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Tree cavity density is a limiting factor for a secondary cavity nester in second-growth Andean temperate rainforests

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ABSTRACT

Cavity-nesting bird populations are most frequently limited by the number of tree cavities available in second-growth forests. However, this possible limitation of a key resource is less clear in old-growth forests. We compared forest attributes (i.e., basal area, density of larger trees, density of dead trees, and tree cavity density) in second-growth and old-growth stands in Andean temperate rainforests in southern Chile. To examine the role of nest-site availability in limiting the populations of *Aphrastura spinicauda* (Thorn-Tailed Rayadito), we monitored their populations in both forest types during a 5-year period (2008-2013), while we conducted an experiment in which nest boxes were added and then, after two years, removed by blocking cavity entrances. In old-growth forests, as compared to second-growth forests, we found a more than double basal area (99.6 vs. 43.7 m^2 ha^{-1}), a 3 times higher density of larger trees (88.2 vs. 36.4 trees ha^{-1}), and a 1.5 times higher number of small cavities (25.9 vs. 10.3 cavities ha^{-1}). The density of cavities also strongly increased with tree diameter and basal area. In second-growth forests, *A. spinicauda* showed a strong response to the addition, and later to the removal of nest boxes, with population abundance increasing by 13% and then decreasing by 50%, respectively. In contrast, we found no impact on old-growth stands. Our experiment emphasizes the importance of maintaining large and dead trees in second-growth, disturbed, and managed forests. These trees provide suitable cavities for *A. spinicauda*, and likely many other secondary cavity nesters, increasing their abundance in a Globally significant Biodiversity Hotspot in southern South America. A Spanish translation of this manuscript is available as Supplementary Material.

Keywords: *Aphrastura spinicauda*, Chile, forest management, resource limitation, secondary cavity-nesting birds, temperate rainforests, Thorn-Tailed Rayadito

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LAY SUMMARY

- Cavity availability is considered a limiting factor, potentially regulating the breeding population density of avian cavity nesters.
- We compared forest attributes in second-growth and old-growth stands and assessed the role of nest-site availability in limiting populations of *Aphrastura spinicauda* (Thorn-Tailed Rayaditos) in Andean temperate rainforests in southern Chile.
- We conducted an experiment in which nest boxes were added and removed in both forest types during a 5-year period (2008–2013).
- In old-growth forests compared to second-growth forests, we found 2.3 times higher basal area, 2.4 times higher density of larger trees, and a 2.5 times higher number of small cavities.
- In second-growth forests, *A. spinicauda* populations increased by 13% after the nest box addition, and then decreased by 50% after removal, in contrast to no change in old-growth forests.
- Our findings highlight the importance of maintaining larger trees that provide suitable cavities for this species in second-growth forests.

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La densidad de cavidades en árboles es un factor limitante para un ave nidificadora secundaria de cavidades en bosques templados andinos de crecimiento secundario

RESUMEN

Las poblaciones de aves que nidifican en cavidades están frecuentemente limitadas por el número de cavidades disponibles en bosques de crecimiento secundario. Sin embargo, esta posible limitación de este recurso clave es menos clara en bosques antiguos. Comparamos los atributos del bosque (i.e., área basal, densidad de árboles grandes, densidad de árboles muertos y densidad de cavidades de árboles) en bosques templados andinos de crecimiento secundario y antiguo del sur de Chile. Para examinar el rol de la disponibilidad de sitios de nidificación en la limitación de poblaciones de *Aphrastura spinicauda*, monitoreamos sus poblaciones en ambos tipos de bosques durante un periodo de 5 años (2008-2013), mientras realizamos un experimento en el que se agregaron cajas nido y, luego de dos años, se removieron bloqueando la entrada. En los bosques antiguos, en comparación con los bosques de crecimiento secundario, encontramos un área basal de más del doble (99.6 vs. 43.7 m^2 ha^{-1}), una densidad de árboles grandes tres veces mayor (88.2 vs. 36.4 árboles ha^{-1}) y un número de cavidades pequeñas 1.5 veces mayor (25.9 vs. 10.3 cavidades ha^{-1}). La densidad de cavidades también aumentó fuertemente con el diámetro de los árboles y el área basal. En los bosques de crecimiento secundario, *A. spinicauda* mostró una fuerte respuesta a la adición y subsecuente eliminación de cajas nido, con un aumento en la abundancia poblacional del 13% y luego una disminución del 50%, respectivamente. En contraste, no encontramos impacto en los bosques antiguos. Nuestro experimento enfatiza la importancia de mantener árboles grandes y muertos en los bosques de crecimiento secundario, degradados y/o manejados. Estos árboles proporcionan cavidades adecuadas para *A. spinicauda*, y probablemente para muchas otras aves que se reproducen en estas, aumentando sus abundancias en un bosque prioritario para la conservación de biodiversidad a nivel mundial en el cono sur de Sudamérica. Una versión en español de este manuscrito está disponible como material suplementario.

Palabras clave: *Aphrastura spinicauda*, bosques templados, Chile, limitación de recursos, manejo forestal, nidicadoras secundarias de cavidades

INTRODUCTION

Cavity-nesting birds form a hierarchically structured community, which are often categorized as excavators or secondary cavity nesters (SCN; Martin et al. 2004, Martin and Eadie 1999). SCN cannot excavate their own cavities and rely on those created by excavators and/or a limited number of decay-formed non-excavated cavities (Aitken and Martin 2007). This community, therefore, depends on a key resource: Tree cavities (Newton 1998). Cavity availability is considered a primary factor that limits the breeding population density of avian cavity nesters (Aitken and Martin 2012, Brawn and Balda 1988, Cockle et al. 2010, Newton 1998, 1994, Tomasevic and Estades 2006). While there is strong evidence of this limitation in second-growth forests, there is less evidence of it in old-growth forests (Newton 1998). Only 19% of studies assessing the limitation in old-growth forests have reported ecologically significant changes in the density of cavity nesters (Wiebe 2011), and the conclusions of experiments in old-growth forests appear less consistent (Cornelius et al. 2008). For example, in the Coconino National Forest (Arizona, Brawn and Balda 1988) and old-growth subtropical forests (Cornelius et al. 2008), no evidence of cavity limitation was found. While these studies improved knowledge about the effect of both spatial and temporal cavity availability on cavity nesters, most cavity limitation evidence is still confined to North America and Europe (Newton 1998).

Cavity-nesting birds depend on some particular forest structural attributes and are especially sensitive to forest disturbance (Díaz et al. 2005, Martin and Eadie 1999, Vergara and Armesto 2009). Reduction of cavity density at the stand level tends to occur mostly as a result of the removal of larger and dead standing trees (Pattanavibool and Edge 1996, Cockle et al. 2010); whereas at the landscape level, land use change (i.e., agriculture or livestock production) is the main factor (Vergara and Armesto 2009). Cavity limitation is, therefore, highly plausible in forests where human activities have changed forest structural attributes (Politi et al. 2010).

South American temperate forests are declining, due principally to fire, selective logging, and land use change associated with agriculture (Armesto et al. 2009, Echeverría et al. 2007). Selective logging takes place mainly for firewood, which is the principal source of energy in rural and urban settlements in central-southern Chile (Burschel et al. 2003). Logging has been highlighted as the main activity responsible for the degradation of native forests (U. de Chile 2012), particularly in the case of small forest fragments (Echeverría et al. 2007, Zamorano-Elgueta et al. 2014). Currently, only 13.1% of the original temperate rainforest areas correspond to an old-growth condition (Armesto et al. 2009, CONAF et al. 1999). Selective logging in these forests targets mainly trees with larger diameters (diameter at breast height [DBH]; Neira et al. 2002) and/or dead standing trees, negatively affecting the number of suitable cavities available for nesting (Lindenmayer et al. 1993, Fan et al. 2003b, Ibarra et al. 2020, Dudinszky et al. 2021).

Several studies have experimentally assessed the responses of SCNs to changes in cavity density, chiefly by installing nest boxes (Brawn and Balda 1988, Tomasevic and Estades 2006, Cockle et al. 2010,) or blocking natural cavities (Aitken and Martin 2008), usually in only one forest type or age. However, only a few experimental studies have both increased and decreased this relevant resource (Aitken and Martin 2012, Robles et al. 2012). Additional information is particularly necessary in the southern hemisphere (Wiebe 2011). In South American temperate rainforests, there is a gap in understanding the effect of differences in stand attributes and cavity limitation on SCN populations in both second-growth and old-growth forests.

In South American temperate forests, 57% of the bird community are cavity nesters, and most of them are SCNs (Altamirano et al. 2017). However, there are only 2 previous studies assessing the population limitation of the cavity-nesting community in these forests, both conducted in second-growth forests (Cornelius et al. 2008, Tomasevic and Estades 2006). Among all the cavity-nesting birds inhabiting the Andean temperate rainforests, *Aphrastura spinicauda* (Thorn-tailed Rayadito) are endemic to these forests, obligate cavity nesters, with relatively small home-ranges, abundant in both second- and old-growth forests (Rozzi et al. 1996), and readily use nest boxes (Moreno et al. 2005, Altamirano et al. 2015). Thus, they are a good model

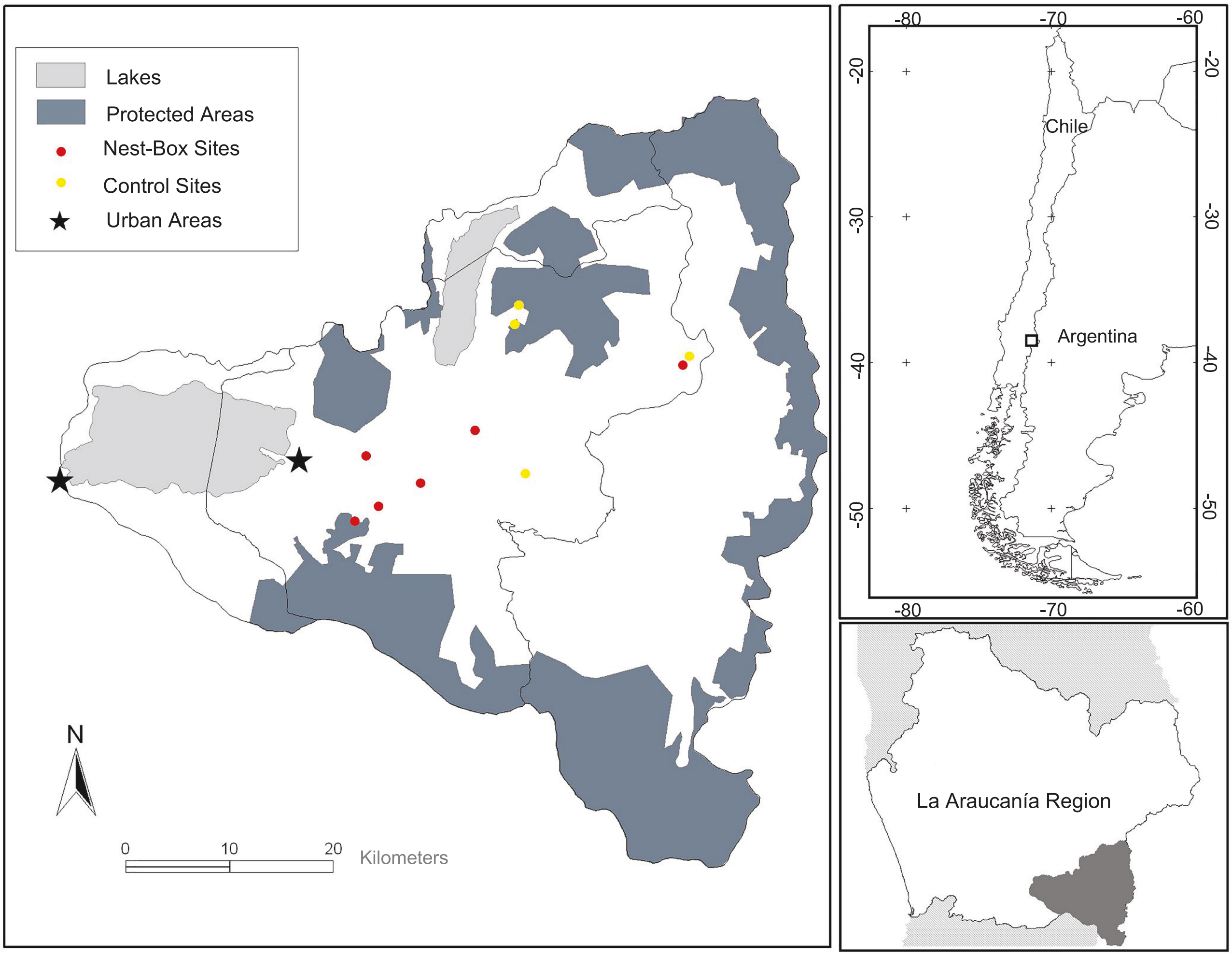

FIGURE 1. Ten forest stands where key resource experimental variation and quantification of forest attributes were conducted in La Araucanía Region, Chile.

species to test if cavity densities are a population-limiting factor in these forests. In the light of the resulting importance of assessing whether the cavity-nesting bird community is being limited by cavity availability in second-growth and old-growth forests, we sought to (1) quantify stand attributes and cavity density (as a proxy of cavity availability) in second-growth and old-growth forests; and (2) determine whether cavity density is limiting the breeding population densities of *Aphrastura spinicauda*s. We predicted that the density of cavities would be higher in old-growth forests than in second-growth forests and, therefore, variation in cavity densities would have a stronger impact on breeding densities in second-growth forests.

METHODS

Study Area

We studied a small-bodied secondary cavity-nesting bird species in the Andean temperate rainforests of southern Chile (*A. spinicauda*, 11.74 g; Altamirano et al. 2020), in the La Araucanía Region (39°16′ S, 71°48′ W; Figure 1). The South American temperate rainforests are 1 out of only 7 of these temperate rainforest ecosystems in the world (Alaback 1991). These forests cover >40,000 km² along the south-western edge of the continent, mainly in Chile and a small adjacent area in Argentina (CONAF et al. 1999, Donoso 1993), stretching in latitude south between 35° and 55° (Armesto et al. 1998). They are characterized by cool summers, with precipitation occurring throughout the year. Furthermore, they have been classified as among the world's 200 biologically most valuable and critically endangered ecoregions (Olson and Dinerstein 1998) and are considered a Global Biodiversity Hotspot (Myers et al. 2000). In Andean areas, native forests have been reduced by 44% over the last 2 decades (Altamirano and Lara 2010), and in coastal areas, 67% of native forests have been replaced by other types of land cover since 1975 (Echeverria et al. 2006).

We quantified forest attributes, cavity density, and the abundance of a secondary cavity nester (SCN) in 10 forest stands with different degrees of disturbance in the Andean Cordillera (Figure 1). The stands ranged from recently burned areas with very low and occasional selective logging, representing second-growth forests (<80 years), to non-burned old-growth forests (>200 years old; Caviedes and Ibarra 2017). Six of the ten stands corresponded to second-growth forests, mainly with a predominance of broadleaf species such as *Nothofagus obliqua*, *Nothofagus dombeyi,* and *Laurelia sempervirens*.

The other four stands corresponded to old-growth stands of conifer-broadleaf mixed forest, principally with *Saxegothaea conspicua*, *Laureliopsis philippiana* and *N. dombeyi*. Forest stands were considered as old-growth when they had a core area with a minimal edge effect and maintained a complex vertical structure and mostly unmodified species composition (Armesto et al. 2009). In both second-growth and old-growth forest stands, understory composition was dominated by bamboo species (*Chusquea* spp.), *Rhaphithamnus spinosus*, and a variety of species of *Azara* and tree saplings. As the home range of the focal bird species is unknown, we assumed a range of 3–4 ha for *A. spinicauda*, given the observed home range for its close relative, *A. masafuerae* (Hahn et al. 2010). Our study stands were separated by a minimum linear distance of 1.6 km, 3.3 to 3.8 times the median natal dispersal reported by Botero-Delgadillo et al. (2017; 490 m females and 420 m males) to ensure that populations in one stand would not affect birds inhabiting adjacent study stands (Wiebe 2011).

Forest Attributes and Cavity Density

To quantify forest structural attributes and cavity density in the stands, we established 5 vegetation plots per stand. These plots had their center at each point where the abundance of *A. spinicauda* was surveyed (details below), with a survey area of 0.04 ha (radius = 11.2 m). Within these vegetation plots, we quantified the following stand attributes: Density of live trees; density of dead standing trees; and for all live and dead trees with a tree DBH ≥12.5 cm, we measured DBH and the number of small cavities per tree. We used tree DBH to calculate the basal area of trees with DBH ≥ 35 cm and the density of larger trees (DBH ≥ 60 cm). Tree cavities, including round or square entrances, crevices, and branch holes, among others, were considered if they had a minimum entrance diameter of 2.5 cm, and a maximum diameter of 5 cm (Cornelius 2008, Altamirano et. al. 2017, Ibarra et. al. 2020). We counted cavities with a minimum depth of 10 cm from the lower lip of the entrance (Altamirano et al. personal observation). Cavity heights between 0.2 and 30 m on the trees were considered, consistent with reports from previous studies (Altamirano et al. 2012, Cornelius 2008, McGehee et al. 2010).

Resource Addition and Removal

We increased the density of suitable cavities by installing 40 wooden nest boxes in each of 6 forests (160 boxes in 4 second-growth forests and 80 in 2 old-growth forests; $n = 240$) during the 2010 nonbreeding season. The remaining 4 forest stands (2 second- and 2 old-growth forests) were used as control stands where nest boxes were not installed. Nest boxes were hung from branches at a height of 1.5 m. The great majority of nest boxes were installed in the forest interior. When there was an open area nearby, nest boxes were placed at least 15 m in from the forest edge. The direction in which the entrance to the nest boxes faced was random. The nest-box entrance diameter and depth of the box were 3.1 and 17.1 cm, respectively (Altamirano et al. 2013, 2015). Nest boxes of this type (i.e., entrance diameter and internal dimensions) were used to improve the probability of their occupancy (Lambrechts et al. 2010) as they had previously been successfully used by *A. spinicauda* (Moreno et al. 2005, Vergara 2007). In the winter of 2012, we blocked all nest boxes, reducing cavity density back to its original level in both second-growth and old-growth forests.

Secondary Cavity-nesting Bird Abundance

We used an experimental design that considered monitoring densities of *A. spinicauda* before and after the cavity addition and removal (Aitken and Martin 2012, Robles et al. 2012). We monitored populations of *A. spinicauda* in experimental and control stands over a 5-year period: 2 years of pretreatment (2008–2010); 2 years of treatment (nest box installation, 2010–2012), 1 year of post-treatment (nest box blocked, 2013). Five-point count stations per forest stand were established, with a diameter of 50 m and a minimum distance of 125 m between stations. All counts were conducted between October and February in each breeding season (total point counts = 660), during the 4 hours after sunrise (06.30–10.30) and had a duration of 7 minutes during which we recorded all the bird species that were detected (heard and/or seen) within the radius. Point count stations were selected instead of transects as they are more efficient in forest conditions (Ralph et al. 1996).

Data Analysis

We compared the following structural attributes of second-growth and old-growth forests: Basal area of trees with DBH ≥35 cm (m^2 ha^{-1}; hereafter, basal area), number of trees with DBH ≥60 cm ha^{-1} (hereafter, density of larger trees), number of dead trees ha^{-1} (hereafter, density of dead trees), and number of small-sized cavities per ha (hereafter, cavity density). We tested statistical differences using the *t*-test for pairs comparison, testing first for normality (Shapiro–Wilk test; $P > 0.05$) and homoscedasticity (Levene's test; $P > 0.05$). A critical tree diameter was established: (1) DBH of 35 cm for the basal area because 80% of the nests of *A. spinicauda* were in trees with a higher DBH; and (2) DBH of 60 cm to calculate the density of larger trees, given that this is the mean diameter of the trees used by this species (Altamirano et al. 2017). We used 2 independent linear regressions to assess how the density of natural cavities was related to 2 different scales: Tree DBH and basal area. For the number of cavities per tree, we used log10 (number of cavities +1) transformation to achieve the normality assumption. We assessed cavity limitation for *A. spinicauda*, analyzing its responses to experimental cavity addition and removal. Although we did not account for detectability, we think this might not have affected our main conclusions, as we compared abundances using consistent methods across forest stands and seasons. To determine the response to experimental increasing and reduction of cavity densities, we used linear mixed-effect models with a Poisson distribution, and the Akaike's Information Criterion (AIC) approach to select the best fit models. Forest type, nest-box treatment (pretreatment, during treatment, and post-treatment), and their interaction were included as fixed effects. Season and forest stand were included as random effects, allowing us to (1) control for any inherent capacity of each season to have lower or higher abundances of *A. spinicauda* (Altamirano et al. 2020), and (2) include repeated measurements in the same forest stands (pretreatment, during treatment, and post-treatment). Models with $\Delta AIC < 2.0$ were considered the best-supported models.

TABLE 1. Paired comparison (mean ± SE; n = 50 vegetation plots; 30 in second-growth and 20 in old-growth forests) of forest attributes: Basal area (medium-sized and larger trees ≥35 cm diameter at breast height), density of larger trees and dead trees, and small-sized cavities (entrance diameter <5 cm) in the Andean temperate rainforest of South America.

Forest attributes	Second-growth forests	Old-growth forests	Univariate statistical test	*P* value
Basal area (m^2 ha^{-1})	43.69 ± 5.34	99.57 ± 10.72	t = 5.14	<0.001
Density of trees ≥60 cm DBH (trees ha^{-1})	36.39 ± 6.86	88.19 ± 11.55	t = 4.56	<0.001
Density of dead trees (trees ha^{-1})	105.78 ± 14.71	76.17 ± 19.32	t = 1.13	0.264
Density of small-size cavities (cavities ha^{-1})	10.27 ± 1.28	25.92 ± 3.11	t = 5.27	<0.001

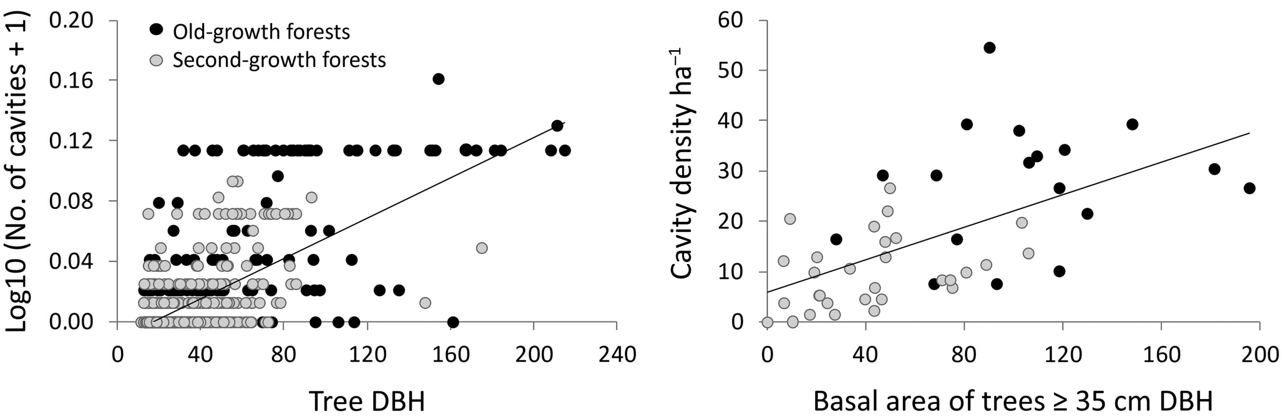

FIGURE 2. Association between cavity density and forest structural attributes in Andean temperate rainforests of Chile. Regression plots show (**A**) the number of cavities and (**B**) the density of cavities as a function of tree diameter at breast height (DBH; cm; n = 1,627) and basal area of trees ≥35 cm DBH (cm^2; n = 50), respectively. Darker circles represent the association between variables in old-growth forests while lighter circles show the variable's associations in second-growth forests.

RESULTS

Forest Structural Attributes and Cavity Density

Among the 50 vegetation plots and 1,627 trees measured, we found structural differences between second-growth and old-growth forests. Old-growth forests had more than twice the basal area found in second-growth forests. The density of large trees (≥60 cm DBH) was almost 3 times higher in old-growth forests whereas the density of small-sized cavities was 1.5 times higher (Table 1). Second-growth forests have a higher average density of dead trees compared to old-growth forests, but this difference has low statistical support (Table 1). Linear models indicated a positive response of cavity density as a function of tree DBH (R^2 = 0.45, F = 1101.70, df = 1 and 625, p < 0.001), with the number of cavities increasing with tree DBH (Figure 2A). A similar result was found for the effect of basal area on cavity density, which increased with basal area (R^2 = 0.35, F = 24.28, df = 1 and 625, p < 0.001; Figure 2B).

Cavities as a Limiting Resource

During the 2 years of treatment, nest boxes were occupied by *A. spinicauda* (54 pairs in 2010–2011 and 96 in 2011–2012, 23% and 40% of the total nest boxes, respectively). The best-supported model to explain variation in abundances of *A. spinicauda* included the interaction between forest type and nest-box treatment (Table 2). We found evidence for a treatment effect of nest box addition on *A. spinicauda* abundance in second-growth forests (b = 0.40; P = 0.005), with a population increase of 13% during the 2 years of treatment (25% in the breeding season 2010–2011, before decreasing by 12% in 2011–2012, with respect to the previous season). Then, when the nest boxes were blocked, population abundance decreased by 50% in the breeding season 2012–2013 (b = –0.37; P = 0.009). This action changed the *A. spinicauda* abundance back to near its 2010 pretreatment level and a level similar to that found in control stands (Figure 3A). In contrast, there was no statistical support for an effect of the experimental addition and removal of cavities on *A. spinicauda* populations inhabiting old-growth forests (Figure 3B; 2 years of treatment, b = –023, P = 0.09; nest boxes blocked, b = 0.14, P = 0.40).

DISCUSSION

This study quantified cavity density and its relationship with forest structural attributes and assessed cavity limitation in both second-growth and old-growth forests in the temperate rainforests of South America. We provide evidence of population limitation for *A. spinicauda* inhabiting second-growth forests, but not in old-growth forests. Furthermore, our findings suggest that the differences associated with forest age in response to experimental manipulation of cavities are likely to be driven by specific forest structural attributes (i.e., tree DBH and basal area) present in both forest types.

Forest Attributes and Cavity Density

As expected, we found that critical forest structural attributes for SCNs (i.e., basal area, density of larger trees, and number

TABLE 2. Model rankings for *Aphrastura spinicauda* abundance in relation to forest types and the nest-box treatment in the south temperate forests of Chile.

Model	k	AIC_c	ΔAIC_c	W_i	LL
Forest_type * treatment	**8**	**2,499.50**	**0.00**	**0.80**	**−1,241.64**
Treatment	5	2,503.20	3.69	0.13	−1,245.53
Forest_type + treatment	6	2,504.40	4.93	0.07	−1,247.17
Forest_type	4	2,518.10	18.64	0.00	−1,255.04
Null	3	2,519.40	19.91	0.00	−1,256.69

Season and forest stand were treated as a random term in all models. Bold indicates the best-supported model. k = number of parameters estimated; ΔAIC = the difference in AIC_c values between each model and the lowest AIC_c model; W_i = model weight; LL = log-likelihood.

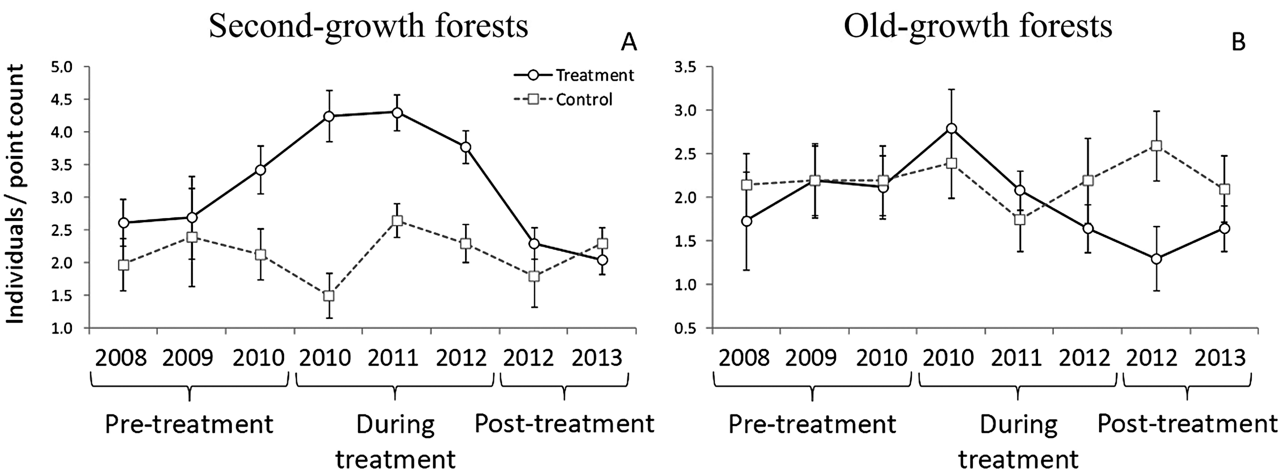

FIGURE 3. Mean bird abundance per point count for *Aphrastura spinicauda* (**A, B**) over 5 years of monitoring, during pretreatment (before nest box addition), treatment (nest boxes added), and post-treatment (nest boxes blocked). Treatment and control monitoring were carried out in 6 second-growth forests and 4 old-growth forests in Andean temperate rainforests of South America. Error bars represent the standard error of mean bird abundance per point count station.

of small cavities) were more prevalent in old-growth forests. This is likely to reflect the effect of selective logging in second-growth forests (Politi et al. 2010). Changes found in basal area and the density of larger trees for forests in different successional stages are quite similar to results from coastal locations (Carmona et al. 2002, Díaz et al. 2005), and also in Andean temperate forests (Dudinszky et al. 2021). In these previous studies, both basal area and the density of larger trees in old-growth forests are at least double those in intermediate and early successional forests. Basal area and density of larger trees have a positive association with larger populations of forest specialist birds, such as *A. spinicauda* (Díaz et al. 2005, Tomasevic and Estades 2006). On the other hand, the density of dead trees did not vary between forests, probably because of the high variability observed in old-growth forests and the large number of dead trees in second-growth forests resulting from past disturbances (e.g., fire; Aravena et al. 2002).

Our findings support the hypothesis that tree DBH and basal area, as indicators of the age of forest stands, are important for cavity formation (Cockle et al. 2010, Koch et al. 2008). Similarly to a study in coastal temperate rainforests (Estades and Tomasevic 2004), we found that tree DBH has a significant effect on the density of cavities present in each tree. Cavity density increased with basal area, a similar pattern found in Atlantic forests (Cockle et al. 2010). This result confirms basal area as a good predictor of cavity density at the stand scale (Fan et al. 2003a). Using basal area to predict cavity density in forests could be useful as an alternative to counting the specific number of small cavities in a stand. However, caution is required because the effects of tree DBH and basal area on the density of suitable cavities could vary in forests with different tree composition, ecological dynamics, and/or abiotic conditions. For example, in forests dominated by conifer species or highland forests near the treeline, where tree growth is influenced by snow and wind.

Nest-Site Limitation

The role of nest sites in limiting the density of cavity-nesting species has been widely studied (Newton 1998). Despite this, experiments manipulating cavity densities to assess nest-site limitation in old-growth forests are rare and the results appear less consistent (Cornelius et al. 2008, Wiebe 2011, Aitken and Martin 2012). In second-growth areas of temperate forests, similar cavity addition experiments (Cornelius et al. 2008, Tomasevic and Estades 2006) concluded that nest sites did limit the population size of *A. spinicauda* in breeding seasons in coastal and island locations. Our experiment suggests that cavity density affects the abundance of *A. spinicauda* in second-growth forests, likely reflecting a population limitation effect, with the number of *A. spinicauda* increasing and decreasing significantly in the treatment stands (nest box additions and removals, respectively), but no changing in the control stands (i.e., no nest-box experiments). This result strongly indicates that, as suggested by previous studies, cavities are a critical resource that may limit the breeding populations of *A. spinicauda* (Cornelius et al. 2008, Tomasevic and Estades 2006). Also, the fact that 63% of the rayaditos' nests in nest boxes were successful in second-growth forests (Altamirano et al. 2015) reinforces the idea that cavities are a limiting factor in these forests. Increasing cavity density leads to more breeding outcomes, under a scenario where there was no experimental manipulation of other potential factors, such as food availability or predation risk. The increase in cavity availability might have offered breeding opportunities for nonbreeding individuals in the treatment sites (Hold and Martin 1997; and/or for individuals dispersing from adjacent sites). The latter, by reducing the territory size occupied by dominant rayaditos, enabling these individuals to breed either in nest boxes or tree cavities that otherwise would have been unavailable for them (Marshall and Cooper 2004, Aitken and Martin 2012). Interestingly, the rayadito abundance did not continue increasing in the second year with the next boxes open. In fact, the slight decrease suggests that another limiting factor(s) might have restricted the maximum abundance.

The larger decline from blocking nest boxes than the addition of them is similar to the response of SCN found in forests of British Columbia (Aitken and Martin 2012), suggesting more sensitivity of *A. spinicauda* to the loss of available cavities than the addition of this resource. A potential underlying mechanism of this population decrease is that, when the nest-site availability is reduced, dominant individuals may expand their territory size (Marshall and Cooper 2004). This expansion may even reduce the cavity availability, and perhaps, forcing subordinate individuals to disperse to other sites (Robles et al. 2012). On the other hand, in agreement with 81% of the studies carried out in old-growth forests (Wiebe 2011 and references therein), nesting density did not change with nest-site density for *A. spinicauda* in old-growth forests. This suggests that another resource, such as food supply, might limit the abundance of this species in forests with a higher basal area, density of larger trees, and cavity density (Newton 1998).

Response to the variation in cavity density might differ across species. *A. spinicauda* compete for cavities with conspecifics, as well as *Tachycineta leucopyga* (Chilean Swallow) and *Troglodytes aedon* (Southern House Wren; Altamirano et al. personal observation). Thus, the addition/removal of this key resource may also affect other species' populations, increasing or reducing their population abundance depending on each species' ability to respond to temporal and spatial changes in key resource density (Aitken and Martin 2008, Norris et al. 2013).

Forest Management Implications

This study provides evidence that the *A. spinicauda* might not be limited by cavity availability in old-growth forests but, in second-growth forests. In the latter, the abundance of rayaditos varied with cavity density, which was highly influenced by the density of larger trees. Our findings highlight the importance of supplying, maintaining, and/or increasing forest attributes that provide suitable cavities for SCNs in second-growth areas, especially in stands that have experienced high forest disturbance. Old-growth forests do have appropriate structures for supporting sustainable populations of rayaditos, but given extensive habitat loss and conversion, old forests are now found mainly in protected areas and at higher altitudes (Armesto et al. 2009, Altamirano et al. 2020).

Maintaining remnant large and dead-standing trees in second-growth forests could improve habitat conditions for *A. spinicauda* (Altamirano et al. 2017), which are negatively affected by the reduction and fragmentation of forest cover (Vergara and Armesto 2009). This would represent an important contribution by silviculture to the conservation of forest specialist birds inhabiting second-growth forest stands. However, most forest policies specify a minimum tree diameter for harvesting, thereby tending to protect younger trees, rather than large and old trees (Cockle et al. 2011, Altamirano et al. 2017). Chile's national forestry policy only superficially mentions tree diameter as a criterion for authorizing tree logging (CONAF 2014). We suggest limiting the maximum diameter of trees for harvesting in order to ensure a sufficient number of larger trees (DBH ≥ 60 cm) to support a sustainable cavity-nesting bird community (Cockle et al. 2010). In addition, stipulating a minimum number of large and medium-sized trees to be maintained (future resource availability; Aitken and Martin 2004), could be very useful in facilitating the breeding of cavity-nesting birds in second-growth forests. These suggestions will also contribute to the Chilean Bird Conservation Strategy, which highlights the importance of maintaining large and dead-standing trees in managed forests (MMA—ONU Medio Ambiente 2022).

Finally, cavity-nester populations may be limited by other factors not measured in this study, such as food abundance, predation rates, or abiotic constraints (Cornelius et al. 2008, Newton 1998, Zarnowitz and Manuwal 1985). Maintaining suitable nest trees may not entirely suffice to conserve the tree cavity-nesting bird community, indicating a need for further studies of population limitation in birds.

Supplementary material

Supplementary material is available at *Ornithological Applications* online.

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Ethics statement

Our research was developed under the permit of the National Forestry Service permission to carry out research in protected areas. Wildlife was not manipulated. We followed the IOU Code of Ethics (https://www.internationalornithology.org/iou-code-ethics).

Conflict of interest statement

The authors declare that they have no conflicts of interest.

Author contributions

T.A.A., C.B., J.T.I., and K.M. conceived the idea, design and experiment. T.A.A and F.N. performed the experiments (collected data, conducted the research). T.A.A., S.N., and F.N. analyzed the data. C.B. and K.M. contributed substantial resources. T.A.A. and J.T.I. wrote the manuscript with substantial support of S.N., K.M., and C.B.

Data availability

Analyses reported in this article can be reproduced using the data provided by Altamirano et al. (2024).

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