggested that although ground surveys may be poor indicators of absolute cavity abundance, they may be sufficient to compare the relative abundance of cavities among sites within a forest type. However, misclassification rates are likely to vary widely among stands in different forest types or of different ages. Since most studies estimate cavity abundance through ground surveys (*e.g.* Sedgwick & Knopf 1986, Bai *et al.* 2003, Boyle *et al.* 2008, Zheng *et al.* 2009), I advise researchers to estimate classification accuracy and be cautious when comparing cavity abundance across continents, forest types, and latitudes.

Although tropical rainforests are proposed to contain abundant tree cavities (Boyle *et al.* 2008, Brightsmith 2005), the density of active nests increased following the addition of nest boxes in my study, suggesting that populations of some cavity-nesting birds may be nest-site limited even in primary forest. My experimental results are consistent with evidence that birds fight over cavities in tropical rainforest (Heinsohn & Legge 2003, Renton 2004) and evidence that the density of suitable cavities may be considerably lower than the density of cavity-nesting birds, preventing some individuals from breeding (Marsden & Pilgrim 2003). Nevertheless, birds occupied only ~25% of the natural cavities I considered suitable. Some cavities may remain unoccupied because birds choose to forego breeding in a given year rather than nesting in a low-quality cavity where the risk of predation may be high. Other cavities may remain unoccupied because they are too small or low for the larger bird species (Whitford & Williams 2002). Unfortunately, only limited anecdotal information is available regarding species-specific cavity requirements in the Atlantic forest (Chapter 3).

There are two important caveats to the interpretation that birds are nest-site limited in primary Atlantic forest. First, little primary Atlantic forest remains, so nest-site limitation in remnant primary forest could be caused by a large supply of food and diminished supply of cavities in the alternate habitat if birds nest inside but forage outside of primary forest (Marsden & Pilgrim 2003). Testing cavity-limitation in large tracts of primary tropical rainforest is no longer possible in the Atlantic forest, but remains an important area for research in more intact regions such as the Amazon. Second, we know little about the demography of Atlantic forest birds so it is not clear whether limitation of nest density translates into population limitation. An increase in nest density on plots with nest boxes could be attributed to nesting by subordinate individuals that would not otherwise have nested, or to immigration of birds from other areas. By adding nest boxes after clutches had been initiated, Holt & Martin (1997) showed that increases in nesting density on box-addition plots in young temperate forest in Canada were best explained by the initiation of nests by individuals that otherwise would have been non-breeding floaters. Nevertheless, although adding nest sites led to an increase in nest density in my study, population size may not necessarily increase if, for example, fewer individuals survive the winter.

The paucity of large trees, cavities, and nests in logged forest suggests that conventional tropical logging has a major impact on habitat quality for cavity-nesting birds. My results should be interpreted with caution because I did not study cavity availability on logged plots prior to logging, and the logged forest could have differed from the primary forest in other ways. However, the most parsimonious explanation for my results on replicated plots is that logging reduces the supply of tree cavities: although logged forest had half the basal area of primary forest, it had nine times fewer cavities and 17 times fewer nests. The conventional practice of harvesting the largest trees may have a strong negative effect on the number of cavities and nests. However, I found no significant interaction between nest-box addition and the availability of natural cavities, and adding artificial cavities did not raise breeding density in logged forest plots to the level of primary forest plots, suggesting that other factors may also limit breeding density in logged forest, or that nest boxes were unsuitable for most species and territoriality limited the density of woodcreepers once nest-site limitation was alleviated. I know of only two other studies to examine the effects of logging on cavity-nesting birds in tropical rainforest. Consistent with my results, Pattanavibool & Edge (1996) and Marsden & Pilgrim (2003) found reduced cavity densities in selectively logged stands in Thailand and Papua New Guinea, respectively. My study appears to be the first experiment to show how reduced cavity availability in logged tropical forest can limit breeding density of cavity-nesting birds. However, longer term experiments over larger geographical areas would be needed to determine the extent to which a limited supply of cavities in tropical forests affects population size and community structure of cavity-nesting birds.

CONCLUSION

In this chapter I showed evidence that the nest density of secondary cavity-nesting birds was limited by the supply of tree cavities in both primary and logged Atlantic forest. The limited supply of cavities in the Atlantic forest was created primarily by natural decay processes in large live trees (Chapters 2 and 3). In Chapter 3 I showed that secondary cavity nesters use excavated cavities in proportion to their availability. However, it is not clear why so few excavated cavities are available in the Atlantic forest. In Chapter 5 I will examine the rates of cavity loss for excavated and non-excavated cavities in the Atlantic forest and compare these patterns to long-term data on cavity persistence at two northern temperate sites.

Table 4.1. Mean ± SE and univariate statistical tests (*t* test and Wilcoxon rank sum test with continuity correction) for basal area, density of medium- and large trees, and density of cavities suitable for nesting birds in primary (*n* = 4 1-ha plots) and logged (*n* = 4 1-ha plots) Atlantic forest in Misiones, Argentina.

	Primary forest	Logged forest	Test statistic	*P*
Basal Area (m^2/ha)	26.8 ± 1.7	11.1 ± 3.8	$t = 3.79$	0.018
Density of trees ≥60 cm DBH (trees/ha)	29.8 ± 2.0	8.8 ± 4.4	$t = 4.32$	0.011
Density of suitable cavities (cavities/ha)[a]	4.5 ± 1.04	0.50 ± 0.29	W = 16	0.028

[a] If 11 inaccessible potential cavities are included (probably an overestimate of total cavity availability), the number of suitable cavities /ha rises to 7.3 ± 1.9 in primary forest but remains 0.50 ± 0.29 in logged forest.

Table 4.2. Ranking of generalized linear mixed models predicting the number of active nests on 1-ha plots in the Atlantic forest, Argentina. Plot was a random effect in all models. *n* = sample size (number of plot*year combinations), k = number of parameters, -2 LL = -2 x log-likelihood, AICc = Akaike's Information Criterion corrected for small sample size, ΔAICc = difference in AICc between this model and the minimum AICc model, w_i = Akaike weight.

Model	k	*n*	-2 LL	AICc	ΔAICc	w_i	R^2
Box + natural cavities	4	32	10.52	20.00	0	0.55	0.61
Box + natural cavities + box*natural cavities	5	32	8.178	20.49	0.49	0.43	0.70
Box	3	32	20.34	27.20	7.20	0.02	0.25
Natural cavities	3	32	23.54	30.40	10.40	0.00	0.14

Table 4.3. Model-averaged parameter estimates for models predicting the number of nests on 1-ha plots in the Atlantic forest, Argentina. z = parameter estimate/SE. Parameters where $|z| > 1.96$ have 95% confidence intervals that do not include 0 (in bold). Higher nest density was associated with a higher number of natural cavities and the addition of nest boxes, but not an interaction between these two variables.

Parameter	Estimate	SE	*t*
Box	**1.81**	**0.58**	**3.13**
Natural cavities	**0.31**	**0.10**	**3.11**
Box * natural cavities	-0.25	0.17	-1.48

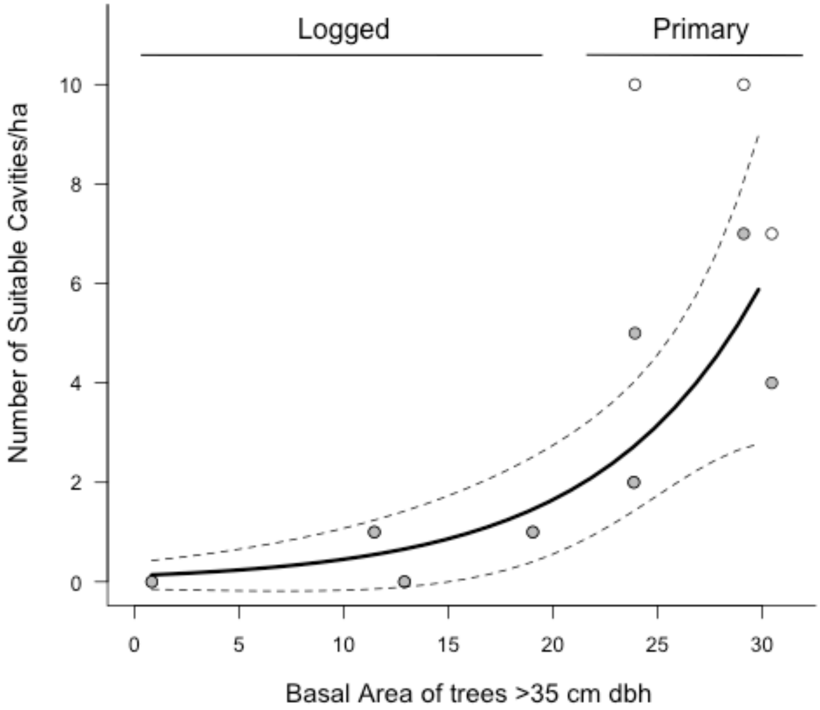

Figure 4.1. Density of cavities suitable for secondary cavity-nesting birds (≥12 cm deep, ≥2.5 m high) as a function of basal area of medium-sized and large trees (≥35 cm diameter at breast height). Filled circles show the total number of suitable cavities on each plot in logged and primary forest. Empty circles also include cavities that could not be accessed and may have been suitable (these were only present in primary forest and were not included in any models). The solid black line shows the predicted values of the generalized linear model of suitable cavities as a function of basal area. The broken lines show the 95% confidence interval on the predicted values. Log-likelihood ratio $R^2 = 0.41$, $b_{\text{BasalArea}} = 0.13$, SE = 0.04, $z = 3.14$.

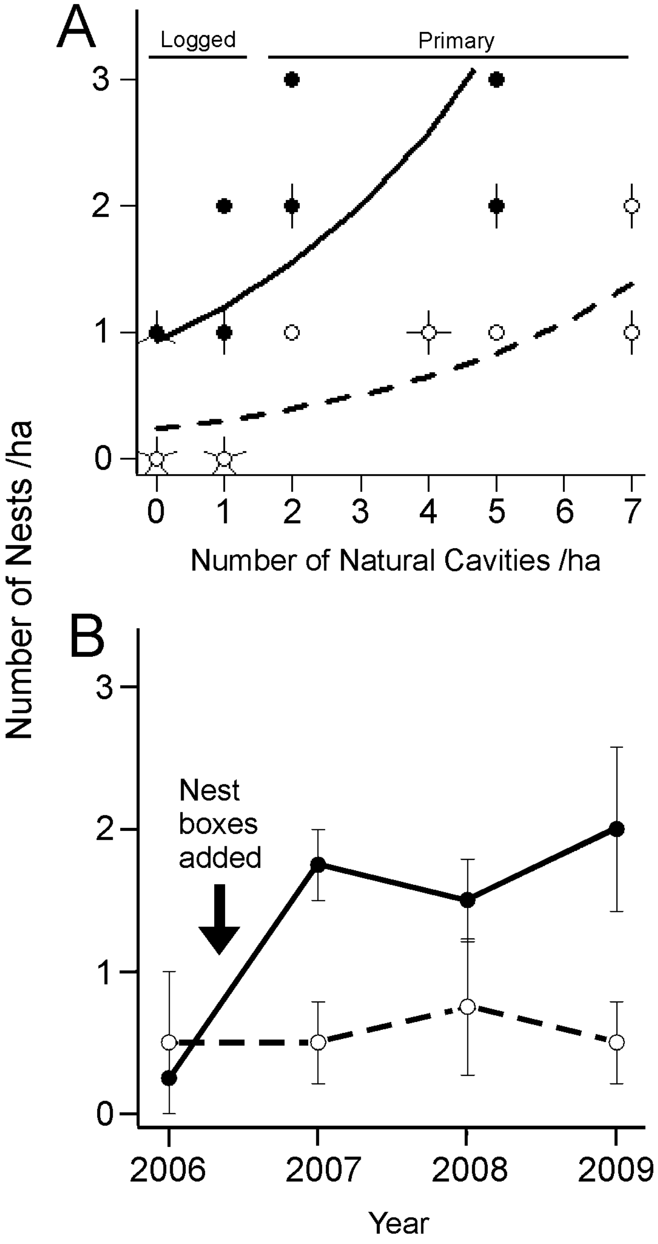

Figure 4.2. (A) Sunflower plot showing the number of nests in each 1-ha plot as a function of the number of natural cavities in the plot and the presence (black dots) or absence (white dots) of nest boxes, with values of the top model predicting the number of nests /ha from the number of natural cavities in the presence (solid line) and absence (broken line) of nest boxes. The lines for predicted nest density in primary and logged forest are not parallel because I used a log link function which creates non-linearities when plotted on an absolute scale. Lines radiating from a

dot indicate the number of observations at that value (*i.e.*, accounting for hidden observations). (B) Mean number of nests in four treatment plots (two in primary and two in logged forest) where nest boxes were added (black dots with solid line) and four control plots where nest boxes were not added (white dots with broken line) over the four years of the study. Bars indicate standard error.

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CHAPTER 5. GLOBAL VARIATION IN THE ROLE OF WOODPECKERS AS TREE CAVITY PRODUCERS AND THE PERSISTENCE OF EXCAVATED AND NON-EXCAVATED CAVITIES

The formation and persistence of tree cavities are key ecological processes that determine the structure and function of communities of cavity-nesting vertebrates. Cavity-nesting species make up 15 to 50% of many forest vertebrate communities globally. The majority of these animals are secondary cavity nesters that cannot create their own cavities (Martin & Eadie 1999). Through bottom-up control of a key resource, vertebrates that excavate tree cavities (excavators) can directly impact the abundance and diversity of secondary cavity nesters (Martin *et al.* 2004, Blanc & Walters 2008, Norris & Martin in press). Much attention has been paid to the role of cavity-excavating woodpeckers as keystone facilitators (Daily *et al.* 1993, Aitken & Martin 2007), ecosystem engineers (Jones *et al.* 1994), and indicators of ecosystem health and biodiversity (Mikusiński *et al.* 2001, Drever *et al.* 2008). However, other natural decay and disturbance processes can also form suitable nesting cavities. In Australia and New Zealand, for example, there are no vertebrate excavators, and cavities are created by fungal decay, insects, broken branches and abiotic processes such as fire and wind (Gibbons & Lindenmayer 2002, Blakely *et al.* 2008). In Chapter 1, I showed that excavators created only 20% of the cavities that were used by secondary cavity nesters in my study in the Atlantic forest.

Variation in the importance of vertebrate excavators (proportion of nests of secondary cavity nesters in excavated as opposed to non-excavated cavities) can be explained partly by the nest-site preferences of secondary cavity nesters. In Europe and Mongolia, for example, some secondary cavity nesters avoided woodpecker cavities (Bai *et al.* 2005, Remm *et al.* 2006, Wesołowski 2007) perhaps because Palearctic woodpeckers can be nest predators (Wesołowski 2007). In comparison, in mature temperate mixed forest in British Columbia, Canada, and mature subtropical mixed forest in Argentina, secondary cavity nesters used woodpecker cavities in proportion to their availability (Aitken & Martin 2007, Chapter 3). The differences in the use of excavated and non-excavated cavities by secondary cavity nesters between Canada and Argentina can thus be explained by differences in the relative abundance of excavated and non-excavated cavities. In Canada, Aitken and Martin (2007) found 11.2 excavated cavities/ha but only 1.1 non-excavated cavities/ha. Outside of North America, in contrast, these figures were approximately reversed, with about 2.2 excavated cavities and 10.9 non-excavated cavities/ha in primeval forest in Poland (Wesołowski 2007; includes only cavities used at least once as a nest), and 0.5 excavated cavities and 4.0 non-excavated cavities/ha in mature subtropical Atlantic forest in Argentina (Chapter 4, Table 5.1).

The abundance of excavated and non-excavated cavities depend on their rate of production and their lifespan (how long each cavity persists; Sedgwick & Knopf 1992, Wesołowski 2007). Cavity production rates and lifespan depend on the nature of the substrate, climate, fungal and other decay processes, and density and behaviour of excavators, all factors that may vary among sites. Here, using data from my study and other published and unpublished studies, I examine global variation in the importance of excavators in the creation of cavities for non-excavating birds (proportion of nests of secondary cavity-nesting birds that were in excavated cavities). Then, using data from my study in Argentina and two long-term studies in Canada and Poland, I compare the persistence of excavated and non-excavated cavities between three forested sites on three continents, to determine whether rates of cavity loss can explain differences in the relative use of woodpecker cavities by secondary cavity-nesting birds at these three sites.

METHODS

To compare the proportion of nests of secondary cavity-nesting birds that were in excavated cavities across a wide range of sites globally, I collected data by reviewing published studies and contacting colleagues known to have monitored whole communities of secondary cavity-nesting birds. I did not compare data on the proportions of available cavities between forests, because definitions of what constitutes a cavity vary widely between studies and necessarily depend on the species composition of the avian community.

To compare the persistence of excavated and non-excavated cavities between three forested sites on three continents, I compiled data collected by K. Martin from 1995 to 2008 in mature and logged temperate mixed forest near William's Lake, British Columbia, Canada (51°52'N, 122°21'W); data collected by T. Wesołowski from 1979 to 2004 in primeval temperate mixed forest at Białowieża National Park, Poland (52°41'N, 23°52'E); and my own data collected from 2004 to 2009 in primary and logged subtropical Atlantic mixed forest in Misiones, Argentina (Chapter 1). The vertebrate excavators known to excavate in wood at these sites include seven species of woodpeckers, one nuthatch (*Sitta canadensis*) and one chickadee (*Poecile atricapillus*) at the site in Canada (Martin *et al.* 2004); seven species of woodpeckers and two species of tits (*Parus* spp.) at the site in Poland (Wesołowski 2007); and 10 species of woodpeckers and two species of trogons (*Trogon* spp.) at my site in Argentina (Chapter 1). For additional details on the study areas see Martin & Eadie (1999), Wesołowski (2007), and Cockle *et al.* (2008). Cavity-nests were found each year by following adult birds, listening for chicks begging, watching for birds entering and leaving cavities, and observing cavity contents using ladders, mirrors, pole-mounted video cameras, and tree-climbing. Cavities were checked every year thereafter, to determine whether they were still useable. Cavities were considered no longer useable when (1) the tree fell down, (2) the branch supporting the cavity fell from the tree, (3) the cavity walls collapsed, or (4) bark grew over and closed the cavity.

To examine the persistence of cavities in Canada, Poland and Argentina, I calculated how long the cavity was available for birds to use (cavity lifespan), from the year the cavity was first found to be used until the year it was no longer useable. Since cavities were not always found in their first year of use, my calculations of lifespan should be considered minimum estimates. I used the survival package (Therneau & Lumley 2009) in R version 9.2.2 (R Development Core Team 2009) to create a Cox's Proportional Hazard model that predicted the odds of cavity loss based on the following explanatory variables: 1) country, 2) formation process (excavated or non-excavated), and 3) country x formation interaction. Cox's Proportional Hazard method models failure rate (loss of cavity) as a log-linear function of covariates, whereby regression coefficients are the natural logarithms of the odds of failure (Tabachnick & Fidell 2001). This method allowed me to include right-censored data; that is, cavities still standing at the end of the study (Tabachnick & Fidell 2001, Crawley 2007). Using right-censored data with a Cox's Proportional Hazard model eliminated problems associated with different lengths of studies in the three countries. Since I found a significant country x formation interaction, I built a separate Cox's Proportional Hazard model for each country, with only formation as an explanatory variable. Cox's Proportional Hazard was used to estimate mean cavity lifespans for each type of cavity (excavated vs. non-excavated) in each country (Therneau & Lumley 2009).

RESULTS

There was strong variation in the importance of vertebrate excavators as creators of cavities for secondary cavity nesters (relative use of excavated and non-excavated cavities by secondary cavity nesters) across the continents (Fig. 5.1). Secondary cavity nesters primarily occupied excavated cavities at seven sites in North America with community-level data (mean: 77% excavated; range: 50–99% excavated), but they primarily occupied cavities made by natural decay processes outside of North America in Eurasia (mean: 31% excavated; range: 16–69% excavated), South America (mean: 25% excavated; range: 20–30% excavated) and Australia and New Zealand (0% excavated; no excavators present).

I studied persistence of 2826 tree cavities: 796 excavated and 42 non-excavated in Canada, 539 excavated and 1368 non-excavated in Poland, and 36 excavated and 45 non-excavated in Argentina. The global model predicting cavity loss showed a significant interaction between site and mode of cavity formation ($b_{\text{Excavated*Canada}} = -2.73$, SE = 0.63, $P = 0.002$; $b_{\text{Excavated*Poland}} = -1.93$, SE = 0.63, $P = 0.002$). Cavities formed by excavators were lost at a similar rate to natural cavities in Canada ($b_{\text{Excavated}} = -0.036$, SE = 0.28, $P = 0.90$, $\text{AIC}_{\text{Model}} > \text{AIC}_{\text{Null}}$) but at a higher rate in Poland ($b_{\text{Excavated}} = 0.75$, SE = 0.070, $P < 0.0001$) and Argentina ($b_{\text{Excavated}} = 2.50$, SE = 0.64, $P < 0.0001$; Fig. 5.2). The odds of cavity loss were 2.1 (95% confidence interval: 1.8–2.4) times as high for excavated cavities as for non-excavated cavities in Poland, and 12.2 (95% confidence interval: 3.5–42.6) times as high for excavated as for non-excavated cavities in Argentina. Thus the two-year survival rate was about 90% for non-excavated cavities in Canada and Poland, and for excavated cavities in Canada, 100% for non-excavated cavities in Argentina, but only 80% for excavated cavities in Poland and less than 50% for excavated cavities in Argentina (Fig. 5.2). The five-year survival rate was approximately 80% for non-excavated cavities in Canada and Poland, and for excavated cavities in Canada, but only 60% for excavated cavities in Poland; and the nine-year survival rate was approximately 60% for non-excavated cavities in Canada and Poland and for excavated cavities in Canada, but less than 40% for excavated cavities in Poland (Fig. 5.2). Estimated cavity lifespans were thus similar for excavated and non-excavated cavities in Canada, but 2 and 12 times as long for non-excavated cavities than for excavated cavities in Poland and Argentina, respectively (Table 5.1).

DISCUSSION

Secondary cavity nesters depend strongly on cavity excavators to provide tree cavities in North America, but rely primarily on other decay processes to provide tree cavities on other continents. This pattern may be explained by a large supply of excavated relative to non-excavated cavities in North America, whereas non-excavated cavities predominate at most sites studied in Eurasia and South America, and make up all of the cavities available in Australia and New Zealand.

Cavity supply depends on local rates of cavity creation and loss. I found equal persistence of excavated cavities compared to non-excavated cavities in North America, but low persistence of excavated cavities in Poland and Argentina. Although the study in Argentina was conducted over a short time span, the result that excavated and non-excavated cavities were lost at different rates is robust because the effect size, the difference between excavated cavities and non-excavated cavities, was very large. The five-year persistence of non-excavated cavities used by birds in temperate forest in Canada and Poland (80%) was similar to that of non-excavated cavities used by marsupials in temperate forest of Australia (73%; Lindenmayer *et al.* 1997). Many factors combine to determine how often cavities form and how long they last. First, excavator species differ in their preference for substrates; some use standing dead trees in advanced stages of decay, others excavate in recently dead trees and live sections of living trees (Raphael & White 1984, Winkler *et al.* 1995). Dead cavity-trees and dead sections of trees fall much sooner than live sections of trees (Lindenmayer *et al.* 1990, 1997; Sedgwick & Knopf 1992, Vaughan *et al.* 2003). Second, Gibbs *et al*. (1993) suggest that disturbance processes such as high precipitation and windstorms may render cavities more ephemeral in tropical forests than in temperate forests. Frequent tropical storms with high winds in the Atlantic forest may lead to strong differences in persistence of cavities between the excavated cavities in dead trees and dead branches, and the non-excavated cavities often found in live sections of trees (Chapter 2). Third, properties of individual sites such as wind exposure and soil depth, and properties of tree species such as lifespan, growth rate, rooting depth, wood density, branch size and resistance to injury, may determine how quickly cavities form, what sizes and types of cavities form, whether they form in live or dead wood, and how quickly they are sealed or collapse (Raphael & Morrison 1987, Lindenmayer *et al*. 1993, 1997, 2000; Gibbons & Lindenmayer 2002, Chave *et al.* 2009). For example, in a study of Wood Duck (*Aix sponsa*) cavities in mostly live trees in Illinois, sycamores (*Platanus occidentalis*) had the highest cavity survival rate and cottonwoods (*Populus deltoides*) the lowest (Roy Nielsen *et al*. 2007). Trembling aspen (*Populus tremuloides*) is the primary tree for excavated and non-excavated cavities at the study site in Canada and many other sites in North America (Kilham 1971, Li & Martin 1991, Aitken & Martin 2007); the relative softness and propensity for rot in aspen heartwood render even live sections of the tree suitable for excavation (Hart & Hart 2001, Losin *et al.* 2006), perhaps explaining in part why excavated cavities last as long as non-excavated cavities at the site in Canada.

To better understand global variation in the importance of woodpeckers as excavators, long-term data on cavity loss and creation are needed from many more sites. Species richness of excavators was highest at the Argentina site, but excavated cavities were most abundant at the site in Canada where excavated cavities lasted longest. Woodpeckers may also be more abundant and/or more productive excavators at the site in Canada than at the sites in Argentina and Poland. Rates of cavity production should be examined using field data on woodpecker abundance and behaviour (*e.g.*, reuse of old cavities), and direct measurements of cavity creation rates. Additionally, cavity formation, loss and density may vary over time within sites, due to episodic natural and anthropogenic disturbances such as fire, hurricanes, and forest clearing (Lindenmayer *et al*. 1997, Murphy & Legge 2007, Roy Nielsen *et al*. 2007). Rates of cavity production by excavators may change over time with changes in food supply, substrate availability, and woodpecker abundance (Martin *et al.* 2006, Norris & Martin in press).

My research only addresses the proximate mechanism of cavity loss to explain global patterns in the importance of excavators; however, it is also important to understand the ultimate mechanisms. Future research should examine global variation in the properties of wood, trees and climate related to the formation and loss of excavated and non-excavated tree cavities, and the role of cavity renovators such as parrots. Finally, a key area for research is how and where non-excavated cavities are formed. Progress has been made on this topic mostly in Australia where there are no vertebrate excavators (Lindenmayer *et al.* 1993, 2000; Harper *et al.* 2005, Koch *et al.* 2008a). Similar research is needed on other continents. While charismatic woodpeckers have received much attention as cavity engineers and contribute to avian diversity in their own right, we understand little about the more prevalent agents that create cavities globally: fungi, insects, and weather.

Table 5.1. Species richness of excavators and secondary cavity nesters, density of excavated and non-excavated cavities, and median lifespan of excavated and non-excavated cavities at sites in Canada, Poland and Argentina.

	Canada	Poland	Argentina
Species richness			
Excavators	9	9	12
Non-excavators	22	22	57
Density of cavities (cavities/ha)			
Excavated	11.2	-	0.5
Non-excavated	1.1	-	4.0
Percentage of nests of secondary cavity nesters in excavated cavities	90%	16%	20%
Cavity lifespan (years)			
Excavated	12	6	2
Non-excavated	12	13	24

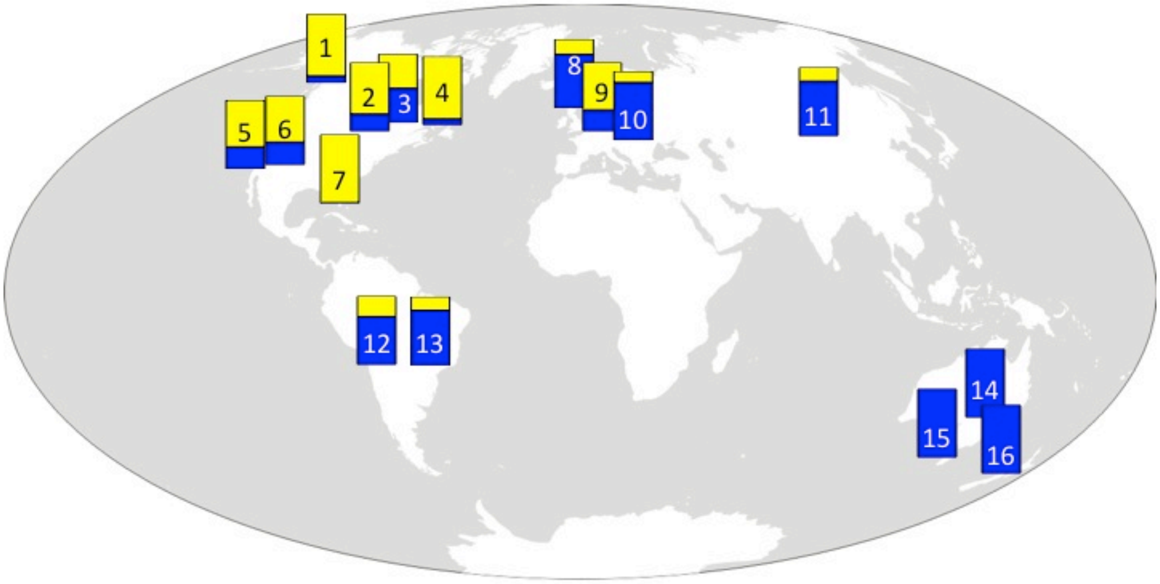

Figure 5.1. Global variation in the importance of excavators as cavity formation agents. Proportion of nonexcavators' nests in cavities excavated by woodpeckers and other birds (yellow) and cavities created by natural decay processes (dark blue) at 16 forest sites worldwide: 1- Aitken & Martin 2007, 2- Stauffer & Best 1982, 3- Bavrlic 2008, 4- P. Drapeau *in litt.*, 5- Waters 1988, 6- Raphael & White 1984, 7- Blanc & Walters 2008, 8- Carlson *et al.* 1998, 9- J. Remm *in litt.*, 10- Wesołowski 2007, 11- Bai *et al.* 2003, 12- Politi in Cornelius *et al.* 2008, 13- Chapter 2, 14- Gibbons & Lindenmayer 2002, 15- Koch *et al.* 2008b, 16- Blakely *et al.* 2008. I only include community-wide studies.

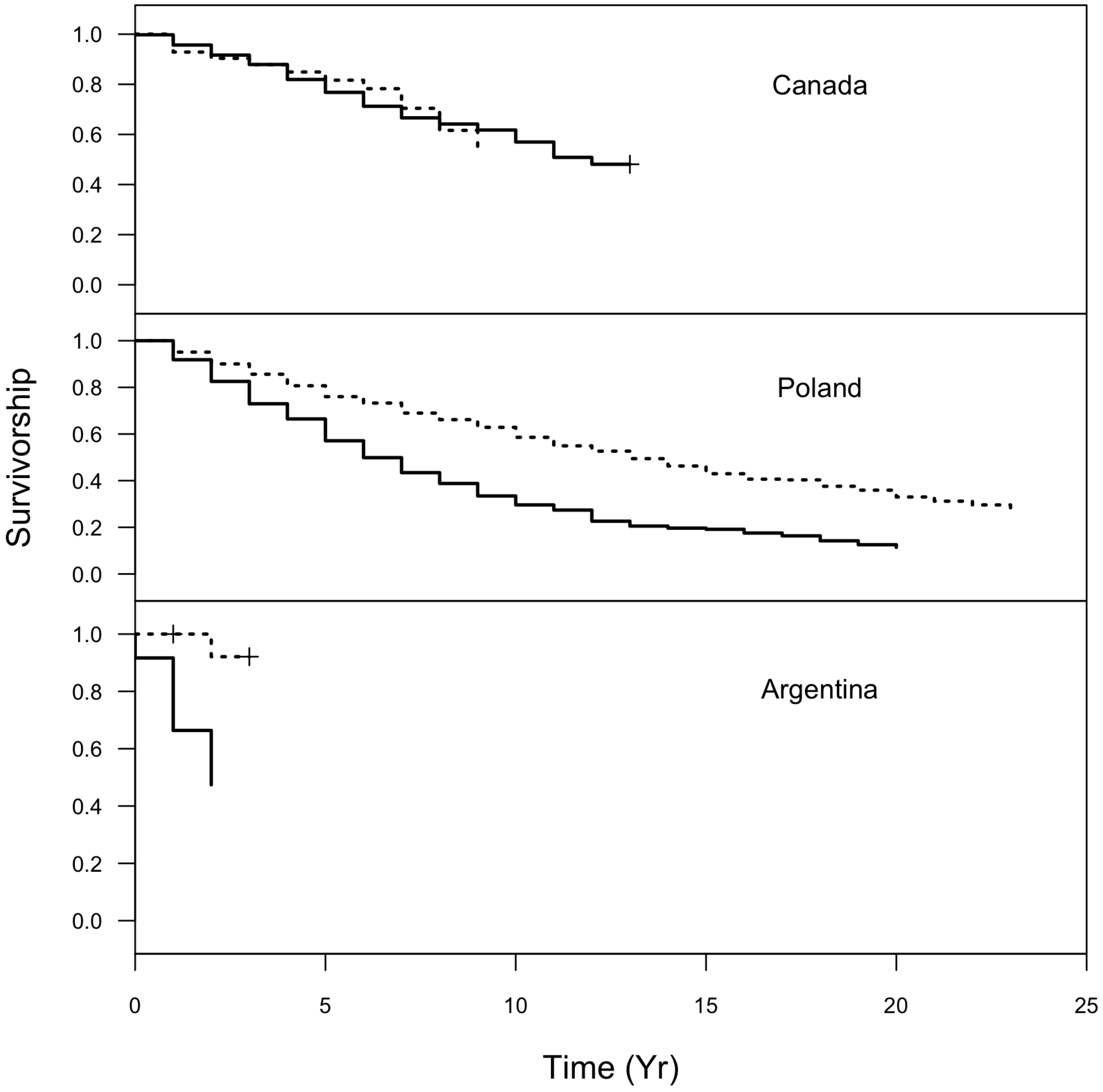

Figure 5.2. Persistence of cavities excavated by birds (solid lines) and created by natural decay processes (broken lines) in temperate mixed forest at William's Lake, interior British Columbia, Canada (n = 836), temperate mixed forest at Białowieża, Poland (n = 1907), and subtropical mixed forest in Misiones, Argentina (n = 81). Crosses on the lines indicate censoring in the data because some cavities were still standing at the end of the observation period. I only include time periods for which there were still at least five cavities in the sample.

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CHAPTER 6. GENERAL DISCUSSION AND MANAGEMENT RECOMMENDATIONS

Communities of cavity-nesting birds are often assumed to be structured around the key resource of tree cavities provided by woodpeckers in standing dead or unhealthy trees, a situation found in many North American forests (*e.g.*, Raphael & White 1984, Martin *et al*. 2004, Cooke 2009). As a result, management recommendations in North America have often focused on managing for excavators, under the assumption that by managing for excavators we can meet the cavity-requirements of most secondary cavity nesters (*e.g.*, Raphael & White 1984). In accordance with this paradigm, Gibbs *et al.* (1993) suggested that the relative rarity of snags and high ratio of secondary cavity-nesting species to excavator species in tropical rainforest might imply that secondary cavity nesters are especially nest-site limited in tropical forests. Like other tropical forests, the Atlantic forest has a high ratio of secondary cavity-nesting species to excavator species, and my work shows that nest sites are indeed limiting in this forest; however, processes other than vertebrate excavation are mainly responsible for determining cavity availability.

Cavity limitation has widespread implications for cavity-nesting birds, not only in terms of conservation and community interactions as discussed in this thesis, but also as a key mechanism driving life history evolution of tropical birds. For example, cavity limitation has been proposed to explain the general pattern of larger clutch size in cavity-nesting birds compared to open cup nesters: if secondary cavity nesters cannot find a suitable cavity every year, they may have fewer opportunities to breed than other birds, and may therefore invest heavily in each nesting attempt (Beissinger & Waltman 1991, Martin 1993). However, Wiebe *et al*. (2006) found more support for alternative hypotheses to explain clutch sizes in cavity excavators; in particular, stronger excavators could access beetles below bark and thus experienced greater annual stability of food resources, migrated less, experienced higher adult survival, and laid smaller clutches. Eberhard (2002) proposed that a lack of closely spaced tree cavities prevents many cavity nesters from breeding colonially, and argued that where parrots are released from this constraint (*e.g.*, when they can nest in cliff faces or build stick nests) they breed colonially. Thus cavity-limitation might affect the evolution of breeding biology. In the Eclectus Parrot (*Eclectus roratus*), extreme nest site limitation and a resulting need for cavity defense has been proposed to explain why females spend up to 11 months of the year in their cavities, sometimes fighting to the death

(Heinsohn & Legge 2003, Heinsohn *et al.* 2005). Since many females cannot acquire a cavity, the operational sex ratio is strongly biased toward males, favouring cooperative polyandry (Heinsohn *et al*. 2007). Heinsohn *et al.* (2005) propose that reverse sexual dichromatism is an ultimate result of this nest site limitation, where green plumage helps male Eclectus Parrots avoid predators while they forage in tree crowns and carry food to the cavity-guarding females, and red plumage helps females defend their cavities from other females. Nevertheless, there have been few direct tests of cavity limitation in the tropics and several authors have recently questioned the assumption that tree cavities are generally limiting (Wiebe *et al.* 2006, Wesołowski 2007), particularly in tropical forests (Brightsmith 2005, Boyle *et al.* 2008). My study (Chapter 4) provides the best evidence yet that cavities can be a limiting resource in tropical forest.

Although nest site availability appears to limit nesting density of some cavity-nesting birds in the Atlantic forest, suggesting the potential for strong direct and indirect effects among populations of cavity-nesting birds, the community is not strongly structured around cavity production by excavators. Excavated cavities made up about 20% of available cavities, and secondary cavity nesters used excavated and non-excavated cavities in proportion to their availability (Chapters 2 and 3), such that natural decay processes, rather than woodpeckers, provided most of the cavity resources for secondary cavity-nesting birds. Likewise, in other parts of the world outside of North America, natural decay processes, not excavators, provided most of the cavities used by secondary cavity nesters, although data are available from only two sites in South America and none in Africa (Chapter 5). The reduced importance of woodpeckers as cavity creators in the Atlantic forest compared to North America is partly because in the Atlantic forest their cavities persist only a short time (Chapter 5). Overall, little is known about the direct mechanisms of cavity loss or the factors influencing the production rate and persistence of cavities created by excavators and natural decay processes globally. We still know little about how and when cavities form through natural decay processes, and which organisms are involved. Future research should examine the relative importance of (1) woodpecker abundance, (2) woodpecker excavation rate (number of new cavities each woodpecker excavates per year), (3) rate of formation of non-excavated cavities, and (4) persistence of excavated and non-excavated cavities, in explaining the global variation in abundance of excavated and non-excavated cavities. Several factors may contribute to the high abundance of woodpecker cavities in North America: multi-annual persistence of excavated cavities in North America (Chapter 5), high abundance of woodpeckers in North America, and/or high rates of excavation by woodpeckers in North America (multiple cavities produced/individual/year). The presence of a suitable decay-prone tree species such as trembling aspen (*Populus tremuloides*) might allow higher woodpecker densities or excavation rates at some sites in North America. Field data and demographic models could be used to compare the relative contribution of these factors to global variation in the abundance of woodpecker cavities.

In the Atlantic forest, research is needed to determine the role of wood-decaying fungi in the creation of tree cavities. Gibertoni *et al*. (2007) have suggested that *Aphyllophorales*, the main group of wood-decaying fungi in the Atlantic forest, may be associated with mature interior Atlantic forest. In my study, *Phellinus* spp. (family *Hymenochaetaceae*) were primarily responsible for enabling the formation of non-excavated cavities in live sections of trees, and were found only in primary forest (7 of 7 fungi, although three of these fungi were within 50 m of forest edge). Since non-excavated cavities in live sections of trees provided most of the nest sites for secondary cavity-nesting birds, and lasted many years longer than excavated cavities in dead sections of trees (Chapters 2, 3 and 5), the possible association of *Phellinus* with primary Atlantic forest merits further study. In more open landscapes with fewer large trees, such as on farms, woodpeckers might take on a more important role as cavity creators (Chapter 2); thus, anthropogenic activities in the Atlantic forest could produce a shift in community structure from a reliance on the slow formation of long-lasting cavities by fungi in large live trees, to a reliance on more quickly produced but ephemeral cavities by woodpeckers in smaller dead trees. Further studies should test this hypothesis with field data on the abundance of fungi, woodpeckers, and excavated and non-excavated cavities across a gradient of anthropogenic disturbance in the tropics.

My preliminary results suggest there is the potential for intra- and inter-specific competition for nest sites among cavity-nesting birds in the Atlantic forest, especially among species of similar body size, but further research is needed to determine the prevalence of nest-site competition in the Atlantic forest and its impact on populations and communities. Demographic studies of Atlantic forest birds using marked individuals would help elucidate the effects of varying cavity supply on fecundity, fitness, and population size. My results suggest that the secondary cavity nesters most likely to be limited by cavity supply are those for which there are many individuals of similar body size in the community, and few appropriately-sized cavities available (Chapters 2, 3 and 4). However, little is known about the absolute abundance of cavity-nesting birds in the Atlantic forest, so it is difficult to speculate on which species are most likely to be nest site limited. Further research in the Atlantic forest should determine the absolute density of birds in different size classes, size-specific cavity selection and availability, and effects of the abundance and diversity of cavities on nest web interactions and species coexistence. To conserve cavity-nesting birds in the Atlantic forest, it is especially important to determine the number and diversity of cavities likely to provide sufficient nest-sites for the whole cavity-nesting community, including subordinate species, and the number of trees that need to be recruited to maintain cavity supply over the long term.

The Atlantic forest has been the subject of several studies on how organisms respond to forest fragmentation, but few studies on other aspects of ecology. Many studies show the importance of conserving large blocks of Atlantic forest wherever possible. In Brazil, smaller, more isolated Atlantic forest fragments have lower species richness of understory birds (Martensen *et al*. 2008) and birds in mixed-species flocks (Maldonado-Coelho & Marini 2004). Birds inhabiting such fragments have less symmetrical morphology, suggesting high levels of genetic or environmental stress (Anciães & Marini 2000). Smaller, more isolated fragments also have reduced species richness of bryophytes (Pereira Alvarenga & Cavalcanti Pôrto 2007), shade-tolerant trees (Metzger 2000), large trees (Oliveira *et al*. 2008) and mammals (Chiarello 1999, Vieira *et al*. 2009), and reduced diversity of tree pollination systems (Lopes *et al*. 2009). However, some taxa are more affected by fragment size, while others are affected by connectivity, landscape context or edge effects (Metzger 2000, Uezu *et al*. 2005, Oliveira *et al*. 2008). The above results are based on studies in extremely fragmented areas of the Atlantic forest. In contrast, across a number of taxa in a landscape dominated by mature Atlantic forest, Pardini *et al*. (2009) showed that secondary forest and shaded cacao plantations harboured more species than interior Atlantic forest, including many forest specialist species, and the main result of converting native forest to other uses was a proliferation of disturbance-adapted native species rather than the disappearance of forest specialists. Based on their results, these last authors suggested that we can manage productive tropical landscapes to maintain most native biodiversity if we avoid creating large tracts of homogeneous converted land. The Argentine Atlantic forest offers just such an opportunity, with corridors connecting patches and large tracts of degraded forest, secondary forest, and isolated trees.

While the Atlantic forest in Argentina represents a type of mosaic landscape common in the tropics, known to be used by many animals, little is known about how resources such as food and shelter, or threats such as predation, vary across such mosaic landscapes, or how these resources and risks affect populations and communities. Indeed, other than fragmentation effects on wildlife, little is known about the ecology of Atlantic forest communities or even the natural history, distributions, and basic biology of many species. The lack of information about Atlantic forest ecology makes it difficult for scientists to understand the mechanisms behind the observed effects of fragmentation and forest loss, or predict the effects of further habitat modification (*e.g.*, Vieira *et al*. 2009).

My thesis focused on cavity-nesting resources in the Atlantic forest and showed that these resources can limit nest density of secondary cavity nesters. However cavity-nesting populations and communities are influenced by many factors other than cavities, including food resources, top-down effects of predators and parasites, and spatial arrangement of habitat (Nilsson *et al*. 1985, Richner & Heeb 1995, Renton 2001, Brightsmith 2005). Indeed, habitat requirements other than cavities may be equally or more important than cavities to the conservation of many cavity-nesting species in the Atlantic forest. During my nest box experiment (Chapter 4), adding nest boxes to logged forest did not increase nest density to the levels of primary forest; although this might be because nest boxes were unsuitable for some species, it might also be because other characteristics such as low food availability or high predation risk reduce the habitat quality of logged forest below that of primary forest. The roles of these other processes remain to be studied.

In Misiones and elsewhere in the tropics, natural history research still has great potential to reveal novel patterns and processes and contribute to improving conservation decisions. For example, several species presumed to be cavity nesters have not had their nests described (Chapter 1). My recent work in Misiones revealed that at least one species in the Piprites genus (*Piprites*, Family: *Incertae sedis*), previously thought to be cavity nesters (Snow 2004), builds a stand-alone nest (Cockle *et al*. 2008a). Areta & Bodrati (2008a, 2010) revealed an unsuspected longitudinal migration system for three species of Atlantic forest birds not previously known to migrate. Their results highlight the importance of conserving Atlantic forest remnants in southern Brazil, to maintain migratory pathways from the coast to the interior. Bodrati & Cockle (2006) and Bodrati *et al*. (2009) recently showed that the globally vulnerable insectivorous White-bearded Antshrike (*Biatas nigropectus*) and Black-capped Piprites (*Piprites pileata*) are habitat specialists on *Guadua trinii* bamboo and *Ocotea pulchella* forest, respectively. To conserve these species, we need to conserve their specific habitats. In the case of the White-bearded Antshrike, this means conserving sufficient bamboo habitat through 30-year cycles of vegetative growth, mass flowering and mass mortality. For the Black-capped Piprites, it means conserving a rare, apparently edaphic forest formation now found only along the arroyo Paraíso in Misiones (Bodrati *et al*. 2009). Another four species of globally or nationally red-listed birds were recently shown to depend, to varying extent, on the mass seed production of *Guadua trinii* and *Guadua chacoensis* (Areta & Bodrati 2008b, Areta *et al*. 2009), appearing in Argentina only every 15 years when these bamboos produce seeds. These findings suggest that many other fascinating ecological patterns and processes remain to be discovered through basic natural history research, with enormous potential to contribute to science and conservation in the Atlantic forest.

MANAGEMENT RECOMMENDATIONS

My results suggest that conventional tropical logging severely reduces nest density of cavity-nesting birds by eliminating most of their nest sites (Chapter 4). I will discuss some of the options for conserving cavity-nesting birds in the tropics, with a particular emphasis on the Atlantic forest. I argue that there is an urgent need to adopt modes of tropical forestry and agriculture that conserve large live cavity-bearing trees.

First, I will briefly discuss the possibility of conserving cavity-nesting birds through nest box programs. Nest box programs have been successful for the conservation and restoration of some cavity nesters in North America and Europe (reviewed in Newton 1998, but see Mänd *et al.* 2005). Although nest box programs can increase the value of young secondary forest for cavity-nesting wildlife and help eliminate some barriers to successful breeding for highly endangered species, wooden nest boxes last only a few years, and many boxes either remain unoccupied or are occupied by non-target ‘pest’ species (Snyder *et al.* 1987, Downs 2005, Lindenmayer *et al.* 2009). In the Neotropics, several nest box programs have been implemented with mixed success. For example, Waugh (2009) reports increased production of chicks of the vulnerable Red-tailed Parrot (*Amazona brasiliensis*) thanks to a nest box program started in 2003 in Brazil. However, nest boxes installed in Peruvian palm swamps failed to attract nesting Blue-and-yellow Macaws (*Ara ararauna*) (Brightsmith & Bravo 2006). The addition of nest boxes apparently eliminated nest-site limitation and led to the successful fledging of 28 chicks of the Puerto Rican Parrot (*Amazona vittata*) between 2001 and 2005 (White *et al*. 2005). However, this parrot continues to experience chronic failure to breed and remains critically endangered despite a large supply of artificial nest sites (Beissinger *et al*. 2008). In my experiment (Chapter 4), few species used the traditional wooden nest boxes and most boxes remained unoccupied. In my pilot study with better-spaced nest boxes in highly degraded forest at Parque Provincial de la Araucaria in 2006, half of the 26 nest boxes were occupied, but only four species of vertebrates used them for nesting: Planalto Woodcreeper (*Dendrocolaptes platyrostris*), Barred Forest-Falcon (*Micrastur ruficollis*), Tropical Screech-Owl (*Megascops choliba*) and White-eared Opossum (*Didelphis albiventris*; Cockle *et al*. 2008b). Five of 60 boxes erected in 2007 were no longer useable in 2009 (four because the tree fell and one because the box rotted and fell from the tree). None of my boxes were occupied by endangered Vinaceous Parrots even though the box dimensions were chosen to reflect their natural nest cavities. Thus, a nest box program might be useful for conservation of some cavity-nesting birds such as woodcreepers (Dendrocolaptinae) in highly degraded forest or open areas, but trials would be needed with other types and sizes of boxes before such a program could be recommended as a conservation strategy for threatened species in the Atlantic forest of Argentina.

Rather than widespread nest box programs, I recommend a concerted attempt to conserve natural cavity-nester habitat. Although the Atlantic forest is already highly fragmented (Fonseca 1985, Ribeiro *et al*. 2009), there remain many opportunities to conserve the key habitat features selected by cavity-nesting birds. Dead and unhealthy trees should be retained for excavators. Large diameter trees, especially grapias, should be retained for secondary cavity nesters. The strategy should aim to conserve all trees >100 cm DBH and a number of trees >60 cm DBH in all forests and on farms. Given the extremely high levels of species richness and endemism in the Atlantic forest and other tropical forests (Myers *et al.* 2000), such measures are likely to have a global impact on biodiversity conservation. Because many cavity-nesting birds are key dispersers of tree seeds in the Atlantic forest (Pizo 1997, Cardoso da Silva & Tabarelli 2000) and elsewhere in the tropics (Holbrook & Loiselle 2009), a reduction in cavity availability that reduces the abundance of seed-dispersing cavity nesters (Chapter 4) could potentially result in reduced tree regeneration and even fewer cavities in the future (*e.g.*, Pizo *et al*. 2008). In this sense, further study is merited to determine the key dispersal mechanisms, regeneration ability and potential for active restoration of the main cavity-bearing tree species in the Atlantic forest (*e.g.*, Holz *et al.* 2009, Rodrigues *et al.* 2009). In the meantime, I recommend two specific complementary strategies to slow the loss of cavity-bearing trees, based on the results of my thesis and seven years of running a bird conservation project in Misiones:

1. Conserve existing and future cavity-bearing trees in legally commercially-logged native forest through regulations and financial incentives

In the 2500 km^2 Yaboty Biosphere Reserve, most landowners practise selective logging of the native forest. Although the logged forest I studied in Chapter 4 had few cavities and very few active nests, not all tropical logging needs to follow this pattern. Current forestry policies impose minimum diameters on harvested trees, encouraging landowners to harvest the trees most likely to provide nest sites for secondary cavity nesters. I recommend new guidelines that stipulate maximum diameters for tree harvest and minimum densities of large trees for retention. Some land owners and forest managers in Misiones already avoid harvesting trees >100 cm diameter and those with fungal conks, because these trees are either too large for the mill or they have extensive heart rot (M. Matuchaka and E. Miott, pers. comm.). If other landowners and forest managers could be educated in the selection of trees for harvest, substantially more cavity-bearing trees could be saved in commercially logged forest. Recruitment of new trees can also be improved through reduced impact logging practices that avoid destruction of non-target trees (Bulfe *et al.* 2009) and liana-cutting that promotes growth of target trees (Campanello *et al.* 2007). Nevertheless, even reduced impact logging can lead to reductions in the abundance of cavity-nesting- and other sensitive birds, and regulations are needed to improve conservation of large trees in such operations (Felton *et al.* 2008). Owners of forested lots in the Atlantic forest provide the world with an important ecosystem service by preserving a biodiversity hotspot. Foregoing exotic plantations and pastures to retain native Atlantic forest carries a high opportunity cost for landowners, a cost that should be subsidized by global conservation interests. Conserving cavity-trees and native forest should be promoted by financial incentives such as subsidies, grants for new tourism initiatives, and a premium price for sustainably harvested tropical wood.

Increasingly, tropical forestry is moving toward monoculture tree plantations subsidized by many national governments, including the government of Argentina. Many of these plantations are certified by international organizations such as the Forest Stewardship Council. As such, I believe it is important to briefly discuss the value of these plantations for native cavity-nesting birds. Two studies in the Atlantic forest have reported high species richness of birds in monoculture tree plantations relative to native forest, and concluded that tree plantations may be valuable for bird conservation if properly managed. Zurita *et al*. (2006) report that 63% of forest generalist species were found in plantations of exotic pines (*Pinus* spp.) in Argentina, and Fonseca *et al*. (2009) report even higher rarefied species richness of birds in 'ecologically managed' exotic *Pinus* plantations than in native Paraná pine forest in Brazil. However, the methods, species richness, and species lists reported in these studies show that the authors failed to record most of the species present in the forest, and the studies were therefore inadequate to detect real differences in species assemblages between native forest and tree plantations. Plantations of native Paraná pine are key for the conservation of the globally near-threatened Araucaria Tit-Spinetail (*Leptasthenura setaria*) in Misiones (Pietrek & Branch in press) and may provide limited foraging opportunities for some cavity-nesting birds (Bodrati & Cockle 2006, A. Bodrati & K. Cockle pers. obs.); however, tree plantations are managed on short (< 30 year) rotations and are unlikely to contain any tree cavities suitable for nesting birds. I agree with Zurita *et al*. (2006) that habitat for cavity nesters could be enhanced in plantations by protecting legacy trees, large old trees that are spared during harvest. Plantations may also help reduce logging pressure in native forest and provide an economic activity that requires less clearing of native forest than tobacco or other annual crops. Nevertheless, conservation efforts to prevent further extinctions of cavity-nesting bird species in Misiones should focus primarily on maintaining native forest with cavity-bearing trees, because such forest supports the greatest richness of native species.

2. Conserve existing cavity trees and initiate reforestation on small farms

In Argentina, the laurel, guatambú and Paraná pine forest I studied is now restricted to three small parks and hundreds of small-holder farms. I found 50% of my nest cavities of forest birds on these farms (Chapter 3). The farms still support relatively well-connected forest patches with the full complement of non-game forest bird species, including the only large breeding population of the endangered Vinaceous Parrot in Argentina (Cockle *et al*. 2007; Fariña *et al*. 2010, A. Bodrati & K. Cockle, unpublished data). Although not all species of cavity nesters in the Atlantic forest use isolated trees in pastures, tree isolation was a characteristic selected by some secondary cavity nesters in this study (Chapter 3), and isolated cavity-bearing trees can be keystone structures that allow threatened species to persist in anthropogenically altered habitat (Manning *et al*. 2006, Manning & Lindenmayer 2009).

To conserve cavity-trees on small farms we need a strategy that includes outreach, policy changes and economic incentives. The small-holder farmers in my study area in Argentina are stewards of lands among the richest in biodiversity globally. Paradoxically, they receive little or no government or NGO support for biodiversity conservation. Instead, current subsidies and land-tenure policy encourage them to replace native forest with plantations of exotic trees and annual crops. Lack of access to emergency credit drives many farmers to sell timber illegally, at prices well below market value. I believe a simple micro-credit program could provide access to emergency funds between crop harvests, preventing this unnecessary and illegal logging of endangered forest.

Several provincial environmental laws help protect native forest on farms. For example, Misiones Provincial Law 854 “Régimen Legal sobre Bosques y Tierras Forestales / Law of Forests and Forested Lands” (1977) requires landowners to have their forestry plans approved before exploiting native forest, and Law 3426 “Bosques Protectores / Protector Forests” (1997) requires native forest to be retained along all stream margins and on land with >20% slope. However, these laws are only weakly enforced and until very recently, have not been accompanied by environmental education. Indeed, some environmental laws have never been implemented, such as Misiones Provincial Law 3136 “Área Integral de Conservación y Desarrollo Sustentable, Corredor Verde / Green Corridor Integrated Conservation and Development Area” (1999), which would have compensated municipalities like San Pedro for retaining native forest rather than converting it to other land uses. Misiones Provincial Law 2380 (1986) protects the critically endangered Paraná pine and prohibits harvesting adult trees. As an unintended result, many farmers eliminate ‘nuisance’ Paraná pine seedlings from their pastures. A better policy would be to use subsidies and outreach to encourage farmers to (1) conserve native forest, (2) establish Paraná pine plantations, and (3) retain natural Paraná pine seedlings and saplings. International governmental and non-governmental organizations should also pressure the government of Misiones to implement and enforce existing environmental laws to protect native forest.

Environmental education can help reduce threats to native forest and cavity-nesting birds. My colleagues and I successfully reduced nest poaching of one endangered cavity nester (the Vinaceous Parrot) through an environmental education program in my study area, now in its seventh year (Fariña *et al.* in press). We currently promote the conservation of cavity-bearing trees through our education program in 14 rural schools and a poster campaign in the department of San Pedro. However, a longer term, province-wide environmental education program is needed to promote the conservation of Atlantic forest and cavity-bearing trees.

Without conservation efforts, isolated large cavity-trees will not be replaced when they fall. Lindenmayer *et al*. (1997) found that cavity-bearing trees in wildlife corridors in Australia fell at twice the rate of cavity trees in continuous forest. Even in a cocoa agroforestry system where standing shade trees are valued, Rolim & Chiarello (2004) found that native Atlantic forest trees were slowly disappearing. Oliveira *et al*. (2008) showed that even without logging, large tree species were rare in Atlantic forest edges, perhaps because higher winds through open habitats caused elevated rates of tree fall. To conserve a supply of mature trees over the long term in agricultural areas, models suggest keeping mortality of existing trees below 0.5%/year, and recruiting new trees at a rate higher than the number of existing trees and at a frequency of about 15% of the maximum life expectancy of trees (Gibbons *et al*. 2008). However, we need studies of the demography of Atlantic forest trees (lifespan, mortality and recruitment) to determine appropriate targets for rural tree conservation. In my study area, colleagues and I will start a pilot replanting effort on 28 farms in August 2010. Grapia may be an especially useful species to plant, but the development of tree cavities in different species of trees needs to be studied further.

In another biodiversity hotspot, the Western Ghats (India), perceiving benefits from forest on farms has been key to preserving a mixed landscape of forest patches and agricultural crops that supports 86% of the bird species found in large intact forest, even after 2000 years of cultivation (Ranganathan *et al*. 2008). However, conserving native trees and tropical forest patches on farms in the Ghats and elsewhere is a complex undertaking requiring a good understanding of the needs and motivations of rural stakeholders (Garcia *et al*. 2009). In the Atlantic forest of Argentina, it is important to study the social, legal and economic drivers that encourage the conservation of native forest on farms, to inform policy measures like new laws, subsidies, and stewardship payments. My conversations with small-holder farmers in Misiones suggest that forest and remnant trees may be retained for multiple reasons. Native forest patches and remnant trees provide services for farmers, including (1) protection of spring-water; (2) a supply of firewood, timber, and limited non-timber forest products such as ornamental plants and planters, meat, and Paraná pine seeds; and (3) shade and shelter for domestic animals, people and some crops. Some farmers view native forest as a long-term investment because trees can be harvested and sold when money is scarce. Laws (mentioned above) dissuade some farmers from harvesting Paraná pines and clearing forest on steep slopes or along streams. Many farmers say they enjoy watching native wildlife, especially large colourful birds, and have left remnant trees and forest so they could see these animals. However, some farmers may conserve forest simply because they have not had the time or capital to clear the land (*e.g.*, Garcia *et al*. 2009). Thus, understanding the motivations and aspirations of farmers is crucial to the conservation of native forest and cavity-bearing trees on farmlands in Misiones. I strongly encourage policy-makers and non-governmental organizations to begin seeking farmers' input on strategies to conserve remnant forest and trees in rural areas, for example through surveys and local workshops.

CONCLUSION

Remaining Atlantic forest in Misiones still supports high biodiversity and a nearly complete community of cavity-nesting birds (Bodrati *et al*. 2006, in press). These birds continue to interact with one another around the limiting resource of tree cavities created mostly through natural decay processes. However, cavity-nesting birds in the Atlantic forest form a fragile community, susceptible to reductions in the key resource of nesting cavities in large live trees. Maintaining these large live trees will allow cavity-nesting birds to continue to perform their functions as seed dispersers, and predators of other birds, arthropods, seeds and small mammals. However, these trees are threatened by conventional logging of native forest and conversion to plantations, inadequate and unenforced regulations, a growing human population, and economic inequality. Some of the problems facing cavity-nesting birds in Misiones can be resolved through local environmental education; however, conserving future cavity-bearing trees on a large scale will require swift and concentrated efforts from governmental and non-governmental organizations, to create strong economic incentives for the preservation of large trees in native Atlantic forest.

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