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STAND ATTRIBUTES AND THE ABUNDANCE OF SECONDARY CAVITY-NESTING BIRDS IN SOUTHERN BEECH (*NOTHOFAGUS*) FORESTS IN SOUTH-CENTRAL CHILE

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Resumen. – Atributos de rodal y abundancia de aves nidificadoras de cavidades secundarias en bosques de *Nothofagus* en el centro-sur de Chile. – La ecología de aves nidificadoras de cavidades secundarias (NCS) ha captado gran interés en el mundo por muchos años, en parte por la relación directa entre la biología reproductiva de estas especies y los impactos del manejo forestal en la disponibilidad de cavidades. Mientras que existe gran cantidad de información sobre la ecología de los NSC para la región Paleártica y Neártica, ésta es escasa en el Neotrópico, especialmente para los bosques templados. Para describir el efecto de los atributos del bosque en la abundancia de aves NCS, realizamos un estudio de dos partes en la cordillera de la costa de la región del Maule, centro-sur de Chile. En primer lugar, usando 40 puntos de conteo distribuidos en un gradiente de bosques de *Nothofagus*, relacionamos las condiciones del bosque con la densidad de cuatro NCS (invierno y primavera austral de 1999 y 2000). En segundo lugar, usando un experimento con cajas anideras (primavera 1999, invierno 2000), probamos si las cavidades limitan la densidad de NCS en un bosque secundario. Los datos de conteos sugieren que no existen relaciones entre la densidad de las NSC para el invierno (ambos años), pero se encontraron relaciones positivas significativas con la altura total, el volumen total de follaje, el diámetro medio y la abundancia estimada de cavidades en la primavera (ambos años). A nivel de especie, las cavidades no entraron en un modelo de regresión lineal múltiple para la mayoría de las especies (las variables más significativas fueron la altura total y el diámetro medio) sugiriendo que nuestra definición de un sitio de nidificación adecuado fue incorrecta o que otros factores como la agregación espacial de las cavidades y la territorialidad podrían haber ocultado una potencial relación. El experimento de las cajas anideras mostró que las densidades del Rayadito (*Aphrastura spinicauda*, $P < 0,05$) y del Chercán (*Troglodytes aedon*, $P < 0,01$) están limitadas por los sitios de nidificación durante la época reproductiva, pero no durante la época no reproductiva.

Abstract. – The ecology of secondary cavity-nesting birds (SCN) has been a matter of great interest for many years throughout the world, in part because of the direct and strong relationship between the breeding biology of these species and the impacts of forest management on the availability of cavities. While there exists a great body of knowledge on the ecology of SCN in the Nearctic and Palaearctic regions, information from the Neotropics is scarce, in particular for the temperate forests. In order to describe the

effect of forest stand attributes on the abundance of SCN, we conducted a two-part study in the coastal range of the Maule region, south-central Chile. First, using 40 point-count stations covering the entire range of *Nothofagus* forest conditions, we related forest-stand attributes to the density of four SCN (austral winter and spring 1999, 2000). Second, using a nest-box experiment (spring 1999, winter 2000), we tested whether cavities were limiting the density of SCN in a second-growth forest. Point-count data suggest no relationships between the abundance of all SCN and habitat attributes during the winter (both years), but a significant and positive association with canopy height, total foliage volume, mean stem diameter and abundance of cavities (estimated) during the spring (both years). At the individual species level, cavities did not enter into a stepwise linear regression model for most species (most significant predictors were canopy height and stem diameter) suggesting that either our definition of what an appropriate nest site is was wrong or that factors such as cavity spatial aggregation and territoriality may have obscured a potential relationship. The nest-box experiment showed that the density of Thorn-tailed Rayaditos (*Aphrastura spinicauda*, $P < 0.05$) and House Wrens (*Troglodytes aedon*, $P < 0.01$) was limited by nesting sites during the breeding season, but not during the non-breeding one. *Accepted 24 October 2005.*

Key words: Secondary cavity-nesting bird, *Nothofagus*, stand attributes, A*phrastura spinicauda, Troglodytes aedon,* Chile.

INTRODUCTION

A significant number of bird species breed inside cavities. While some of these bird species can make their own cavities (known as primary cavity-nesting birds, hereafter PCN), a greater number cannot (called secondary cavity-nesting birds, hereafter SCN). In forests, cavities are usually excavated in tree trunks or branches by woodpeckers and are used by a variety of species (Raphael & White 1984, Sedgwick & Knopf 1990, Martin & Eadie 1999).

Old forests usually have a higher number of suitable cavities than second-growth forests, because of a higher availability of dead trees and a higher proportion of dead wood on bigger live trees (Newton 1994). There are many mechanisms that can lead trees to die: suppression by light competition, injuries, wind-throw, disease or insect infestation (Newton 1994, Oliver & Larson 1996, Lindenmayer *et al.* 2000, Jackson & Jackson 2004), thus favoring natural cavity formation (Lindenmayer *et al.* 1993, 2000) or becoming substrate to PCN to build new cavities (Raphael & White 1984, Newton 1994, Martin & Eadie 1999).

Some forest attributes may be strongly related to habitat quality for cavity-nesting birds (Raphael & White 1984, Sedgwick & Knopf 1990). For example, the number of snags (i.e., standing dead trees) or live large trees per hectare can affect the abundance of some SCN species (Newton 1994). These dead and old trees can provide food (Raphael & White 1984), roosting places (Aubry & Raley 2002) and can have territoriality significance, especially for woodpeckers (Wilkins & Ritchinson 1999, Imbeau & Desrochers 2002).

The most widely recognized conservation issue about cavity-nesting birds is their limitation in population size because of the provision of nesting sites, especially for SCN (Brush 1983, Raphael & White 1984, Wiens 1992, Ingold 1998, Newton 1998). This association with old-growth forests attributes (presence of old or dead trees for PCNs and cavity trees for SCNs) makes them especially sensitive to forest management strategies that prevent the occurrence and permanence of such trees (Newton 1994, Gibbons & Lindenmayer 1996).

The Maulino Forest is located in the coastal range of south-central Chile (34º55' to

36°20'S, San Martín & Donoso 1996). It is dominated by deciduous trees of the genus *Nothofagus* (Lara *et al.* 1996). The former distribution range of Maulino forest covered c. 500,000 ha, but since the early 18th century, the Maulino Forest has been cleared and fragmented to provide land for agriculture and for the production of timber and charcoal (San Martín & Donoso 1996). By the 1980s, most of the landscape had been transformed into exotic Monterrey pine (*Pinus radiata*) plantations, leaving only scattered fragments of forest remnants embedded in a matrix of pine woodlands (Hormazábal & Benoit 1987, Gajardo 1994, Estades & Temple 1999). Nowadays these remnants only cover c. 43,000 ha (CONAF/CONAMA 1999) and are structurally degradated because of the lack of a forest management scheme (Olave 1984) leaving second-growth stands with few old trees and old-gwoth conditions restricted to narrow strips along creeks (Donoso 1993, San Martín & Donoso 1996). These two forest types can be found in a gradient of conditions, from more mesic sites (old-growth) to more xeric sites (second-growth).

Bird communities of the Maulino forest have been matter of study only since the recent years. Estades & Temple (1999) found 31 species in a 10,000 ha native forest area. Without considering raptors and ground cavity-nesters, the bird species that use secondary tree cavities to nest are the Thorn-tailed Rayadito (*Aphrastura spinicauda*), the House Wren (*Troglodytes aedon*), the Plain-mantled Tit-spinetail (*Leptasthenura aegithaloides*), the White-throated Treerunner (*Pygarrhichas albogularis*), and the Chilean Swallow (*Tachycineta leucopyga*). Both the Thorn-tailed Rayadito and the White-throated Treerunner are resident endemic species of the temperate forests of southern South America (Willson *et al.* 1994, Rozzi *et al.* 1996) and can be considered true forest species (Vuilleumier 1967). The Thorn-tailed Rayadito is a small foliage gleaner insec-

tivorous bird that can ecologically remind a tit (Paridae) (Johnson 1967, Jaramillo 2003). It is one of the most abundant bird species on the Chilean forests (Willson *et al.* 1994, Estades & Temple 1999). The White-throated Treerunner is a foliage and bark gleaner insectivorous that can resemble (in appearance and behavior) to a Nuthatch (*Sitta* spp.) (Johnson 1967). This species is not as common as the Rayadito. It can be found joining mixed-flocks with the Rayadito and other species during the non-breeding season (Vuilleumier 1967, Ippi & Trejo 2003, Estades *et al.* pers. observ.). The Chilean Swallow, the House Wren, and the Plain-mantled Tit-spinetail are widespread insectivorous species that are not restricted to forests. None of these species have been listed in a threat category in Chile (Glade 1988). Primary-cavity nesters that can provide cavities for SCN species are the Striped Woodpecker (*Picoides lignarius*), and the Chilean Flicker (*Colaptes pitius*). The presence of the largest woodpecker in the southern temperate forests, the Magellanic Woodpecker (*Campephilus magellanicus*), was reported by Estades & Temple (1999), but in such low densities that it is unlikely that it may provide a significant number of cavities. A portion of the cavities may be provided by the White-throated Treerunner (a weak cavity excavator). Its antagonistic behavior against some SCN species for nesting-site utilization suggests competition more than facilitation for this resource (Estades *et al.*, pers. observ.). Unfortunately, the nest-web (sensu Martin & Eadie 1999) has not been studied in these forests so there are no data on interspecific interactions for nest sites.

Forest management strategies that benefit cavity-nesters include insert (like nest boxes, but inserted inside tree trunks, see Saenz *et al.* 2001) and snag provision (e.g., Peterson & Grubb Jr. 1983, Caine & Marion 1991, Lohr *et al.* 2002) for PCNs, nest boxes for SCN birds (e.g., White & Seginak 2000, Twedt & Henne-
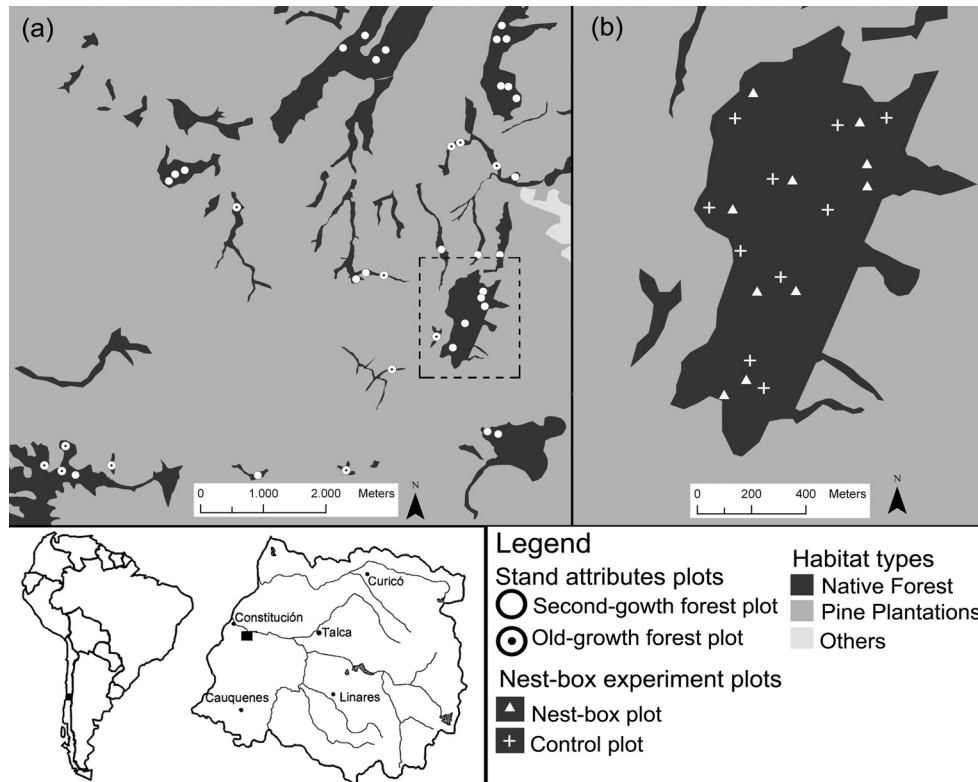
FIG. 1. Study area in the Maule Region on south-central Chile where fragmented remnants of native *Nothofagus* forests (dark grey) are imbedded in *Pinus radiata* plantations (light grey). This study was conducted in two parts at two different scales: (a) the abundance of four species of secondary-cavity nesting (SCN) birds was related to a gradient of *Nothofagus* forests attributes (from second-growth to old-growth conditions) with forty sampling plots (notice that the radius of the plots in the figure does not show the actual radius of sampling plots), and (b) a nest-box addition experiment to test the nest-site limitation hypothesis in a second-growth *Nothofagus glauca* stand.

Kerr 2001), and retention of cavity trees (Gibbons & Lindenmayer 1996) for both.

Our objective through this study was to determine the relationships between stand attributes and the abundance of secondary cavity-nesting bird species. It consisted of two parts. First, SCN species abundance was related to stand attributes in a natural experiment, and second, a nest-box experiment was conducted in order to determine whether nesting sites were limiting SCN density in a second-growth *Nothofagus glauca* stand.

METHODS

Study area. The study was conducted during part of the austral breeding (October and November) and non-breeding (June) seasons of 1999 and 2000 in the coastal range of the Maule Region, at the Pantanillos Forest Research Station of the University of Chile (35°26'S, 72°17'W; Fig. 1). The area is dominated by Monterrey pine plantations while native forest is severely fragmented and reduced to less than 10% of its original extent

(Estades & Temple 1999). Native vegetation is dominated by trees of the genus *Nothofagus*. Along creeks, there are narrow strips of old-growth *Nothofagus dombeyi* forests that reach up to 25–30 m in height. Upland remnants are dominated by second-growth *Nothofagus glauca* forests that have suffered human activities such as wood, charcoal and firewood collection. Frequent human-caused wildfires have impeded these forests from growing more than 15–20 m in height in the best places.

Stand attributes and the abundance of SCN. Forty 50-m radius circular sampling plots (except during non-breeding season 2000, N = 35, due to the excess of rainy days during the field season) were set randomly distributed in the study area (Fig. 1a). Twenty-eight plots were set in second-growth forest and 12 in old-growth forests according to availability in the study area. The altitude of these plots ranges from 300 up to 540 m a.s.l. (mean 430 m. a.s.l.). The mean distance between neighboring plots was 557 m, ranging from 85 up to 3190 m. The closest plots, only 85 m away (when measured in the map), were considered independent because one was on the top of a hill and the other was more than 100 m away downhill. Both habitat attributes and bird densities were estimated at each of these plots.

Habitat attributes. In the sampling plots described above some habitat variables were measured and others were estimated. Canopy height (estimated in meters) was the maximum height reached by trees in the plot. Diameter at breast height (dbh) was measured with an aluminum caliper for every individual larger than 5 cm. The number of trees (larger than 5 cm dbh) per plot was also accounted and expanded to the hectare. Total basal area was calculated as the sum of dbh per plot, and expanded to the hectare. Mean dbh (in cm) was calculated as the squared root of total basal area divided by the number of trees per

hectare. To assess the total foliage volume, the sampling plots were divided in four quadrants. In each of these quadrants, the foliage cover was visually estimated in four height layers (0–0.3 m, 0.31–2 m, 2.01–6 m, and over 6 m) according to natural vegetation stratification. Then, total foliage volume was calculated as the sum of foliage cover per layer times its height in meters (Estades 1997, Estades & Temple 1999). The number of cavities potentially suitable for breeding was counted using a standard searching effort (time spent on each tree) as an estimate of the abundance of cavities. However, the presence of a nesting chamber inside the cavity, especially for the higher ones, could not be verified so this should be considered a coarse estimator of the actual number of cavities. Stand attributes from second-growth plots and old-growth plots were pooled to consider a wider range of *Nothofagus* forests attributes in the analyses.

Bird counts. Bird densities were estimated using variable-radius point counts (Buckland 1987, Buckland *et al.* 1993). Point counts were preferred because the observer is concentrated on detection, location and identification of birds, and because they are more efficient in forest conditions than other methods (Buckland *et al.* 1993, Ralph *et al.* 1996). Using a maximum radius of 50 m, every bird detected within 10 m concentric rings was recorded. Two consecutive 5-min counts with a 5-min interval between them were used in order to maximize the time spent in point counts relative to the time traveling between them (Estades & Temple 1999). All counts were conducted by CFE from sunrise to midday (06:30 to 11:00, breeding season; 07:30 to 12:00, non-breeding season) on non-rainy days. Individuals that flew over the plot were not considered unless they were highly-mobile species (e.g., hummingbirds or swallows) showing evident use of the vegetation of the plot (e.g., flycatching). For the latter,

only the individuals that were present at the beginning of the counting period were recorded. Every plot was visited twice, and only once during the breeding and non-breeding seasons, respectively.

Analyses. All SCN species were considered for the analyses with the only exception of the Plain-mantled Tit-spinetail which is too scarce in the area. The White-throated Treerunner was included due to its weak-cavity excavation abilities, and possible competition with the SCN species.

Density of each species was corrected by its detectability (Buckland *et al.* 1993). Detectability was calculated using the total frequency of observations at every 10-m increment divided by the annular area encompassed by that increment and then divided by the maximum frequency in order to give values between 0 and 1. The correction factor was calculated by dividing the cilinder of height 1 and radius 50 m (i.e., no detectability decline) by the volume resulting of the rotation the observed frequency distribution. Finally, the abundance of all species was log-transformed [i.e., Ln (density +1)]. To determine the relationships between species densities and stand attributes, simple and multiple linear regressions were used (Sokal & Rohlf 2003). In multiple regression model analyses, non-significant predictors were eliminated using a stepwise procedure (backward, alpha to remove = 0.15). If non-significant ($P > 0.05$) variables were still present in the model, the less significant one was manually removed, and the stepwise regression was run again with remaining variables.

Nest-box experiment. Fifty nest boxes were set in 10 plots (five boxes per plot) during the non-breeding season of 1999 (June). These plots were paired with 10 control plots (i.e., without nest-boxes) with similar characteristics. No differences were found in mean diameter (Paired-t test, t = 0.96, df = 9, $P = 0.181$), number of trees per hectare (Paired-t test, t = 0.243, df = 9, $P = 0.407$), and basal area (Paired-t test, t = 1.188, df = 9, $P = 0.133$), but trees were slightly taller in control than in nest-box plots (Paired-t test, t = 2.104, df = 9, $P = 0.032$). Nest-box and control plots were located at variable distances (from 70 to 180 m apart, mean ± SD = 132.6 ± 46.6 m). To avoid bias due to plot location, treatment (nest-boxes) and control plots were randomly located within the forest stand in study (Fig. 1b). None of the nest-box plots was located near those used for the first experiment. Nest-boxes were designed based on authors' observations of Thorn-tailed Rayadito nests in the study area. Nest-boxes were made on wood and had a base of 11 x 13 cm and a height of 27 cm in the front and 30 cm in the back. Wood thickness was variable, but the mean was c. 7 mm. The entrance hole had 3 cm in diameter, and it was placed 25 cm above the nest-box bottom. In order to facilitate checking nest-box content, they had a hinged-roof. Nest-boxes were attached only to *Nothofagus glauca* trees, at 3–4 m in height. They were oriented facing the center of the plot, and no farther than 25 m from it. Bird abundance was estimated with point-counts carried-out by JAT, using the same method as above, except for the maximum distance (30 m), and only for one year (breeding 1999 and non-breeding 2000). Each plot was visited four times and twice, during the breeding and the non-breeding seasons, respectively. Mean bird abundances on nest-box plots were compared to control plots using Student's paired t-test (Canavos 1988, Sokal & Rohlf 2003) for the breeding (October–November 1999) and the non-breeding (June 2000) seasons.

RESULTS

Stand attributes and the abundance of SCN. Stand attributes found in both forest types are

TABLE 1. Stand attributes in two types of *Nothofagus* forests in the coastal range of south-central Chile. Mean value and range (minimum–maximum) are shown.

Forest types	Canopy height (m)	Number of trees per ha	Total foliage volume (m^2)	Mean diameter (cm)	Basal area (m^2/ha)	Number of cavities
Second-growth *Nothofagus glauca* plots (N = 28)	10.74 (6.0–21.0)	1611 (326–4450)	523.88 (184.9–1046.0)	12.23 (4.6–23.0)	16.51 (2.3–38.1)	1.46 (0–10)
Old-growth *Nothofagus dombeyi* plots (N = 12)	23.05 (13.2–37.0)	625 (54–3055)	876.6 (418.9–1571.0)	28.28 (8.4–41.4)	18.14 (7.3–34.6)	10.17 (3–25)
All (N=40)	14.43 (6.0–37.0)	1315 (54–4450)	629.7 (184.9–1571.0)	17.04 (4.6–41.4)	17.00 (2.31–38.07)	4.07 (0–25)

TABLE 2. Density (ind./ha) $\pm$ SD of four secondary cavity nesting birds species in *Nothofagus* forests in the coastal range of south-central Chile.

Species	1999		2000	
	Non-breeding	Breeding	Non-breeding	Breeding
Aphrastura spinicauda	0.81 $\pm$ 1.38	1.82 $\pm$ 1.92	1.12 $\pm$ 1.52	1.02 $\pm$ 1.53
Troglodytes aedon	0.46 $\pm$ 0.60	0.66 $\pm$ 0.80	0.09 $\pm$ 0.32	0.63 $\pm$ 0.62
Pygarrhichas albogularis	0.15 $\pm$ 0.53	0.19 $\pm$ 0.36	0.07 $\pm$ 0.25	0.10 $\pm$ 0.20
Tachycineta leucopyga	0.05 $\pm$ 0.17	0.42 $\pm$ 0.59	0.00 $\pm$ 0.00	0.35 $\pm$ 0.67
All	1.48 $\pm$ 1.93	3.10 $\pm$ 2.79	1.29 $\pm$ 1.59	2.10 $\pm$ 2.23

shown in Table 1. As expected, the most abundant species was the Thorn-tailed Rayadito followed by the House Wren for all seasons (Table 2). The simple regression analysis showed a significant positive effect of most stand attributes on total SCN density during the breeding season for both years, but not during the non-breeding season (Table 3). In the multiple regression analysis, the pattern was consistent between breeding seasons. However, after removing the total basal area and the number of cavities from the model, the effect of total foliage volume was negative in 1999 (Table 3). At the species level, during the breeding season, patterns were consistent between years for most species (except for the House Wren) (Table 4). On the other hand, some significant relationships were found during the non-breeding season, but without an evident pattern (Table 4).

Nesting-site limitation on SCN density. Only two species nested in the boxes during the 1999 breeding season. Eleven active nests of Thorn-tailed Rayaditos and seven of House Wrens were recorded. Additionally, 14 nest-boxes showed some nesting materials and 18 were not used. During the breeding season (Fig. 2a), the density was significantly higher

7

TABLE 3. Effect of different forest-stand attributes alone (simple regression analysis) and combined (multiple regression analysis) on the density (log-transformed) of four secondary cavity-nesting bird species in Nothofagus forests in the coastal range of south-central Chile. Regression coefficients are shown. In multiple regression analysis, attributes were selected using the stepwise-backward procedure (see Methods). Significance is expressed as follows: P > 0.05 (ns), P < 0.05 (*), P < 0.01 (**), P < 0.001 (***), P < 0.0001 (****).

Season	Year	Canopy height (m)	Number of trees per ha	Total foliage volume (m³)	Mean diameter (cm)	Basal area (m²/ha)	Number of cavities
Simple regression analysis							
Non-breeding	1999	ns	ns	ns	ns	ns	ns
	2000	0.033*	ns	ns	ns	ns	ns
Breeding	1999	0.082****	ns	0.0009***	0.051****	ns	0.098****
	2000	0.080****	ns	0.0011**	0.053****	ns	0.098****
Multiple regression analysis							
Non-breeding	1999	ns	ns	ns	ns	ns	ns
	2000	0.033*	ns	ns	ns	ns	ns
Breeding	1999	0.083****	ns	- 0.0006*	0.028***	ns	ns
	2000	0.057****	ns	ns	0.033***	ns	ns

in nest-boxes plots than in control plots for the Thorn-tailed Rayadito (one-tailed Paired t-test, t = 2.05, df = 9, P = 0.035), and the House Wren (one-tailed Paired t-test, t = 3.02, df = 9, P = 0.007). No differences were found during the non-breeding season (Fig. 2b), for both the Thorn-tailed Rayadito (one-tailed Paired t-test, t = –0.13, df = 9, P = 0.450), and the House Wren (one-tailed Paired t-test, t = –0.97, df = 9, P = 0.187).

DISCUSSION

Stand attributes and bird abundance. Our results show a significant and consistent relationship between the degree of development of the forest and the density of SCN during the breeding season. In fact, total height and mean diameter, both of which increase with stand age, were the most important predictors of the abundance of SCN. The latter stand attributes have been recognized as having important effects on the abundance of SCN in several studies (Raphael & White 1984,

Newton 1994, Berg 1997, Estades & Temple 1999). Raphael & White (1984) highlight the importance of stem diameter as a key variable in habitat selection by SCN, although different species show different specific requirements (Sedgwick & Knopf 1990). Old forests contain a higher proportion of larger trees (diameter and height) with a large number of different types of cavities, which, in turn, can be used by a larger number species (Newton 1994).

In our study, the number of cavities was an important predictor of the abundance of SCN when considered separately from other stand variables. However, when analyzed in a multiple regression model, the number of cavities was eliminated by the stepwise procedure, probably because of two non-exclusive factors: 1) our definition of "cavity" was not functionally correct, mostly due to the impossibility of checking their internal structure (particularly for the higher ones), and 2) the number of cavities present in a site might not reflect the number of cavities available for

TABLE 4. Effect of different forest-stand attributes on the density (log-transformed) of four SCN birds species in *Nothofagus* forests at the coastal range of south-central Chile. Attributes were selected using the stepwise-backward procedure in a multiple regression analysis (see Methods). *Tachycineta leucopyga* was not analyzed in non-breeding season due to migratory movement. Regression coefficients are shown. Significance is expressed as follows: $P > 0.05$ (ns), $P < 0.05$ (*), $P < 0.01$ (**), $P < 0.001$ (***), $P < 0.0001$ (****).

Species	Year	Canopy height (m)	Total foliage volume (m^3)	Mean diameter (cm)	Basal area (m^2/ha)	Number of cavities
Breeding season						
Aphrastura spinicauda	1999	0.062****	ns	0.026***	ns	ns
	2000	0.061****	ns	0.026***	ns	ns
Pygarrhichas albogularis	1999	0.028***	ns	-0.0003*	ns	ns
	2000	0.020***	ns	-0.009**	ns	0.021**
Tachycineta leucopyga	1999	0.016*	ns	0.020****	ns	ns
	2000	0.014*	ns	0.014**	ns	ns
Troglodytes aedon	1999	ns	-0.0005**	ns	ns	0.042****
	2000	ns	ns	0.016*	ns	ns
Non-breeding season						
Aphrastura spinicauda	1999	ns	ns	ns	0.024**	ns
	2000	0.04*	ns	ns	ns	ns
Pygarrhichas albogularis	1999	ns	ns	ns	ns	ns
	2000	ns	ns	ns	ns	ns
Troglodytes aedon	1999	ns	ns	-0.012*	ns	ns
	2000	ns	-0.0003**	ns	0.012**	ns

birds, due to the effects of territoriality (Newton 1994).

Canopy height had the most explanatory power of all studied variables and that is likely not only due to the fact that the size of trees is correlated with the abundance of cavities (Lindenmayer *et al.* 1993, 2000; Estades & Tomasevic 2004), but also because height per se may be important for birds as taller trees may bear cavities that are more difficult to reach by predators (Newton 1994).

The positive effect of foliage volume on spring SCN density in the simple regression analysis may be explained by the association between foliage biomass and food biomass for many birds (Mills *et al.* 1991), or simply by the correlation between foliage volume and overall tree size. Although this is mere speculation, the negative effect of the total foliage volume in the spring of 1999 (Table 3) might

reflect the fact that, given a large size of trees (positive effects of height and stem diameter), less foliage volume could be an indication of tree decay.

The lack of a clear pattern during both winter seasons suggests that the measured attributes are not sufficiently related to variables limiting SCN populations during the winter, such as food and refuge. During the winter eight bird species in the *Nothofagus* forests join mixed flocks (Estades 2001) that move throughout the landscape rather than defending a foraging territory.

Nesting sites as a limiting factor. Differences in abundance of Thorn-tailed Rayaditos and House Wrens between treatment and control plots suggest that the density of both species is limited by nesting sites in the breeding season. This pattern was not observed during
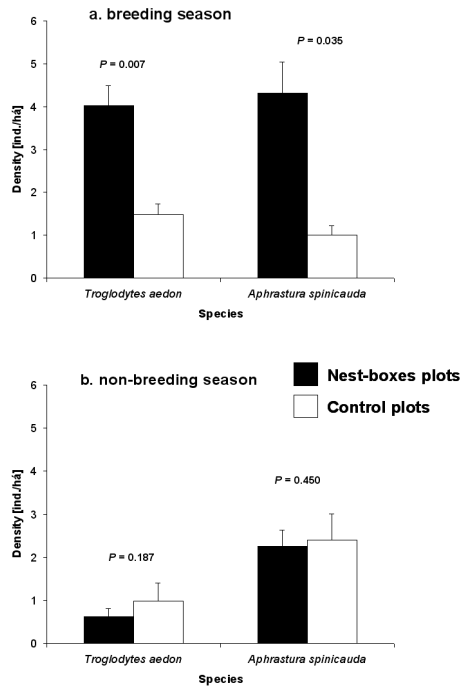
FIG. 2. Mean abundance (with 1 SE lines) of two secondary cavity-nesting bird species on nest-boxes (black bars) and control plots (white bars) for (a) breeding and (b) non-breeding season. Abundances were corrected by detectability, except for *Troglodytes aedon* on the non-breeding season. Significance of one-tailed paired t-tests is shown.

winter when nesting sites are not supposed to limit populations. The lack of nests of White-throated Treerunners and Chilean Swallows can be explained by the relatively low density of these species in the second-growth stand (Tomasevic 2002), although both species have successfully used other nest boxes in the area (including pine plantations). In addition, these boxes were also used by one small-mammal species (*Thylamys elegans*) for breeding, hibernating, roosting, and as bird nest predator.

Because of the small average diameter of trees in the studied forest (Tomasevic 2002) we expected Thorn-tailed Rayaditos to be

limited by the abundance of cavities. However, because of the high flexibility of the House Wrens nest-site selection (McCabe 1965, Johnson 1967), we did not expect this species to respond as intensively to nest boxes as it did. The significant increase in the density of House Wrens in treatment plots might be explained by the habit of male House Wrens selecting more than one cavity to attract females (Kendeigh 1941, Alworth & Scheiber 2000). The important increase in density of both species in plots with nest boxes (Fig. 2a) may be due to the fact that densities in the natural condition (control plots) were very low, with areas were the studied birds were almost absent. In places with high densities, the response to manipulations in nest-sites availability may not be as high (Brush 1983), probably due to density-dependent factors.

In our study site, the highest abundance of large dead trees and natural cavities is found along ravines dominated by the evergreen old-growth *Nothofagus dombeyi* (coihue) forests. It is expectable that nest sites may not be the main factor limiting populations of SCN. However, the long and narrow shape of these forest patches may prevent "area-sensitive" species from using them. This is the case of the the Magellanic Woodpecker (*Campephilus magellanicus*), and the Austral Parakeet (*Enicognathus ferrugineus*). Both species are very scarce in the study area, and no sign of breeding activity has been found in the area. The Magellanic Woodpecker could play a major role in the formation of new cavities for the rest of CN community (Ojeda 2004). On the other hand, the Rufous-legged Owl (*Strix rufipes*), a cavity nester believed to be an old-growth specialist (Martínez & Jaksic 1996, Pavez 2004), appears to cope with the scarcity of cavities in a landscape dominated by secondary forests and fast-growing pine plantations It has been found nesting on the ground in second-growth *Nothofagus glauca* forests

(Vukasovic *et al.* unpubl.) and in mature Monterrey pine plantations (Estades *et al.* 1998).

Forest management to favor SCN should focus on increasing diameter and height of trees specially in second-growth stands. Reducing tree density by extracting some individuals (thinning) has been tested in order to increase growth in diameter in several *Nothofagus* forests in south-central Chile (Rocuant 1969, Grosse *et. al* 1987, 1996; Pincheira 1993, Del Fierro 1998, Grosse & Quiroz 1999). However, because of the severe degradation of some of these forests, their response to thinning may be marginal to nil (Donoso pers. com.). Soil fertilization should be necessary to improve trees response to thinning but also may help trees to grow faster in height.

Long-term management of secondary *Nothofagus* forests to favor SCN should necessarily consider improving and restoring habitat conditions for PCN. The addition of snags (Caine & Marion 1991) or inserts (Saenz *et al.* 2001) for breeding, or artificial trees as roosting places (Peterson & Grubb Jr. 1983) may be of limited application due to elevated costs. An easier and less expensive way of providing substrate for PCN would be killing pines (Schultz *et al.* 1992) that have invaded most secondary forests in the area (Estades & Temple 1999, Tomasevic 2002). The impressive growth rate of these exotic trees allows them to reach high diameters in few years, which make them suitable for nest building by woodpeckers and similar birds. White-throated Treerunners have been seen nesting in dead pines (Estades pers. observ.). However, a downside of the use of pine trees to produce snags may be their short duration as opposed to snags of hardwood trees (Estades pers. observ., McKensen & Bauhus 1999).

In the mean time, nest boxes were shown to provide appropriate nesting sites for most of the SCN in south-central Chile, and could be easily used to improve habitat conditions for most of SCN species in secondary *Nothofagus* forests.

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