BIOTROPICA
THE JOURNAL OF TROPICAL BIOLOGY AND CONSERVATION

BIOTROPICA 41(3): 354–360 2009 10.1111/j.1744-7429.2008.00481.x

Nest Selection by Cavity-nesting Birds in Subtropical Montane Forests of the Andes: Implications for Sustainable Forest Management

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ABSTRACT

Development of sustainable forestry has been hampered in tropical countries by a scarcity of research on the ecological effects of logging. We focused on cavity-nesting birds, a group known to be sensitive to logging. Cavities used for nesting were not a random subset of all available suitable cavities. Birds selected cavities that were relatively high above the ground, had smaller entrances, and were excavated by woodpeckers. The use of tree species was also not random: *Calycophyllum multiflorum*, *Blepharocalyx gigantea*, and *Podocarpus parlatorei* were disproportionately important. Cavity nests were also more likely to be found in areas with trees with high mean diameter at breast height. This study emphasizes the need to maintain some unlogged forest patches within logging areas and retain certain species of trees. This study has implications for forest management in Argentina, where a new law mandates the sustainable use of forest resources and where many landowners are interested in forest certification.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp.

Key words: Argentina; forestry; logging; selva Tucumano-Boliviana; woodpeckers.

Sustainable forest management has gained worldwide support among conservationists, foresters, legislators, and the public (Lindenmayer & Franklin 2002). However, in most tropical countries, a scarcity of studies on the effects of logging on biodiversity has hampered efforts to develop guidelines for sustainable forestry (Fimbel *et al.* 2001). Currently, the stage is being set in some countries to move in this direction. Specifically, in Argentina a new federal law mandates: the sustainable use of forests without negatively affecting biodiversity, people, or the landscape; increasing the goods and services that forests provide; and maintaining or increasing the current forest land cover (Law 26331). However, this law has not been accompanied by guidelines on how to achieve these goals.

Both domestic and international wood demand in Argentina has been increasing steadily and this has significantly increased the extent of forest lands under exploitation (Pacheco & Brown 2006). Among Argentina's diverse forest ecosystem types the subtropical montane forest is particularly rich, harboring at least 20 economically valuable tree species and 50 percent of Argentina's avifauna (Brown *et al.* 1993). However, at least 30 percent of the subtropical montane forest has already been transformed to agricultural lands (Brown *et al.* 2002) and most remnant forests are highly degraded by inappropriate forest logging (Grau & Brown 2000, Pacheco & Brown 2006). Furthermore, as the forest stock becomes depleted, forests lose their economic value and are more likely to be transformed to other land uses (McComb 2007). Therefore, it is essential to develop management guidelines that maintain both the economic and ecological value of forests (Fimbel *et al.* 2001).

Some initiatives have promoted better management of subtropical montane forest in Argentina. For example, the Forest Stewardship Council has certified two land owners (both international corporations) although the certification standards used were generic, with little, if any, specific recognition of the particular characteristics of Andean subtropical montane forest. Another initiative—Developing Good Forest Practices—has been undertaken by an environmental group, ProYungas, with funding from the French Global Environment Facility. This program focuses on using ecological information to increase forest productivity but also includes biodiversity aspects; however, it too is hindered by a lack of scientific information.

Our research was catalyzed by this opportunity to influence sustainable forest-management strategies during a critical period of policy development. While this study is focused on Andean subtropical montane forest in northwestern Argentina we believe that it will be also useful in formulating management guidelines in other regions where sustainable forestry is under development.

We focused on cavity-nesting birds because: (1) they are likely to be particularly sensitive to logging due to loss of nesting sites (Grieser Johns 1997); (2) their status may be indicative of the welfare of a large suite of species that are dependent on older, often dead or dying, trees (McComb & Lindenmayer 1999); and (3) they are relatively easy to study. Therefore, understanding the effects of logging on cavity-nesting birds is a straightforward and significant

Received 10 June 2008; revision accepted 3 September 2008.
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step toward understanding the effects of logging on ecosystem integrity. More specifically, we examined nest-site use in relation to cavity, tree, and forest stand characteristics and developed predictive models to determine the probability of occurrence of a cavity nest. This is the first study that addresses the nesting requirements of cavity nesters in Andean forests; previously, there were only anecdotal records of cavity-nesting sites for some species (*e.g.*, de la Peña 1998).

METHODS

STUDY SITE.—Fieldwork was conducted in the subtropical montane forests of the Andes in northwestern Argentina known as Yungas or selva Tucumano-Boliviana (Cabrera 1994); this is the southernmost limit of Neotropical montane forests (Hueck 1978). The study area lies in the tropical–subtropical transition at 23–24° S (Fig. 1). We studied both piedmont forest, *i.e.*, *ca* 400–750 m asl, and cloud forest, found at 1500–2200 m asl. Climate in both forest types is highly seasonal with rainfall concentrated (75–80%) during the summer (*i.e.*, November to March). Annual rainfall averages *ca* 800 mm in the piedmont and 1300 mm in the cloud forest (Brown *et al.* 2001). Mean annual temperature averages 21.1°C for the piedmont forest and 11.7°C in the cloud forest (Arias & Bianchi 1996). We selected six 100-ha sites in the piedmont and five 100-ha sites in the cloud forest (Fig. 1).

Most of the forestland (estimates of 50–90% [Brown *et al.* 2001, Brown & Malizia 2004]) in the piedmont region of northwestern Argentina has been transformed to agricultural fields because of the relatively flat terrain, good soils, and proximity to urban areas. Remnant piedmont forests are subject to extensive high-grade selective logging, focusing primarily on 10 valuable timber species (Brown & Malizia 2004). Piedmont forest in relative good conservation status has a continuous canopy of 20–25 m of height, a basal area of 30–35 m^2/ha, and around 40 trees species/ha (Brown *et al.* 2006). Cloud forest remnants are also subject to intense selective logging, primarily of one species (*i.e.*, *Cedrela lilloi*). Until recently (late 1990s) *Podocarpus parlatorei* was intensively logged for paper pulp production, but now paper pulp is made from sugar cane. Cloud forests are also frequently replaced by grasslands through intentional fires set to facilitate extensive cattle grazing (Brown *et al.* 2001). Cloud forests in good conservation status have around 15–20 species/ha, a high basal area that can be > 40 m^2/ha, and a height of 25–30 m (Brown *et al.* 2006).

In the subtropical montane forest of Argentina there are 214 forest-restricted bird species (around 140 bird species in the piedmont and 130 in the cloud forest) (Blendinger & Alvarez, in press). Of those, eight are cavity excavators (*i.e.*, golden-green woodpecker *Piculus rubiginosus*, ocellated woodpecker *Picumnus dorbignyanus*, white-barred woodpecker *P. cirratus*, smoky-brown woodpecker *Veniliornis fumigatus*, dot-fronted woodpecker *V. frontalis*, lineated woodpecker *Dryocopus lineatus*, cream-backed woodpecker *Campephilus leucopogon*, crimson-crested woodpecker *C. melanoleucos*) and an additional 42 species are obligate cavity nesters (*e.g.*, toco toucan *Ramphastos toco*, blacked-banded woodcreeper *Dendrocolaptes picumnus*, great rufous woodcreeper *Xiphocolaptes major*, alder amazon *Amazona tucumana*, turquoise-fronted amazon *A. aestiva*, mitred parakeet *Aratinga mitrata*, scaly-headed parrot *Pionus maximiliani*, Hoy's screech-owl *Otus hoyi*, Yungas pygmy-owl *Glaucidium bolivianum*,

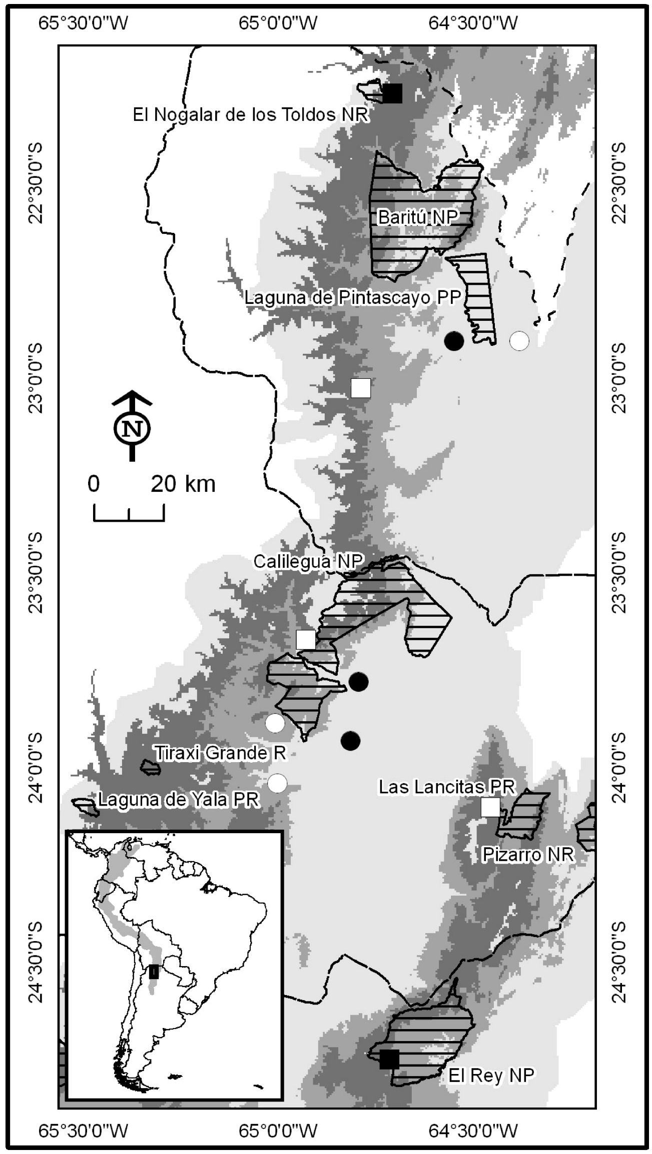

FIGURE 1. Location of study sites in the subtropical montane forests of the Andes. Lightest gray (almost white) and circular symbols = piedmont forest, intermediate gray = montane forest of intermediate elevation that were not studied, darkest gray and square symbols = cloud forest. Hatched areas represent protected areas, NP = National Park, NR = National Reserve, PP = Provincial Park, PR = Provincial Reserve, filled symbols = control sites, open symbols = harvested sites. Left-bottom corner map shows (in gray) the distribution of subtropical and tropical montane forest of the Andes and the box shows the study area.

barred forest-falcon *Micrastur ruficollis*, collared forest-falcon *Micrastur semitorquatus*, etc.; de la Peña 1998).

DATA COLLECTION.—At each site we established 20 variable-width, random direction, 300-m long transects that were at least 150 m apart. Cavity sampling was conducted during the dry season (April–August) when many trees are leafless (piedmont forest is deciduous and cloud forest is semi-deciduous). We marked every cavity encountered, regardless of location in the tree (*i.e.*, branch or bole), that had a diameter entrance > 3 cm and a height > 2 m and < 15 m and all the cavities were inspected with a camera system attached to an extendible pole of 15 m (Richardson *et al.* 1999). We made monthly inspections during two breeding seasons (August–February 2005–2006 and 2006–2007) to cavities that we knew to be suitable for avian cavity-nesting (*i.e.*, hollow chambers surrounded by sound wood [not collapsing wood] accessed by entrance holes with a floor to harbor an incubation chamber, and a roof to provide overhead protection; hereafter referred as potentially usable cavities). In total we monitored 192 cavities in piedmont forest and 107 in cloud forest to determine if avian cavity nesters made use of the cavities. We probably missed some potentially usable cavities, (notably those > 15 m) but this was true at all sites and thus should not unduly influence our key comparisons. Also, our methods excluded two species (*P. dorbignyanus* and *P. cirratus*) that use cavities with entrance diameters < 3 cm.

For each potentially usable cavity, we recorded: tree species, dbh, tree height, tree type (living with no signs of decay; living with signs of decay; dead), cavity height, cavity entrance area (by measuring the horizontal and vertical diameters of the entrance), internal cavity diameter (the horizontal diameter from the entrance to the opposite wall), internal cavity height (or depth; measured from the entrance to the incubation chamber), and origin of the cavity (*i.e.*, excavated or decayed). All trees with active cavities (those that had evidence of current or past nesting [*e.g.*, when we found eggs, chicks, or egg shells that were not previously found]) were made the center of a 0.05-ha circular plot in which we counted every tree species of dbh > 10 cm and measured diameter at breast height. A random subsample ($N = 84$ in the piedmont, $N = 42$ in the cloud forest) of the potentially usable cavities that did not have nests was also used as the centers of 0.05-ha circular plots. We compared active cavities to suitable but unused cavities to assess habitat selection.

DATA ANALYSIS.—We compared cavity, tree, and stand-level characteristics between active and potentially usable cavities using comparisons of means (*i.e.*, Kolmogorov–Smirnov tests for non-normally distributed variables). We used Manly's selection index to determine nest-site selection in relation to availability in each forest type of the subtropical montane forest (Manly *et al.* 2002). We calculated a selection coefficient and the 95% CI for categorical nest-site variables including cavity origin, tree species, and decay category. Selection coefficients were calculated as $w_i = o_i/p_i$, where w_i was the selection coefficient for cavity category i, o_i was the ratio of the number of active cavities in category i to the total number of active cavities, and p_i was the ratio of the number of cavities in category i to the total number of cavities. Standard errors of selection coefficients were calculated as $SE(w_i) = \sqrt{\{[o_i\ (1\text{-}o_i)]/Up_i\}}$, where U was the total number of active cavities. Selection coefficients were tested for significance using the log-likelihood ratio (G test; Manly *et al.* 2002).

Logistic regression was used to build a model that could distinguish between active and potentially usable cavities. Logistic regression is particularly suitable for habitat association studies because habitat variables often have non-normal distributions, and are categorical, and the sampling design is retrospective (Ramsey *et al.* 1994). The final selection of the model involved backward elimination of nonsignificant effects and testing the individual significance of each variable using deviance tests. Akaike's information criterion (AIC) was used to determine the most parsimonious model fitting the data (Burnham & Anderson 2002). We used ΔAIC (*i.e.*, the difference between the best model and other models) to provide insight into the amount of uncertainty in model selection, and we used the model weight to assess the relative plausibility of each model (Burnham & Anderson 2002). The logistic regression analysis also provided jack-knife estimates of the classification rates of both nest and potentially usable cavities. Before this analysis was conducted, a correlation matrix including all parameters was generated. Highly correlated parameters ($r > 0.50$) were not all included in the analysis (Table S1). If the predictor variables were highly skewed, the variables were transformed to $\log_{10}$ (Quinn & Keough 2002). To compare the effects of quantitative predictors having different units, variables were standardized (Agresti 1996). The logistic regression model classifies an observation as a nest or a potential nest site according to the parameters in the model.

RESULTS

Of the 192 piedmont cavities that were potentially usable for bird breeding, 31 had evidence of bird nests (16%). We found seven nests of *O. hoyi*, three of *C. leucopogon*, two of *P. maximiliani*, two of lesser woodcreeper *Lepidocolaptes angustirostris*, two of *P. rubiginosus*, one of bat falcon *Falco rufigularis*, and one of *M. semitorquatus*; the remaining were unidentified. In the cloud forest, of the 107 potentially usable cavities examined, birds nested in 29 (27%). Seven nests belonged to *A. mitrata*, five to *A. tucumana,* two to *C. leucopogon*, one to *Otus choliba*, one to green-cheeked parakeet *Pyrrhura molinae*, and the others were unidentified. In the piedmont forest, cavities occupied for breeding were, compared to potentially usable cavities, significantly more frequently: found in *Calycophylum multiflorum*, snags, and live trees with signs of decay; excavated; higher above the ground; located in plots with significantly greater mean tree dbh; and had smaller cavity entrances (Table 1; Fig. 2). In the cloud forest, cavities occupied for breeding were, compared to potentially usable cavities, significantly more frequently: found in *Blepharocalyx gigantea*, *P. parlatorei*, and live trees with signs of decay; excavated; located in plots with greater mean tree dbh and basal area; and had smaller cavity entrances (Table 1; Fig. 2).

TABLE 1. *Cavity, tree, and plot characteristics of nests and potentially usable cavities in the piedmont and cloud forest. Abbreviations of parameters are in brackets. Means with different superscripts in a row show significant differences (Kolmogorov–Smirnov tests,* P *< 0.05); means not followed by superscripts did not differ significantly (*P *> 0.05).*

Forest type	Characteristics	Nests Mean	Nests SE	Usable Mean	Usable SE	*P*-value
Piedmont		$N = 31$		$N = 138$		
Plot	Mean dbh (cm) [PMD]	27.0[a]	2.80	22.6[b]	4.10	0.00
	Basal area (m^2/ha) [PBA]	30.2	9.56	24.1	6.02	0.31
	Stem density (ind/ha) [PSD]	427	112	397	90.5	0.69
Tree	dbh (cm) [TD]	48.9	17.7	43.3	20.3	0.06
	Height (m) [TH]	15.1	4.46	14.7	5.00	0.60
Cavity	Height (m) [CH]	9.50[a]	2.75	6.99[b]	3.16	0.00
	Entrance area (cm^2) [CEA]	166[a]	191	601[b]	847	0.02
Cloud		$N = 29$		$N = 77$		
Plot	Mean dbh (cm)	35.9[a]	13.2	26.9[b]	4.90	0.00
	Basal area (m^2/ha)	47.7[a]	21.3	31.9[b]	10.5	0.00
	Stem density (ind/ha)	361	116	431	134	0.14
Tree	dbh (cm)	69.8	23.8	64.1	25.2	0.34
	Height (m)	21.8	9.93	17.2	8.18	0.42
Cavity	Height (m)	9.39	3.10	8.65	3.05	0.26
	Entrance area (cm^2)	674[a]	628	1160[b]	1024	0.00

In the piedmont, the model that best predicted whether a cavity was used as a nest was based on the plot dbh, stem density, cavity height, and internal height (Table S2); all four parameters had a positive relationship with the probability of encountering a nest. The model correctly classified nests 91 percent of the time. The model that best predicted (82% correct) whether a cavity was used in the cloud forest was based on two characteristics (plot mean dbh and cavity entrance area; Table S2). Cavities with smaller cavity entrance area and within plots that had greater mean dbh were predicted to be more likely to be used for nesting.

DISCUSSION

Cavities used for nesting were not simply a random subset of all available cavities. Birds were selective, thus rendering a proportion of apparently available cavities unsuitable. We found that birds select cavity nests at three different scales, at the cavity, tree, and stand levels. These findings have important implications for forest management because Argentinean foresters and loggers currently manage primarily at the tree level; *e.g.*, choosing minimum diameters and valuable species (Brown & Pacheco 2006).

The structural characteristics of a cavity can affect both its microclimate and the level of protection from predators. For example, cavities that were higher above the ground and had greater internal cavity depth (or height) were more likely to be used in the piedmont forest and both these features have been associated with lower risks of predation in previous studies (Nilsson 1984, Peterson & Gauthier 1985, Li & Martin 1991). Higher and deeper cavities may be particularly relevant in piedmont forest, where there is a greater diversity of predators than in cloud forest where, for example, snakes are almost absent. We also found that nest cavities had smaller entrance areas than potentially usable cavities. Presumably, species prefer cavities with entrances not much larger than themselves, thus excluding entry of larger predators (Tidemann & Flavel 1987) or more competitively dominant species (Short 1979). Furthermore, small cavity entrances may provide better shelter from weather extremes (Barclay *et al.* 1988). In this study, cavities excavated by woodpeckers were used more often than expected based on their availability, highlighting the key role that woodpeckers have in providing preferred cavities for many species (Martin *et al.* 2004, Cornelius *et al.* 2008).

The use of particular tree species was also not random: piedmont cavity-nesters used *C. multiflorum* far more often than would be expected by chance, while in the cloud forest, *B. gigantea* and *P. parlatorei* were disproportionately important. These preferences represent a potential conflict between cavity nesters and loggers. By comparing forests that have been logged recently to those that are relatively undisturbed, we found that potentially usable cavities in *C. multiflorum* and *P. parlatorei* were reduced by 82 percent (from 1.73 potentially usable cavities/ha in control sites to 0.31/ha in logged sites) and 62 percent (from 1.37 potentially usable cavities/ha in control sites to 0.52/ha in logged sites), respectively (Politi 2008). These reductions are partly due to the fact that loggers do not avoid cutting trees with cavities because these species have a good ability to compartmentalize rot.

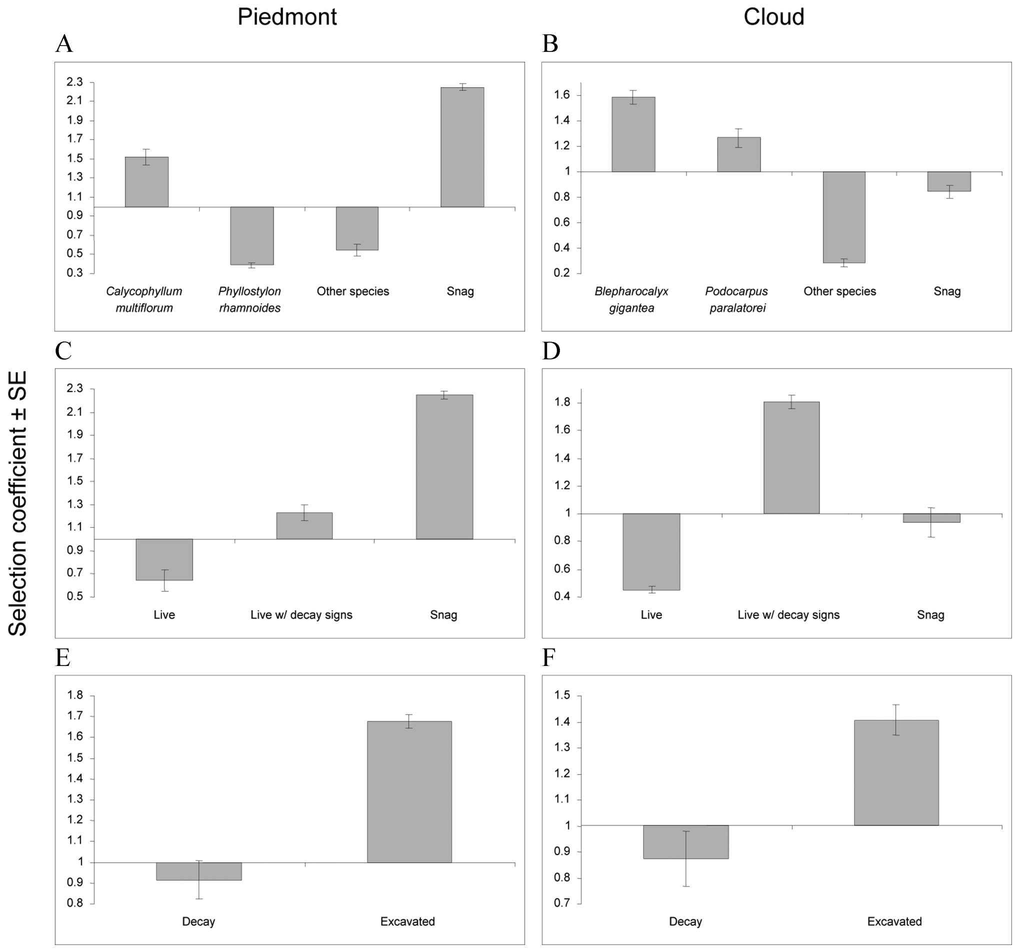

FIGURE 2. Cavity selection in the piedmont forest (A, C, E) and cloud forest (B, D, F) in relation to (A, B) tree species, (C, D) tree condition, and (E, F) cavity origin. The selection coefficient is the proportion of cavities used versus available: values > 1 implies preference; < 1 implies avoidance (Manly *et al.* 2002). Number of nests (N) = 31 in the piedmont forest; N = 29 in the cloud forest.

In both the piedmont and cloud forests, the probability of encountering a nest increased with a stand variable, increasing plot dbh, and in the piedmont forest it also increased with a related variable, plot stem density. In many studies, cavity nesters have been associated with larger trees (Scott *et al.* 1980, Raphael & White 1984, Harestad & Keisker 1989), thus suggesting that patches with large trees should be retained during logging. Furthermore, in a survey of cavity abundance in logged and relatively undisturbed control forests we found logged stands had a significantly lower number of potentially usable cavities than control sites (six times less in piedmont, and half the number in cloud forest; Politi 2008). In sum, logging in northwestern Argentina has reduced both suitable nesting habitat and the availability of nest sites for cavity-nesting species.

This study emphasizes the need to develop forest-management strategies based on at least two scales; *i.e.*, at an intermediate scale by maintaining some unlogged patches (at least of 0.05 ha based on our study) with high mean dbh within logging areas subject to selective logging and at a finer scale by retaining certain species of trees. The retention of unlogged patches will increase the probability of avian cavity nesters finding suitable nesting habitat and will benefit other species associated with mature stands (Fimbel *et al.* 2001, Lindenmayer & Franklin 2002). Ideally, we would like to know the optimal number of unlogged patches and their spatial arrangement, especially considering behavioral issues such as conspecific competition, predation, or food availability, but until detailed information is available we can work with the best judgment of ecologists who are familiar with this ecosystem. It is also important that in logging operations a large majority of existing trees with suitable cavities are retained, especially in *C. multiflorum* and *P. parlatorei* that harbor most of the potentially usable cavities. Furthermore, because of the high loss rate of potentially usable cavities in forests (23% per year in piedmont, and 40% in cloud; Politi 2008) it is important to also retain trees that currently do not harbor cavities but are likely to in the future (Ball *et al.* 1999, Politi 2008). Of course, beyond the ideas of leaving uncut patches and preferred tree species there are many other ways to mitigate the effects of timber management such as reduced impact logging techniques (Felton *et al.* 2008).

We are aware that our study encompasses a limited component of biodiversity; however, by studying cavity nesters and, incidentally, the trees that dominate the birds' habitat, we have focused on two of the most sensitive groups to logging operations (Grieser Johns 1997, Politi 2008). If forest management sustains cavity nesters, many other taxa are likely to thrive as well (Fimbel *et al.* 2001) and future research can address those species that may not be covered under the umbrella provided by cavity nesters.

This study is the first step in a process of building a bridge from scientific information to on-the-ground application. Our study has implications for sustainable forest management in the subtropical montane forests of Argentina, where a new law mandates sustainable forest use and where many landowners are interested in forest certification (Fimbel *et al.* 2001). Additional research on both ecological and economic aspects of forest management will be required, and ecologists, economists, and policy specialists will need to collaborate in designing a process by which economic and ecological goals can be balanced through sound forestry.

ACKNOWLEDGMENTS

Financial support for fieldwork was provided by: Rufford Small Grant for Nature Conservation, Wildlife Conservation Society Research Fellowship Program, UNESCO–MAB Young Scientists Award, University of Maine, and Idea Wild. N.P. undertook this project with support from a Fulbright Fellowship and a Prince Bernhard Scholarship for Nature Conservation (WWF). We are grateful to L. Wood for teaching us how to make a camera system to inspect cavities and for allowing us to use his camera system. This work benefited greatly from discussions with S. Chalukian, E. Simons, L. Malizia, A. White, C. Burns, W. Krohn, and F. Servello. Two anonymous reviewers and M. Pinard provided helpful comments on the manuscript. We thank Ledesma Industry SAAI, the Kolla Community of Finca Santiago, the Bracamonte and Cuñado families, the National Park Administration of Argentina, and the Salta and Jujuy Natural Resources Administration for giving us permission to work on their land. We are especially grateful to the park rangers and staff of El Rey National Park and Regional Technical Delegation. M. Cuevas and M. Gutierrez provided constant support. This publication is No. 3203 of the Maine Agricultural and Forest Experiment Station.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Correlation matrix between variables in the cloud forest and piedmont forest.*

TABLE S2. *AIC values for top models and parameter estimates for the best model on cavities occupied by birds to nest in the piedmont and cloud forest.*

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