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Breeding ecology of cavity-nesting birds in the Andean temperate forest of southern Chile

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To the southern forests of the world and my roots in the earth: my parents and mountains of Chile.

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Abstract

Over 1,000 bird species globally depend on tree cavities to provide critical nesting and roosting sites, which are a shortage resource in most forested ecosystems. Cavity-nesting birds are particularly vulnerable to habitat loss; however, little is known about their ecology and life history variation across elevational forest-gradients that may influence a shift to a "slow" reproductive strategy in birds. I studied the reproductive life-history traits along elevations (at the species-level), population limitation by cavity availability (at the population-level), and cavity-nest web composition and structure (at the community-level) in South-American temperate forests, Chile. For my model species, the thorn-tailed rayadito, I found a shorter breeding season, smaller clutch size, lower number of broods, and longer nestling period in highland than in lowland forests. Tree-basal area was larger, density of large trees was higher, and the availability of small cavities was higher in old growth compared to secondary forests. Cavity availability was a limiting factor for thorn-tailed rayadito populations in secondary forests. Cavity-nesting birds (n=28) comprised a major component of the southern temperate forest bird community (55%). Seventy five percent of nests were in tree-cavities created by natural processes (crevices, broken branches), and the remaining 25% were excavated cavities. Cavity-nest web structure had a low dominance and evenness, but showed a strongly preference for large trees in advanced stages of decay. These results stress the importance of maintaining large decaying trees and dead trees, in order to conserve an enough and long-term supply of cavities for the cavity-nesting community in temperate forests.

Keywords: Bird conservation, community structure, elevational gradient, forest management, life-history traits, population limitation, thorn-tailed rayadito.

General introduction

Many birds in the world require tree-cavities for nesting or roosting (Newton, 1998; Sedgwick and Knopf, 1990), being a cavity-dependent community (Cockle *et al.,* 2011). These species are called cavity nesters, and represent an important section of the forest bird communities in the world (e.g. 50% in Oregon, Dobkin *et al.,* 1995; 32-43% in Colorado, Sedgwick and Knopf, 1986; 21% in Venezuela, 23-25% in Costa Rica, and 26-30% in Belize; Gibbs *et al.,* 1993). Cavity-nesting species are classified in different nesting guilds depending on how they obtain this key resource (cavities). Thus, there are two general cavity nesting guilds: Primary Cavity Nesters (PCNs), species that excavate their own cavities (e.g. woodpeckers), and Secondary Cavity Nesters (SCNs) who cannot excavate their own cavities and depend on pre-existing holes excavated by PCNs or generated by tree decay processes (Martin and Eadie, 1999).

Despite the high ecological relevance of cavity-nesting birds (Mahon *et al.,* 2008; Bernardz *et al.,* 2004), their knowledge is mainly attributable to the northern hemisphere (Tomasevic and Estades, 2006; Moreno *et al.,* 2005). The specific breeding ecology of cavity-nesting birds has been studied a lot more in this section of the world (Auer *et al.,* 2007). Thus, their breeding ecology, interspecific interactions, and geographic patterns of variation, are largely unknown in southern hemisphere (Martin *et al.,* 2006).

Temperate rainforests only exist in specific and limited places in the world (Willson *et al.,* 2005). In South America, they are located in a narrow strip associated to the Andean Range, between 36º S and 56º South Latitude. This forest has insular environment features, with low species richness, high endemism (Vuilleumier, 1985; Armesto *et al.,* 1996, 1998; Willson *et al.,* 2005), and taxonomic singularity (Heywood, 1995 in Aizen *et al.,* 2002). Forty one percent of the avian community of the Temperate Rainforest of South America (TRSA) is endemic (Vuilleumier, 1985). However, these forests have been extensively deforested during the last decades (Echeverría *et al.,* 2006), being replaced by silvicultural activities (Lara *et al.,* 1996). This has resulted in fragmentation and habitat loss (Cornelius *et al.,* 2000; Didham *et al.,* 1996), leading to biodiversity loss (Sala *et al.,* 2000) and native instability of native forests (Hoffmeister *et al.,* 2005). This situation is especially negative for some guilds of forest birds, as cavity-nesting avian species. Cavity-nesting birds experienced a strong decline in small patches, isolated and surrounded by open farming areas (Scott *et al.,* 1977; Willson *et al.,* 1994; Sallabanks *et al.,* 2000; Díaz *et al.,* 2005; Vergara and Marquet, 2007), often depending on artificial nesting sites (Alen *et al.,* 1952). This habitat loss in TRSA could have serious implications for species that depend on high quality habitat and structural complexity (Amico *et al.,* 2008; Díaz *et al.,* 2005; Vergara and Schlatter, 2004), because some structural elements of forests are key to the maintenance of viable populations (Tews *et al.,* 2004). For example, tree density and dead standing trees availability could be determinant factors to predict cavity-nesting bird abundance (Díaz *et al.,* 2005).

Breeding ecology of cavity-nesting birds across elevational gradients

Worldwide, there is a vast diversity of life-history traits across co-occurring species within a given taxa, but also within the same species along environmental gradients (Roff, 1992). Elevation is an environmental gradient that has been considered as an important factor in the evolution of life-history traits (Badyaev, 1997; Badyaev and Ghalambor, 2001; Camfield *et al.,* 2010; Ogden *et al.,* 2012). Indeed, extreme conditions encountered at high altitudes, such as cold temperatures, prolonged snow cover, variable weather, and shorter warm seasons have been shown to influence most of the life-history traits associated with avian reproduction (Martin, 2013).

Reproductive life-history traits of temperate forest birds have been poorly studied in south-temperate systems (Martin, 2004), and even fewer on cavity-nester species. In the temperate forest of southern Chile, most bird species inhabit and breed across wide elevational gradients (Vuilleumier, 1985). However, life-history variation along this gradient remains scarcely documented because the majority of studies have focused on coastal areas (e.g. Cornelius *et al.,* 2000; Estades and Tomasevic, 2004; Tomasevic and Estades, 2006; Vergara and Marquet, 2007; Quilodrán *et al.,* 2012), and island systems (e.g. Willson *et al.,*1994, 2005; Rozzi *et al.,* 1996; Reid *et al.,* 2004; Vergara and Schlatter 2004; Moreno *et al.,* 2005; Díaz *et al.,* 2005, 2006; Ippi *et al.,* 2009).

Nest-site limitation

Population size limitation by cavity availability for nesting has been the main conservation issue around cavity nesting birds, even more so for SCNs (Ingold, 1998; Newton 1998; Raphael and White, 1984; Brush, 1983). The presence and abundance of structures that create cavities could be a strong limitation, especially in managed forests (Newton, 1998, 1994; Holt and Martin, 1997).

Secondary cavity-nesting birds cannot excavate their own cavities and thus rely on those created by excavators and/or a limited number of decay-occurring non-excavated cavities (Aitken and Martin, 2007). There is strong evidence which supports this limitation in managed forest, but less evidence for such limitation in unmanaged and old growth forests (Newton, 1998). Only 19% of the studies which assess limitation in old growth forests have reported significant changes in density of cavity-nesters (Wiebe, 2011). Hence, the conclusions from experiments carried out in mature forests appear less consistent (Cornelius *et al.,* 2008). In TRSA, there is a gap in the understanding of differences in stand attributes and cavity limitation for SCN populations in both managed and old growth forests.

Cavity-nest web and tree selection

Cavity-nesting bird assemblages are arranged in hierarchical structures, analogous to food webs, within cavity-nest webs (Martin and Eadie, 1999). In cavity-nest webs, tree cavities are a vital resource around which birds interact, where PNCs are “cavity-producers” and SCNs are “cavity-consumers” (Martin *et al.,* 2004). SCNs can nest in either excavated cavities (e.g. Beaudoin and Ojeda, 2011;

Robles and Martin, 2013), or in those created by decay processes (Cockle *et al.,* 2012). Descriptions of the composition and structure of cavity-nest webs can provide us strong evidence about the magnitude of the relationship between cavity-nesting birds and forest structure (Blanc and Walters, 2008; Cockle *et al.,* 2012; Koch *et al.,* 2008; Martin *et al.,* 2004). Thus, the management of key resource could be a strong human driver for conservation of cavity-nester communities (Drever and Martin, 2010; Walter and Maguire, 2005). Therefore, conservation of cavity-nesting communities requires a deep understanding of how tree-cavities are created and used (Cockle *et al.,* 2012).

Cavity-nest webs and interspecific relationships between cavity-nesting birds have not been studied in TRSA. Similar to other forest ecosystems in the world (Bednarz *et al.,* 2004), most studies of cavity-nesting birds in TRSA have been focused at the species level (e.g. Ibarra *et al.,* 2014, 2012; Carneiro *et al.,* 2013; Peña-Foxon *et al.,* 2011; Ippi *et al.,* 2012; Moreno *et al.,* 2005; Vergara and Schlatter, 2004; Vergara and Marquet, 2007), and only a few have explored cavity-nesting birds at the community level (e.g. Díaz *et al.,* 2005; Ippi and Trejo, 2003). Furthermore, it is not clear how many species actually rely on tree-cavities for nesting in TRSA, which is the degree of dependence for cavities (i.e. obligate, facultative, marginal, and accidental cavity nesters), and even less information is available on tree characteristics selected for nesting.

This thesis is oriented to improve the knowledge about cavity-nesting birds, and their relationship with forest structures and management, in Andean temperate rainforests of Chile. In this way, it contributes to forest bird conservation and sustainable forest management in an isolated and highly endemic ecosystem.

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Thesis objectives

General objective

To study how cavity-nesting birds, at population and community level, are related to elevation, cavity availability and forest attributes, assessing the breeding ecology, population limitations, and the structure of cavity-nest web in the temperate rainforest of South America.

Specific objetives

Chapter 1: To provide detailed information of the breeding ecology of the thorn-tailed rayadito (*Aphrastura spinicauda*) in Andean locations, and to determine elevational differences in reproductive life-history strategies.

Chapter 2: To quantify forest attributes and density of tree-cavities, and to determine whether cavity availability is limiting breeding population densities of small secondary cavity-nesting birds, in both managed and old growth forests in the Andean temperate rainforest Chile.

Chapter 3: To assess the cavity-nest web composition and structure, comparing the role of tree decay and excavation processes in structuring this cavity-nest web, and to determine characteristics of nest-trees selected.

Chapter 1

Shifting to a slower life-history strategy on a secondary cavity-nester as a result of increased elevation in Andean temperate forests of southern Chile

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Summary. Elevational gradients have been proposed as a driver of change in avian reproductive life-history strategies. The eventual shorter breeding season, due to environmental conditions and the potentially higher predation risks, can produce a decline in fecundity and a reduction in clutch sizes at higher altitudes, which in some species appears to lead to an increase in parental care and offspring survival. However, this phenotypically plastic and potentially adaptive individual response has only been documented in a handful of species in the Northern Hemisphere. Here we studied whether the breeding strategy of the Thorn-tailed Rayadito varied predictably along an elevational gradient in the Andean temperate forests of Chile. We installed 240 nest-boxes between 260 and 1,115 of elevation, and monitored the breeding activity of 162 nests over two seasons (2010-2011, 2011-2012). As expected, the breeding season was shorter in highland forests compared to lower elevations by 28% and 55% over the two successive seasons. Although laying pulse (1 egg every second day) and incubation period (average 15 days) did not vary with altitude, clutch size (average 4.1 vs. 4.5) and number of broods (average 3.5 vs. 4.2) were significantly smaller at higher altitudes. The extent of parental care, expressed as nestling period, was slightly but significantly longer in highland than lowland forests (22.2 vs. 21.6 days). Despite the increased nestling period at higher elevations, breeding success declined with altitude, mainly due to nest predation. Our findings suggest that Thorn-tailed Rayaditos change their reproductive strategy along elevational gradients to a slower one. Yet, these changes do not appear to compensate for the increased predation rates at higher elevations, questioning the adaptive significance of this strategy.

Keywords: Cavity nesters, elevational gradient, life-history traits, temperate forest, Thorn-tailed Rayadito.

INTRODUCTION

Worldwide, there is a vast diversity of life-history traits across co-occurring species within a given taxa, but also within the same species along environmental gradients (Roff 1992). Elevation is an environmental gradient that has been considered as an important factor in the evolution of life-history traits (Badyaev 1997; Badyaev & Ghalambor 2001; Camfield et al. 2010; Ogden et al. 2012). Indeed, extreme conditions encountered at high altitudes, such as cold temperatures, prolonged snow cover, variable weather, and shorter warm seasons have been shown to influence most of the life-history traits associated with avian reproduction (Martin 2013). Within of a fast-slow continuum gradient of reproductive strategies (Sæther 1987), an expected adaptation to harsher conditions is a shift to a “slow reproductive strategy”, in which lower breeding outputs (e.g. clutch size and number of broods) are compensated by increased offspring survival from increased parental care while nesting (Badyaev & Ghalambor 2001). This general response has been observed in both multiple (Badyaev 1997; Sandercock et al. 2005) and single species (Bears et al. 2009; Martin et al. 2009) in the northern hemisphere. However, very few studies have evaluated direct and indirect effects of the environmental stress gradient, plastic behavioural responses, and the consequent offspring survival during nestling period and post fledgling.

Although few studies have been able to quantify changes in birds' life-history traits across elevational gradients (Martin 2001), and even fewer on cavity-nester species, some patterns emerge from the small number of studies in Alpine systems. For example, within an assemblage of 84 cardueline species, clutch size sharply decreased and incubation period significantly increased with increasing elevations occupied by different species (Badyaev 1997). These changes can be understood as direct consequences of decreased energy availability to reproduction at highlands due to harsh environmental conditions. It is unclear, however, whether nestling period is significantly greater in higher altitude species, which would be indicative of a change in reproductive strategy. Intraspecific variation in reproductive traits across elevation has also been documented. For instance, Dark-eyed Juncos (*Junco hyemalis*, a ground-nester) show a shift in their reproductive life-history traits with elevation, reducing their breeding period and decreasing the number of nestlings per nest (Bears et al. 2009). On the other hand, Pacific Wren (*Troglodytes pacificus*, a cavity-nester), reduce their annual fecundity with increasing elevation possibly in response to a 61% shorter breeding season at higher altitudes; however, there is no evidence of a shift in breeding parameters and behavioural attributes that could increase offspring survival at highlands (as a shift to a slower reproductive strategy; Ogden et al. 2012).

Reproductive life-history traits of temperate forest birds have been poorly studied in south-temperate systems (Martin 2004). In the temperate forest of southern Chile, most birds species inhabit and breed across wide elevational gradients

(Vuilleumier 1985). However, life-history variation along this gradient remains scarcely documented because the majority of studies have focused on coastal areas (i.e., Cornelius et al. 2000; Estades & Tomasevic 2004; Tomasevic & Estades 2006; Vergara & Marquet 2007; Quilodrán et al. 2012) and island systems (i.e., Willson et al. 1994, 2005; Rozzi et al. 1996; Reid et al. 2004; Vergara & Schlatter 2004; Moreno et al. 2005; Diaz et al. 2005, 2006; Ippi et al. 2009).

The Thorn-tailed Rayadito (*Aphrastura spinicauda*) is a small furnariid species endemic to the forests of southern South America (Martínez & Gonzalez 2004). Previously to this study, its breeding biology and general ecology had only been studied in coastal temperate forests located below 100 m of elevation. In one of these studies, conducted in Chiloé island, Moreno et al. (2005) described clutch sizes ranging between three and six eggs (mode of four eggs), with broods of 2-5 nestlings (mode of three chicks), and incubation period between 9-16 days (mode 14 days), and a nestling period between 16-23 days (Moreno et al. 2005). In a mainland coastal exotic plantation of pines (*Pinus radiata*), Quilodrán et al. (2012) reported clutch sizes ranging between 2-4 eggs (mode of three eggs), broods between 1-4 nestlings (mode of three chicks), incubation period between 14-18 days (mode of 16), and a nestling period of 21 days. However, The Thorn-tailed Rayadito inhabits from sea level up to 2,400 m in the Andes (Housse 1945), and is therefore a good subject to examine how reproductive life-history traits may change across an elevational gradient.

We investigated changes in reproductive life-history traits of this species by examining nesting birds over two consecutive breeding seasons that used experimental nest-boxes deployed in an elevational gradient. We determine whether changes in reproductive traits are indicative of a plastic and potentially adaptive change in reproductive strategy. Specifically we i) provide a detailed description of the breeding biology of the Thorn-tailed Rayadito in Andean locations, contrasting it to previous research conducted on coastal populations, and ii) determine elevational differences in reproductive life-history strategies, mainly in the length of the breeding season, clutch size, incubation period, number of broods, nestling period, and nesting success.

METHODS

Study area and species

The study was conducted in the Andean mountains of southern Chile, within the Araucanía district near the city of Pucón (39º16’ S, 71º48’ O) (Fig. 1). We selected study sites in six different forests across an elevational gradient, from 271 m to 1,063 m of elevation. A minimum linear distance of 1.6 km separated sites. Four of them were dominated by broadleaf species such as *Nothofagus obliqua*, *Nothofagus dombeyi* and *Laurelia sempervirens*. The other two sites were conifer-broadleaf mixed forests dominated by *Saxegothaea conspicua*, *Laureliopsis philippiana* and *N. dombeyi*. The understory composition, in low and highland forests, were dominated by bamboo species (*Chusquea spp.*), *Rhaphithamnus* *spinosus*, and different species of *Azara* and tree saplings, showing similar habitat conditions for all sampling sites where nest-boxes were placed.

The Thorn-tailed Rayadito is a forest-specialist bird, being classified as large tree user (Diaz et al. 2005). The diet of this species consists mainly of insects (Martínez & Gonzalez 2004), although there are incidental records of individuals feeding on plant seeds (Estades 2001; McGehee 2007). Rayaditos are obligate cavity nesters, and are mostly found in tree-cavities and to a lesser extent in bank-cavities (Jaramillo et al. 2003; Altamirano et al. 2012b). Their nests are located at different heights off the ground, from 0 to 29 meters (Cornelius 2008; McGehee et al. 2010; Altamirano et al. 2012a), and been found to be very attracted to artificial cavities (nest-boxes; Moreno et al. 2005).

Experimental design and reproductive monitoring

In winter 2010, we installed 240 wooden nest-boxes (40 per site) of 16.5 x 13.2 inner space, a depth 17.1 cm from entrance to base, and an entrance hole 3.1 cm in diameter, which followed the design used successfully by Moreno et al. (2005). The nest-boxes were hung 1.5 m above ground from a tree branch (random entrance aspect), and were systematically placed in a grid separated by 25 m. All nest-boxes were placed at least 15 m from the forest edge in order to reduce edge effects. During two breeding seasons (i.e., October 2010 – February 2011, October 2011 – February 2012), nest-boxes were monitored by direct observations and using camera traps (Reconyx RC 55, Reconyx Inc., Holmen, Wisconsin, United States) to examine the activities of the cavity users, nestling feeding, nesting success, and to identify any potential nest predators (Altamirano et al. 2013) (Appendix 2). Furthermore, for clutch size and number of brood, we included some nests data from a third season (i.e., October 2012 – December 2012). A nest-box was considered occupied when it had at least one egg or chick. Nest-boxes were checked weekly to determine the initial date birds started using them. The status of each nest-box (adult activity, clutch size, egg temperature and number of broods) was monitored every 2-3 days, or every day near to the hatching or fledging dates, in order to obtain the exact dates of these processes and accurately calculate breeding periods and nest fates.

The variables recorded per nest-box were: laying date of each egg, incubation period, clutch size, hatching date, number of broods, breeding period, and fledging date. Incubation period was defined as the duration of time from when eggs were warm for the first time, until completion of hatching (Magrath et al. 2000). To calculate nestling period, hatching day was considered the day 0 (Moreno et al. 2005), until the first nestling fledged. We considered a successful nest (fate value = 0) when all eggs resulted in nestlings that fledged, partially successful (fate value = 1) when at least one chick fledged, and unsuccessful (fate value = 2) when no nestling fledged.

Data analysis

All fecundity data were $\log_{10}$ transformed before statistical comparison to improve normality and variance homogeneity. Data are presented as mean ± SD, and statistical tests were considered significant with $p<0.05$. Nests that were not incubating by the end of the observation were excluded from clutch size analysis, because we were not sure whether the laying period had ended. Linear models were used to assess the response of clutch size, number of broods, incubation period and nestling period to elevation. *F* values are presented as $F_{\mathrm{df(effect),df(error)}}$. Differences in fecundity between two categorical elevations, lowland (< 700 m above sea level – a.s.l) and highland (> 700 m a.s.l.) forests, were assessed using univariate *t*-test or *Mann-Whitney U* rank-based test where data were not normally distributed (Quinn & Keough 2002). We used an inflection point of 700 m a.s.l. between our two elevation categories because most precipitation above this elevation falls as snow during Andean winters. We calculated nesting success as the proportion of successful nests between the two elevation categories and breeding seasons. This is a valid approach because, being a study of nest-boxes with known locations, all nests had the same probability of being found, independent of nest stage (Mayfield 1961, 1975; Cooch & White 2006).

RESULTS

Life-history traits of Rayaditos

We monitored 162 nests of the Thorn-tailed Rayaditos, and also include (only for clutch size and number of brood) 50 additional nests observed in the third breeding season (2012-2013). Nest-box use rates were higher in the second year (55 vs. 107 nests). Considering all nesting attempts, clutch size ranged from 2 to 7 eggs, with a mode of 5 (41.8% of 158). Thirty three percent had four eggs, 15.2% six eggs, 7.0% three eggs, 1.9% two eggs, and 1.3% seven eggs. Mean clutch size was 4.65 ± 0.93 eggs. With the exception of one clutch, all eggs within a nest hatched synchronically on the same day (within a period of 24 hours). Number of broods ranged between 2 and 7 chicks, with a mode of 4 (36.2% of 105). Thirty three percent had five nestlings, 17.2% had three nestlings, 6.6% had six nestlings, 5.7% had two nestlings, and 1.0% had seven nestlings. The mean was 4.21 ± 1.03 nestlings. Rayaditos layed eggs every two days during the laying period, with a maximum laying period of 13 days (mean = 7.2 ± 1.6, n=103). Incubation period was 15.3 ± 1.0 (n=92), ranging between 14 and 18 days. Nestling period was 21.7 ± 0.8 days (n=85), ranging between 19 and 23 days.

Effects of elevation on reproductive strategy of Rayaditos

Length of breeding season

During the two years of monitoring, the breeding season was 28% (62 vs. 82 days) and 55% (35 vs. 77 days) shorter in highland forests compared to low elevation areas. The nesting birds in lowland forests showed two peaks in clutch initiation periods (bimodal distribution), whereas only one initiation period occurred in highland forests (unimodal distribution). The latter period was between the two peaks at lowlands for the season 2010-2011 (Fig. 2A), and almost simultaneously with the second peak period at lowlands for the season 2011-2012 (Fig. 2B). The second breeding season started and finished earlier than the first breeding season at lowland forests, while at high elevations the breeding phenology was almost identical (Fig. 2). Rayaditos started laying eggs at lowlands forests on October 10th, 2010 and October 3rd, 2011. At high elevations, Rayaditos started laying eggs approximately one month later than in lowlands: November 22nd, 2010 and November 1st, 2011. The last fledging dates for lowland forests were February 12th, 2010 and January 26th, 2011. In highland forests, the last fledging dates were almost one month earlier than at low elevations: January 23rd and January 2nd for the first and second breeding seasons respectively. Re-nesting attempts differed between elevations, with no second attempts in highlands and 17 in lowlands.

Clutch size and number of broods

Elevation had a negative effect on both clutch size ($F_{1,156}$ = 6.64, p = 0.01; Fig. 3A) and number of broods ($F_{1,103}$ = 6.69, p = 0.01; Fig. 3B). Rayadito pairs breeding in highland forests had significantly smaller clutches than those at lowlands (*t value* = 2.18, d.f. = 156, p = 0.03), with a mean clutch size of 4.1 ± 0.8 and 4.5 ± 0.9 respectively. We found a lower number of broods per nest (*t value* = 2.27, d.f. = 103, p = 0.02) in highland forests, with a mean of 3.5 ± 1.0 vs. 4.2 ± 1.0 in lowlands. The latter resulted in fewer nestling fledges per nest in highland forests than at low elevations (3.2 ± 1.4 vs. 3.7 ± 1.6; Table 1).

Incubation and nestling periods

Elevation did not have a significant effect on incubation period ($F_{1,90}$ = 0.672, p = 0.41; Fig. 3C), but a significant positive effect on nestling period ($F_{1,83}$ = 5.827, p = 0.01; Fig. 3D). Furthermore, there was not a significant difference in incubation period between low and highland forests (*t value* = 0.36, d.f. = 90, p = 0.71), with an overall mean of 15.3 ± 0.7 days and 15.5 ± 1.1 days at high and lowland elevations respectively. Nestling period was marginally longer at high elevations (*t* *value* = -1.87, d.f. = 83, *p* = 0.06), with a mean of 22.3 ± 0.5 days in highlands and 21.7 ± 0.9 days in lowlands (Table 1).

Nesting success

Breeding pairs of Rayaditos showed lower nesting success at high elevations vs. low elevations. For 2010-2011, we found marginal differences between elevation categories (Mann-Whitney *U* test; *U* = 182; p = 0.08; Fig. 4). For 2011-2012, breeding at high elevations was less successful in the number of fledged nestlings (Mann-Whitney *U* test; *U* = 465; p < 0.01; Fig. 4). Most unsuccessful nests failed during laying period (79%) for highlands, and during incubation period (45%) for lowlands. Predation was the main factor of nest failure, especially in highland forests, where accounted for 84% for the second breeding season (Table 1).

DISCUSSION

We have provided the first assessment of the effects of elevation on the reproductive strategy of a cavity-nesting bird, controlled for latitude (same latitudinal degree), in temperate forests of South America. Across a fast-slow continuum gradient of reproductive strategies (Sæther 1987), we found a shift in reproductive life-history traits (i.e., clutch size, number of broods, and nestling period) from faster to slower reproductive strategies with increasing elevation in Thorn-tailed Rayaditos. This result is similar to the shift in reproductive strategy documented for an open-cup nester (Dark-eyed Junco, Bears et al. 2009) and a ground nester (Savannah Sparrow, *Passerculus sandwichensis*, Martin et al.

2009). There was a pronounced reduction in the length of the breeding season at high elevations (28% and 55% shorter than low elevations for two breeding seasons). This reduction is comparable to the one founded by Ogden et al. (2012) for a cavity-nesting bird, the Pacific Wren, along an elevational gradient in British Columbia, Canada. Furthermore, the patterns of clutch initiation dates for Rayaditos are similar to those of Pacific Wren, which also show bimodal and unimodal distribution at low and highland forests respectively. However, the outcomes for Rayaditos differed to those observed by Ogden et al. (2012); the shorter breeding season at high elevations was translated to smaller clutch sizes and number of broods, and a longer nestling period. These results may be associated with lower annual fecundity (fewer offspring per breeding season) and apparently greater parental care at high elevations. The latter two shifts at high elevations agree with patterns found for both open and cavity- nesting birds (Badyaev & Ghalambor 2001), and suggest a trade-off between parental care and number of offspring produced. Since we only assessed a set of specific reproductive life-history traits for the Thorn-tailed Rayadito, we lack knowledge of other stages in their life cycle. In conjunction with the results we have presented, an examination of offspring and adult survival in Rayaditos could provide a greater understanding of how their reproductive life-history traits respond to elevation. Despite the lack of an overall picture, our results are consistent and suggest the presence of intra-specific variation of reproductive traits across elevational gradients in Andean forests.

We found a lower nesting success at high elevations, mainly associated with predation (Skutch 1985; Roper & Goldstein 1997). This pattern match with the hypothesis that greater parental care is related to higher predation risk, since the predators can use parental activity to find nests (Skutch 1949). In temperate forests of South America, the main cavity-nester predators, Austral Opossums (*Dromiciops gliroides*, Celis-Diez et al. 2012) and Güiña (*Leopardus guigna*, Altamirano et al. 2013) (Appendix 2), are nocturnal, whereas Thorn-tailed Rayaditos are active during the day. Therefore, predation rate is likely not influenced by the diurnal activity of birds. We suggest that the higher predation rate observed at high elevations is related to a higher density of native predators at highland forests due to lower habitat disruption in these areas (Ibarra et al. 2012). However, is necessary to assess conjunct effects between nest sites and parental care to understand current patterns of nest predation (Martin et al. 2000).

Our results differ from the breeding biology of Thorn-tailed Rayaditos exhibited in coastal locations (Moreno et al. 2005; Quilodrán et al. 2012). Quilodrán et al. (2012) suggest that, consistent with the hypothesis proposed by Lack (1947), clutch size increases at higher latitudes, with a mean clutch size of 3.3 at 35 °S and 4.1 at 42 °S. However, we found a larger clutch size (mean = 4.7) at an intermediate latitude (39 °S). This suggests that there could be not linear differences in reproductive life-history traits along a latitudinal gradient, even more so when contrasting breeding parameters at similar elevations (< 500 of elevation). Our findings also support the idea that differences in clutch sizes along elevational gradients co-vary with latitude and are reflected in avian life-histories (Camfield et al. 2010). However, potential interactions between elevation and latitude, as drivers behind these differences, are still unknown. To identify these drivers, we would have to assess differential effects across elevational gradients at different latitudes. Nevertheless, implementing such experimental design is complex as many independent variables (e.g. weather, food and/or nest-site availability, predators) may interact with population life-histories (Tieleman 2009).

Using artificial cavities (nest-boxes) is useful to assess the effects of environmental gradients on cavity nesting birds (e.g. Johnson et al. 2006). This artefact allows the control of cavity-level conditions (i.e., entrance size, depth, internal volume, among others) that could have interfered with breeding parameters, such as clutch size and nesting success (Karlsson & Nilsson 1977; Llambias & Fernandez 2009). Nonetheless, nest-boxes are artificial tools and, as such, conclusions obtained from their utilization should be interpreted with caution. For example, results from nest-boxes on predation rates and nest fate do not necessarily reflect the real success of predation attempts (Altamirano et al. 2013) (Appendix 2).

We conclude that Thorn-tailed Rayaditos may have an adaptive response to shorter breeding seasons at higher elevations: they have smaller clutches sizes, lower number of broods, and invest more time taking care of nestlings (Badyaev & Ghalambor 2001). Furthermore, they do not appear to show second nesting attempts at higher elevations. However, these potential adaptations do not seem to compensate for the increased predation rates at higher elevations; this brings to question the adaptive significance of this strategy, and suggests that individuals at these higher elevations could make only a marginal contribution to overall population abundance. Finally, the reproductive life-history traits of Rayaditos in Andean locations were different to those of coastal locations, resulting in a higher number of offspring per nest. Our results highlight the importance of studying the ecology of birds in southern Andean locations, and examining the effects of elevational gradients on bird communities in temperate forests of South America.

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Tables

Table 1. Thorn-tailed Rayadito breeding outputs at low and high elevations in Andean temperate forests of Chile. Values are presented as mean ± SD. * Categorical variable, where 0 are completely successful nests, 1 at least one nestling fledge, and 2 completely unsuccessful nests. ** This category included adult dead and bad eggs. See text for details of statistical analysis.

	Low elevation (260-476 m a.s.l.)		High elevation (789-1,115 m a.s.l.)	
	2010-11	2011-12	2010-11	2011-12
A. Breeding parameters				
Clutch size (#)	4.2 ± 0.7	4.7 ± 0.9	4.1 ± 0.9	4.2 ± 0.8
Number of broods (#)	4.1 ± 0.8	4.3 ± 1.1	3.5 ± 0.9	3.7 ± 1.2
Nestlings Fledge (#)	3.7 ± 1.3	3.8 ± 1.8	3.4 ± 0.9	2.7 ± 2.5
Laying period (d)	6.4 ± 1.5	7.7 ± 1.5	6.3 ± 2.0	7.0 ± 1.2
Incubation period (d)	15.0 ± 0.3	15.9 ± 1.3	15.0 ± 0.0	16.0 ± 1.0
Nestling period (d)	22.1 ± 0.8	21.4 ± 0.8	22.3 ± 0.5	22.0 ± 0.0
B. Nesting success				
General Fate*	0.6 ± 0.8	1.1 ± 0.9	1.0 ± 0.9	1.8 ± 0.5
Successful nests (%)	79.1	54.5	66.7	10.5
Predated (%)	7.0	36.4	25.0	84.2
Abandoned** (%)	14.0	9.1	8.3	5.3

Figure legends

Figure 1. Locations of the six forest stands where 40 nest-boxes were installed for two breeding seasons (2010-2011 and 2011-2012) near the city of Pucón, Araucanía district, Chile.

Figure 2. Rayadito breeding temporality at lowland and highland Andean temperate forests of Chile. X axis shows the date of first egg since October 1 (day 0) for all nesting attempts. Y axis shows the proportion of active nest-boxes for breeding season 2010-2011 (A) and 2011-2012 (B).

Figure 3. Association between breeding parameters (raw data) and the elevational gradient (271-1,063 m) in Andean temperate forests of Chile. Regression plots show clutch size (A) and number of broods (B) for three breeding seasons (2010-2013), and incubation period (C) and nestling period (D) for two breeding seasons (2010-2012).

Figure 4. Nest fate (measure of nesting success, we considered a successful nest -fate value = 0- when all eggs resulted in nestlings that fledged, partially successful -fate value = 1- when at least one chick fledged, and unsuccessful -fate value = 2- when no nestling fledged) of Thorn-tailed Rayaditos for two breeding seasons, at high and low elevations in the Andean temperate forests of Chile. * shows statistical significance (Mann-Whitney *U* Test; $p = 0.002$).

Figures

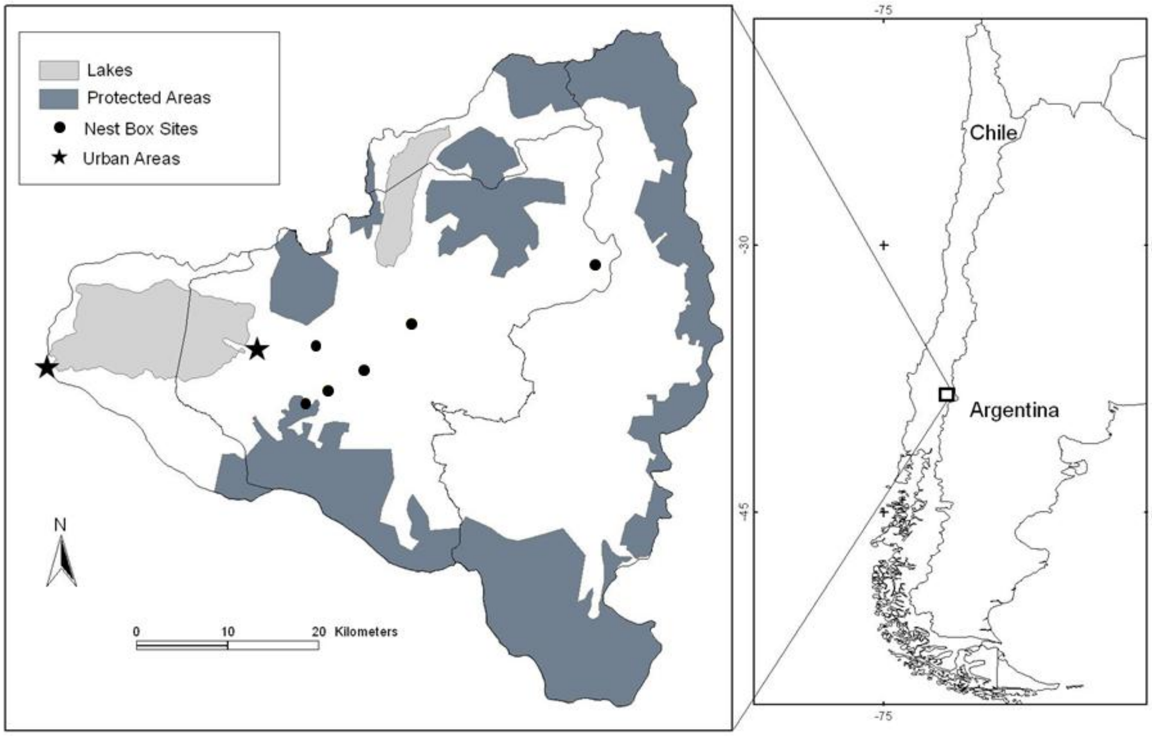
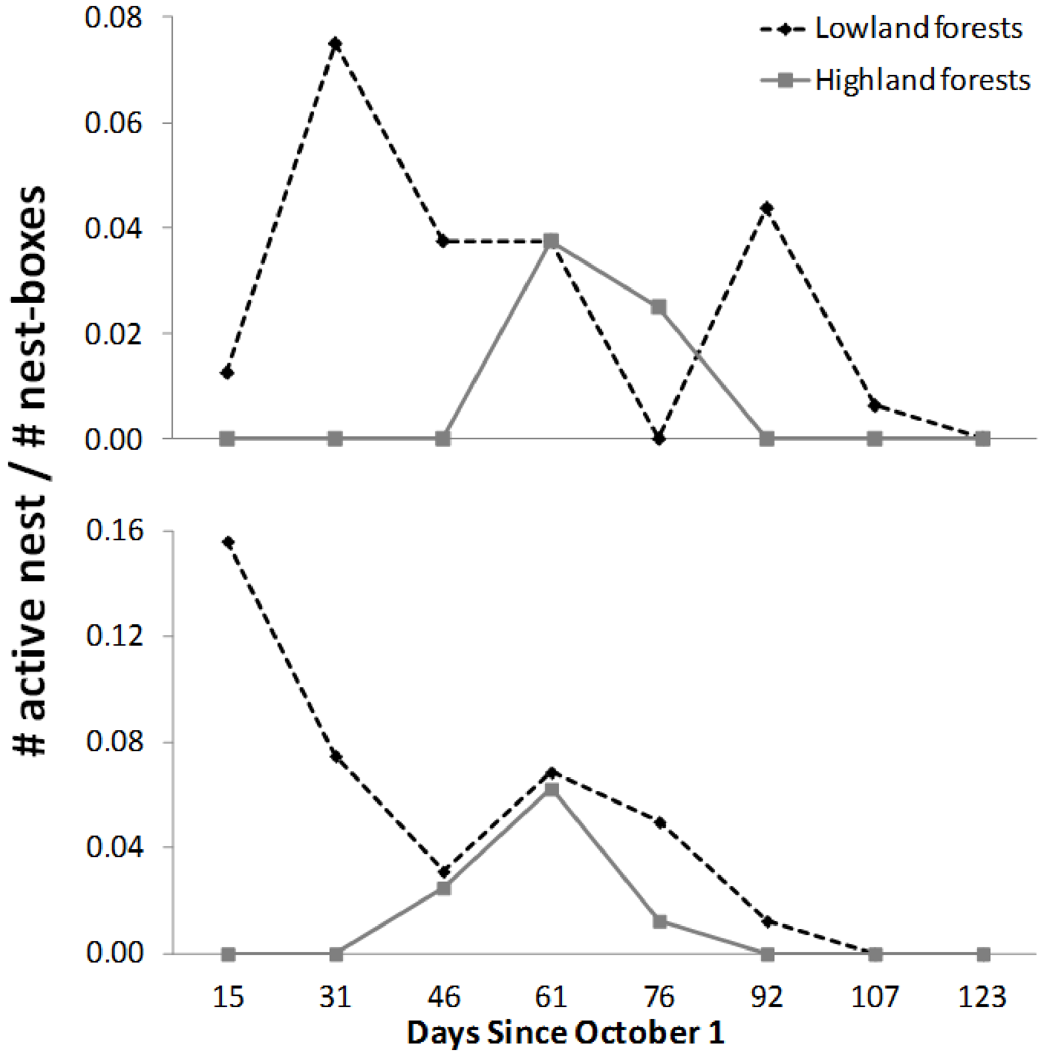


Figure 1



0.08
0.06
0.04
0.02
0.00
0.16
0.12
0.08
0.04
0.00
Lowland forests
Highland forests
active nest / # nest-boxes
15
31
46
61
76
92
107
123
Days Since October 1

Figure 2

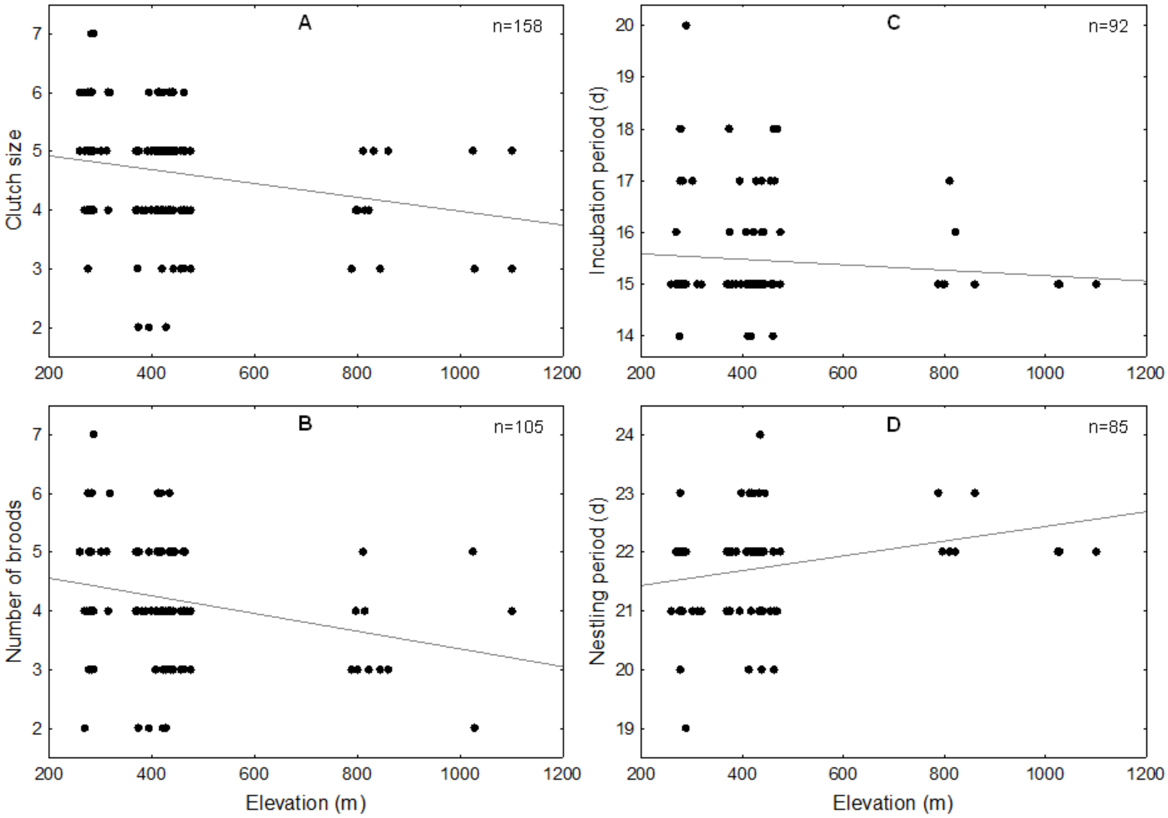
A
n=158
Clutch size
7
6
5
4
3
2
C
n=92
Incubation period (d)
20
19
18
17
16
15
14
B
n=105
Number of broods
D
n=85
Nestling period (d)
24
23
22
21
20
19
200
400
600
800
1000
1200
Elevation (m)

Figure 3

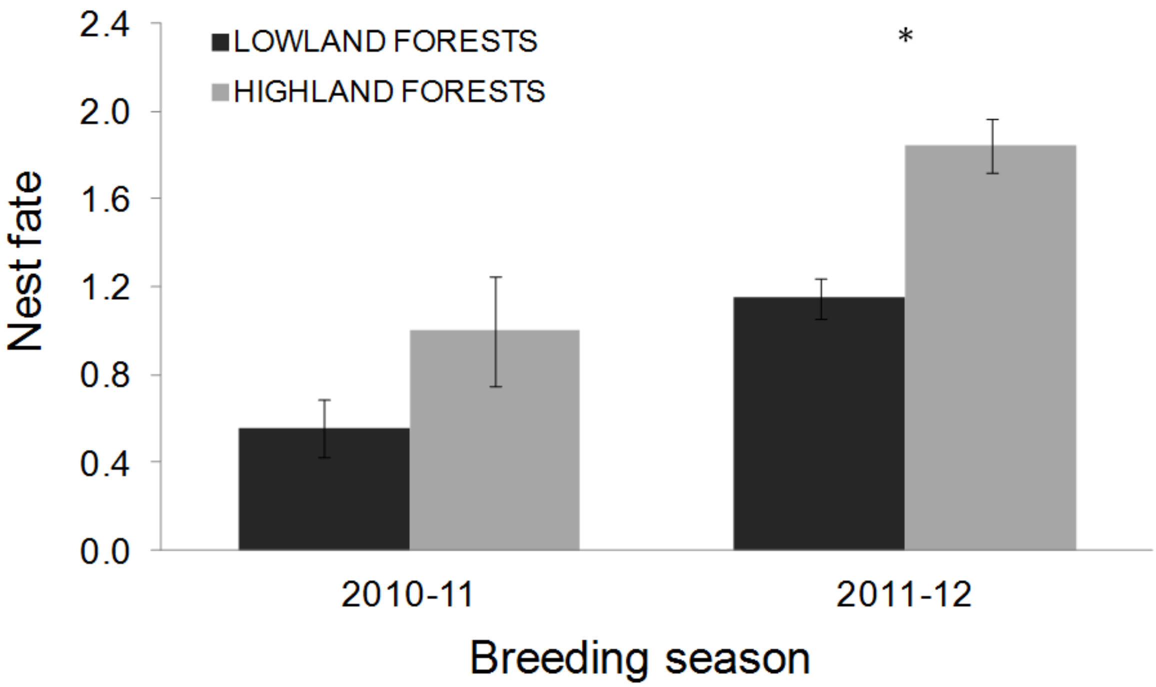

2.4
2.0
1.6
1.2
0.8
0.4
0.0
Nest fate
■ LOWLAND FORESTS
■ HIGHLAND FORESTS
*
2010-11
2011-12
Breeding season

Figure 4

Chapter 2

Cavity-nesting birds response to experimental variation of a critical resource in managed and old growth temperate rainforests of South America

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Abstract. Populations of cavity-nesting birds often are limited by the number of tree cavities available in forests subjected to intensive management. The possibility that this critical resource can be limitating in old growth and unmanaged forests is much less clear. We compared forest attributes and bird populations between managed and old growth stands of temperate rainforests of southern Chile. To examine the role of nest-site availability in limiting populations of secondary cavity-nesting birds, we conducted a replicated experiment between 2008 and 2013, in which nest-boxes were added to forest stands and two-years later removed. Tree-basal area was two times larger (99.6 vs 43.7 m^2/ha), large trees were three times denser (88.2 vs 36.4 trees/ha), and the number of small cavities was 1.5 times higher (25.9 vs 10.3 cavities/ha) in old growth forests compared to managed forests. Thorn-tailed rayaditos showed a strong response to experimental cavity addition in managed forests, increasing 13% in abundance during two years. Removal of cavities led to a large (50%) and rapid decrease. In contrast, in old growth forests there were no measurable effects of cavity addition and posterior removal. Chilean swallows and southern house wrens did not show any significant response in either type of forest. This experiment, the first one carried out simultaneously in both managed and old growth forests in Chile, revealed that older forests have appropriate attributes and unlimited cavity availability to support populations of rayaditos. Our findings highlight the importance of maintaining larger trees that supply suitable cavities to this species within managed areas.

Key words: Chile, forest management, resource limitation, secondary cavity-nesters, temperate rainforests, thorn-tailed rayadito.

INTRODUCTION

Cavity-nesting birds comprise a hierarchical and strongly structured community. These birds are often categorized as excavators which can generate their own cavities, and secondary cavity-nesters (SCNs) (Martin and Eadie 1999, Martin et al. 2004). Secondary cavity-nesting birds cannot excavate their own cavities and thus rely on those created by excavators and/or a limited number of decay-occurring (non-excavated) cavities (Aitken and Martin 2007). Cavity availability is considered a critical primary resource, potentially limiting breeding population density of avian cavity-nesters (Brawn and Balda 1988, Newton 1994, 1998, Tomasevic and Estades 2006, Cockle et al. 2010, Aitken and Martin 2012). However, the evidence supporting nest-site limitation comes mainly from managed forest, which typically have small trees and scarcity or absence of old growth trees (Newton 1998). Only 19% of the studies that have assessed nest-site limitation in old growth forests have reported significant changes in density of cavity-nesters (Wiebe 2011). Thus, experiments carried out in mature forests show that nest-site limitation is much more variable across species and regions (Cornelius et al. 2008). For example, in mature forests of Coconino National Forests (Arizona, Brawn and Balda 1988), and unmanaged subtropical forests (Cornelius et al. 2008) no evidence of cavity limitations was found. In contrast, in old growth temperate forests of Canada, nest abundance of some SCN species (including birds and mammals) were influenced by nest-site availability (Aitken and Martin 2012). These experimental studies have improved our understanding of the effects of spatial and temporal cavity availability on bird populations, and provide a mechanistic basis for the commonly observed negative effects of intensive forest management on some components of the bird assemblage. They also show the need to conduct simultaneous studies in old growth and managed forests if we are to draw conclusions about the factors limiting cavity-nesting bird populations and the impact of forestry practices. Unfortunately, most experiment and empirical evidence of cavity limitation comes from studies in North America and Europe (Newton 1998), and virtually none from the temperate rainforest of South America, which has already been heavily disturbed.

Cavity-nesting birds depend on some particular forest structures, being especially sensitive to forest disturbance (Martin and Eadie 1999, Diaz et al. 2005, Vergara and Armesto 2009). Cavity availability within a stand can be significantly reduced by the removal of the larger and dead standing trees (Pattanavibool and Edge 1996, Cockle et al. 2010), whereas at the landscape level, land use change (to agriculture or livestock production) is the main factor affecting this key resource availability (Vergara and Armesto 2009). Therefore, cavity limitation is highly plausible in forests where human activities have changed forest structures (Politi et al. 2010).

The main human disturbances responsible for the decline in temperate rainforest of South America (TRSA) are human caused fire, selective logging, and land use change associated to agriculture and forest plantations (Echeverría et al. 2007, Armesto et al. 2009). The main purpose of selective logging is firewood, which is the primary source of energy in rural and urban settlements in south-central Chile (Burschel et al. 2003). Thus, this activity has been highlighted as the main factor degrading native forests (U. de Chile 2012), which is especially intense in small forest fragments (Echeverría et al. 2007, Zamorano-Elgueta et al. 2014). Currently, only 13.1% of the original temperate rainforest areas represent the old-growth condition (CONAF et al. 1999, Armesto et al. 2009). The specific reduction of selective logging in TRSA is focused mainly on trees of larger diameters (DBH; Neira et al. 2002) and/or dead standing trees, negatively affecting the number of suitable cavities for nesting (Lindenmayer et al. 1993, Fan et al. 2003b).

Several studies have experimentally assessed the responses of SCNs to changes in cavity resources, mainly using addition of nest-boxes (Brawn and Balda 1988, Tomasevic and Estades 2006, Cockle et al. 2010), or blocking existing cavities (Aitken and Martin 2008). Nevertheless, few studies have used both increasing and reducing nest-site availability (Robles et al. 2012, Aitken and Martin 2012). In TRSA, there is a large gap in knowledge not only of whether cavities are a limiting resource for bird populations, but also about the magnitude of differences of cavity availability and forest attributes between managed and old growth forests. Therefore, information is especially required for the southern hemisphere (Wiebe 2011).

Fifty-five percent of the forest bird community in TRSA are cavity-nesters, and most of them are SCNs (Altamirano et al. 2012b; see chapter III). However, there are only two previous studies that have assessed nest-site limitation carried out in managed forests (Tomasevic and Estades 2006, Cornelius et al. 2008), and no studies have been conducted in old growth forests. Our objectives in this study were to: (1) quantify stand attributes and cavity availability in managed and old growth forests, and (2) experimentally determine whether cavity availability is limiting breeding population densities of small SCN birds, with spetial attention to thorn-tailed rayaditos (*Aphrastura spinicauda*), Chilean swallows (*Tachycineta meyeni*), and southern house wrens *(Troglodytes musculus*), comparing managed and old growth forests. We predicted that in old growth forests there will be higher density of cavities compared to managed forests and, consequently, we expected that nest-site availability limit bird populations in managed forests and not in old growth forests.

METHODS

Study area

We studied small body sized SCN birds in Andean temperate rainforests of southern Chile, in the Araucanía district, Pucón (39º16’ S, 71º48’ O) (Fig. 1). The TRSA is one of only seven of these ecosystems in the world (Alaback 1991). This forest covers more than 40,000 km^2 along the south-western margin of the continent, mainly in Chile and a small adjacent area of Argentina (Donoso 1993, CONAF et al. 1999), including an extensive latitudinal range between 35° and 55° LS (Armesto et al. 1998). The predominant weather characteristics are cool summers, and precipitations distributed throughout the year. Natural fires do not play a key role in this forest type. This ecosystem has been classified among the 200 biologically most valuable and critically endangered ecoregions of the world (Olson and Dinerstein 1998). Despite this classification, it has been and continues to be widely disturbed, resulting in 30% of the original remaining vegetation and being considered a biodiversity hotspot (Myers et al. 2000). In coastal areas, 67% of native forests have been replaced by other land cover types since 1975 (Echeverria et al. 2006), while in Andean locations, native forests were reduced in 44% in the last two decades (Altamirano and Lara 2010).

We quantified stand attributes, cavity availability, and SCNs densities in 10 forest stands with different degrees of disturbance (Fig. 1). Within these, six were recently burned stands with occasional selective logging, representing managed forests (secondary growth, < 60 years), and four were unburned and unmanaged forests representing old growth condition (> 200 years). Managed forests were mainly dominated by broadleaf species as *Nothofagus obliqua*, *Nothofagus dombeyi* and *Laurelia sempervirens*. The old growth stands were conifer-broadleaf mixed forests, dominated by *Saxegothaea conspicua*, *Laureliopsis philippiana* and *N. dombeyi*. We considered areas as old growth stands when these had a core area where edge effect was minimal, maintaining a complex vertical structure, and the species composition had not been significantly modified (Armesto et al. 2009). The understory compositions, in both managed and old growth forests were dominated by bamboo species (*Chusquea spp.*), *Rhaphithamnus spinosus*, and different species of *Azara* and tree saplings. As the home range of focal species is unknown, we considered 3 – 4 ha of home range of thorn-tailed rayadito, based in results found for *Aphrastura masafuerae* (Hahn et al. 2010). Thus, sites were separated by a minimum linear distance of 1.6 km among them to ensure that adding and removing nest-boxes in one site would not affect birds in the other sites (Wiebe 2011).

Forest attributes and cavity availability

To quantify forest structures and cavity availability in the stands, we established five vegetation plots per stand. These plots had their center in each point count station, with a total surface of survey of 0.04 ha (radius = 11.2 m). We quantified following stand attributes within these vegetation plots: live trees density, dead standing trees density, tree diameter at breast height (DBH), and number of small cavities per tree. All variables were recorded in trees with DBH ≥ 12.5 cm. We used tree DBH to calculate basal area of the trees with DBH ≥ 35 cm, and the density of larger trees (DBH ≥ 60 cm). Cavities were considered if they had a minimum entrance diameter of 2.5 cm, including round or square hollows, crevices, fallen branches, among others (Cornelius 2008). We counted cavities with a minimal depth of 10 cm, because we had recorded nests from this internal depth for thorn-tailed rayaditos and southern house wrens (Altamirano et al. unpublish data). Cavities from 0.2 m until 30 m were considered, due to reports from previous studies (Cornelius 2008, McGehee et al. 2010, Altamirano et al. 2012a).

Resource addition and removal

We increased the availability of suitable cavities by adding 40 wooden nest-boxes in six forest stands (n = 240; four managed forests and two old growth forests) during non-breeding season of 2010. These wood-made nest-boxes were installed hanging from branches, approximately at 1.5 m height. All nest-boxes were placed at least 15 m from the forest edge in order to reduce edge effects. The entrance aspect of nest-boxes was oriented randomly. The entrance diameter and depth were 3.1 cm and 17.1 cm respectively, with our focus on smaller body sized SCN birds (Altamirano et al. 2013) (Appendix 2). These kind of nest-boxes (i.e. diameter of entrance and internal dimensions) were used to improve the nest-box occupancy probability (Lambrechts et al. 2010), as they had been successfully used by thorn-tailed rayaditos and southern house wrens (Moreno et al. 2005, Vergara 2007, Llambias and Fernandez 2009, Ippi et al. 2012). Despite that the nest-boxes could be used for any of the three focal species, we prioritized the specific installation sites which were more likely suitable to be used by thorn-tailed rayaditos. This is due primarily to southern house wrens nesting mainly in the forest edge, and Chilean swallows can breed in both forest edge and interior, but when nesting in the forest interior, they mainly use higher cavities (Altamirano et al. unpubl. data). In winter of 2012, we blocked all nest-boxes, reducing cavity availability to its original status in both managed and old growth forests. Blocking was effective in preventing further use of the nest-boxes in 100% of the cases. The remaining four forest stands were used as control sites, where nest-box addition and removal was not carried out.

Secondary cavity-nesting bird abundance

We used a replicated experimental design (Robles et al. 2012, Aitken and Martin 2012). We monitored SCN birds' population in experimental and control sites over a six-year period; two year pre-treatment (2008-2010), two years during treatment (nest-box addition, 2010-2012) and two year post-treatment (nest-box removal, 2012-2013). Five point count stations per forest stand were established, of variable diameter (25 and 50 m), and with a minimum distance of 125 m among them. All counts were conducted during four hours from sunrise (6:30 – 10:30), with a duration of seven minutes where we recorded all bird species that were detected (hear and/or seen) within the radio. Point count stations were preferred because they are more efficient in forest conditions than other methods (Ralph et al. 1996).

Data analysis

We compared the following forest structures between managed and old growth forests: basal area of trees with DBH ≥ 35 cm (m^2/ha; hereafter basal area), number of trees with DBH ≥ 60 cm per ha (hereafter density of larger trees), number of dead trees per ha, and number of small size cavities per ha. We tested the statistical differences using *t*-test for comparing two groups. A critical tree diameter was established in: i) 35 cm for basal area because an 80% of the nests from these three focal species are in trees with higher DBH, and ii) in 60 cm to calculate density of larger trees because it is the mean diameter used by these species (see Chapter III). We used linear regression to assess how the availability of natural cavities was related to tree DBH and basal area. We assessed cavity limitation directly on thorn-tailed rayadito, and indirectly on Chilean swallow, and southern house wren. Therefore, we analysed responses to experimental key resource addition and removal for two forest specialist birds (the first two), and one shrub user (the last one) (Diaz et al. 2005). Opposite to Tomasevic and Estades (2006), we did not consider the white-throated tree-runner (*Pygarrhichas albogularis*) as SCN, because in four years of cavity nesting community monitoring we have not found this species using pre-existent cavities (see Chapter III). We conducted repeated measures ANOVA to determine the response to experimental increasing and reduction of critical resource over the years.

RESULTS

Forest structures and cavity availability

Within 50 vegetation plots and 1,627 trees measured, structural differences were found between managed and old growth forests. Old growth forests had more than twice the basal area found in managed forests (t = 5.14, $p < 0.001$). Density of large trees (≥ 60 cm DBH) was almost three times higher in old growth forests (t = 4.56, $p < 0.001$), while density of small size cavities was 1.5 times higher (t = 5.27, $p < 0.001$) in old growth and unmanaged forests. However, density of dead trees did not vary between kinds of forests (t = 1.13, $p = 0.264$) (Table 1). Linear regression showed a significant response in cavity availability in function of tree

DBH ($R^2 = 0.45$, $F = 1101.70$, $p < 0.000$), increasing the number of cavities with the increase in tree DBH (Fig. 2A). A similar result was found for basal area effect on density of cavities, which increased significantly with the increase in basal area per ha (Fig. 2B; $R^2 = 0.35$, $F = 24.28$, $p < 0.001$).

Cavities as a limiting resource

During two years of treatment, nest-boxes were widely occupied by thorn-tailed rayadito (54 in 2010-2011, and 96 in 2011-2012), while only two and one were used by southern house and by Chilean swallow respectively (see Chapter I). We found a strong treatment effect in thorn-tailed rayaditos inhabiting secondary forests, where population increased significantly by 24% in 2010, and a further 1% in 2011, and decreased by 12% in 2012 (respect to the previous year), resulting in a total increase in population abundance of 13% over the three years of treatment. Then, when the critical resource was blocked, population abundance decreased by 39% in 2012, and further 11% in 2013, resulting in a total decrease in population abundance of 50%, returning to near pre-treatment levels in 2010 (Fig. 3A) and reaching similar levels to control sites ($F = 25.81$; $p = 0.005$). However, this pattern was not observed in old growth forests, where populations of rayaditos did not vary between treatment and control sites over all years (Fig. 3B, $F = 2.79$; $p = 0.175$). Thus, experimental addition and removal of cavities did not impact in bird populations inhabiting old growth forests.

On the other hand, despite the increase of Chilean swallows in more than twice their population abundance during the first year of treatments (2010), there was no statistical difference in managed forests between population abundance over all years (Fig. 3C, F = 0.83; p = 0.497). The same result was observed in old growth forests, with similar patterns in populations of Chilean swallows in both control and treatment sites (Fig. 3D, F = 3.64; p = 0.126). Southern house wrens showed no pattern associated with treatment over all years in both secondary and old growth forests (Fig. 3E, 3F; p >> 0.05).

DISCUSSION

This is the first study that quantifies cavity availability, its relation with main forest structures, and assesses the key resource limitation in both secondary and old growth forests, in temperate rainforests of South America. We provide evidence of a consistent and strong population limitation on thorn-tailed rayaditos inhabiting in secondary and managed forests (Brawn and Balda 1988, Tomasevic and Estades 2006, Cornelius et al. 2008), but not in old growth forests. Furthermore, our findings suggest that the spatial differences associated to forest age in the responses to experimental cavities manipulation, are likely to be driven by specific forest structures (i.e. tree DBH and basal area) present in both kinds of forests.

Forest attributes and cavity availability

We found, as expected, that critical forest structures for SCNs (i.e. basal area, density of larger trees, and number of small cavities) were higher in old growth forests. This is likely to reflect the effect of selective logging in managed forests (Politi et al. 2010). Changes found in basal area and density of larger trees, between forests in different successional stages, are quite similar to results from coastal and island locations (Carmona et al. 2002, Diaz et al. 2005). In these locations, both basal area and density of larger trees, are at least twice higher in old growth forests compared to intermediate and early successions. These variables that had been highlighted, have a positive relation with forest specialist birds (e.g. cavity-nesters; Diaz et al. 2005, Tomasevic and Estades 2006). This is probably to explain the higher number of small cavities found in old growth forests, suggesting that the cavity availability drives the positive relationship between these forest structures and the densities of cavity-nesting birds. On the other hand, density of dead trees did not vary between managed and old growth forests, which is likely due to the maintenance of a large number of these trees resulting from past disturbance (e.g. fire; Aravena et al. 2002).

Our findings match the idea that tree DBH and basal area, as indicators of age of forest stands, are important for cavity creation (Koch et al. 2008, Cockle et al. 2010). Similar to a study in coastal temperate rainforests (Estades and Tomasevic 2004), we found that tree DBH have a significant effect on the density of cavities present in each tree. Cavity availability increased along with the increase in basal area. A similar pattern was found in Atlantic forests (Cockle et al. 2010). This result, confirms basal area as a good predictor variable affecting cavity availability at stand level (Fan et al. 2003a). Therefore, using basal area to predict cavity density in forests could be very useful instead of counting the specific number of small cavities in a stand. However, it must be considered with caution, as the effects of tree DBH and basal area on density of suitable cavities could vary in other forest circumstances (e.g. tree composition or dominant species), and abiotic conditions.

Nest-site limitation

The role of nest-sites in limiting densities of cavity-nesting species has been widely studied (Newton 1998). Despite this, experiments with key resource management assessing nest-site limitation in old growth forests are rare and results appear less consistent (Cornelius et al. 2008, Wiebe 2011). In managed areas of TRSA, similar key resource addition experiments (Tomasevic and Estades 2006, Cornelius et al. 2008), conclude that nest-sites did limit population sizes of thorn-tailed rayaditos in breeding seasons in coastal and island locations. However, both of these studies were of relatively short duration (one and three years respectively), only assessing nest-site limitation on population densities in managed forests. Furthermore, they did not use an experimental design that considered both an increase and reduction of the suitable cavities for SCNs in the same habitats (Robles et al. 2012). Our experiment revealed that cavity availability limits density population of thorn-tailed rayaditos in second growth and managed forests; thus, the number of rayaditos increased and decreased significantly in the treatment sites (nest-boxes addition and removal) but did not change in the control sites where nest-boxes were not added or subtracted. This result confirms the suggestion of previous studies that cavities are a critical resource that may limit rayaditos breeding populations (Tomasevic and Estades 2006, Cornelius et al. 2008). On the other hand, in agreement with the 81% of the studies carried out in mature forests (Wiebe 2011 and references there in), nest-site did not limit populations sizes of rayaditos in old growth forests. This suggests that another resource is a limiting factor the abundance of this species in forests with a higher basal area, density of larger trees, and cavity availability, such as food-supply (Newton 1998).

The response to the variation in cavity availability was different between species. Rayaditos may compete for cavities with swallows and house wrens (Altamirano et al. unpubl. data). Therefore, addition of key resource might reduce potential competition for cavities, and increase the population abundance of other species that do not used nest-boxes, and vice versa when the resource is removed (Norris et al. 2013). Contrary to this, swallows and house wrens did not respond to the increase or decrease of the cavity resource. The low effect of cavity addition and removal on Chilean swallows and southern house wrens, could be explained for one or more of the following non exclusive hypotheses. First, these species nest in cavities located at different conditions. For example, Chilean swallows prefer higher cavities (> 4 m from the ground; Altamirano et al. 2012a), whereas southern house wrens inhabit mostly open areas and forest edges, and their presence is occasional in forest interior (Rozzi et al. 1996, Diaz et al. 2005). Other hypothetical explanation could be that thorn-tailed rayaditos and Chilean swallows are dominant and subordinate competitors respectively, each species having different abilities to respond to temporal and spatial changes in critical resource availability (Aitken and Martin 2008). Thus, in the first year of nest-box addition (2010) thorn-tailed rayaditos concentrate their focus on nest-boxes, justifying the increase in Chilean swallow population the first year (Fig. 3C). The next year of treatment, abundance of rayaditos is large enough to use nest-boxes and compete for natural cavities, in detriment of swallow populations. On the other hand, southern house wrens have been reported as a species with high plasticity in nest site selection (Altamirano et al. 2012a). Hence, they can utilize a broader range of cavity characteristics to reduce interspecific competition (Forstmeier and Weiss 2004, Aitken and Martin 2008). This results in no effects of the experimental changes of cavity resource, differing from significant effects found by Tomasevic and Estades (2006) in managed forests. The final idea is that swallows and house wrens are not limited by cavity availability in managed forests, similar to tree swallows (*Tachycineta bicolor*) in North America (Aitken and Martin 2008). However, these hypotheses should be proved with experimental changes in critical resource with focusing on specific nest-site selection of these species. Thus, adding and/or blocking cavities with appropriate characteristics and locations for their breeding requirements would be necessary. Unfortunately, the species specific cavity characteristics selection is still unknown to many species inhabiting temperate rainforests of South America.

Forest management implications

This study provides the first evidence that the thorn-tailed rayadito is not limited by cavity availability in old growth forests. However, in managed forests, suitable cavities are a limiting resource for this species. In these areas, the abundance of rayaditos varied with cavity availability, which was highly influenced by the density of larger trees. Our findings highlight the importance of maintaining forest attributes that supply suitable cavities to SCNs in managed areas. Old growth forests have appropriate structures to support sustainable populations of rayaditos. However, these kinds of forests are mainly found in protected areas and higher altitudes (Armesto et al. 2009). Therefore, maintaining large and dead trees in managed forests could improve habitat conditions for thorn-tailed rayaditos, which are negatively affected by the reduction in forest cover and fragmentation (Vergara and Armesto 2009), being a real contribution from silviculture to the conservation of forest specialist birds inhabiting managed areas. Most of forest policies specify a tree diameter limit to be harvested, many times protected younger trees more than large and old trees (Cockle et al. 2011). National forestry policy of Chile only superficially mentions tree diameter in the authorization for tree logging (CONAF 2014). We suggest limiting the maximum diameter of trees for harvest 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 size trees (future resource availability; Aitken and Martin 2004) could be very useful to allow breeding of cavity-nesting birds in managed forests.

Finally, the cavity-nester populations could be limited by other factors not measured here, such as food abundance, predation rates, or abiotic constraints (Zarnowitz and Manuwal 1985, Newton 1998, Cornelius et al. 2008). Therefore, at community level, maintaining suitable nest-trees may not be enough to conserve the cavity-nesting bird community, and more studies examining population limitation in birds are required.

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Tables

Table 1. Comparisons of forest attributes between managed and old growth forests (mean ± SE; n = 50 vegetation plots): basal area (medium size and larger trees ≥ 35 cm DBH), density of larger trees, dead trees, and small size cavities (entrance diameter < 5 cm), in the Andean temperate rainforest of South America.

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

Figure legends

Figure 1. Ten forest stands where experimental variation of critical resource and quantification of forest attributes were carried out. Pucón, Araucanía district, Chile.

Figure 2. Association between suitable cavity availability and forest structures in Andean temperate rainforest of Chile. Regression plots show number of cavities (A) and density of suitable cavities (B) as a function of tree DBH (n = 1,627) and basal area of trees ≥ 35 cm DBH (n = 50) respectively. Black circles represent the association between variables in old growth forests, while grey circles show the variables association in managed forests.

Figure 3. Mean bird abundance per point count by Thorn-tailed Rayadito (A, B) Chilean Swallow (C, D), and Southern House Wren (E, F) for six years of monitoring, including pre-treatment (before nest-boxes addition), during treatment (nest-boxes added), and post-treatment (nest-boxes removal). Treatments and control monitoring were carried out in six managed forests (A, C, E), and four old growth forests (B, D, F) in Andean temperate rainforests of South America. Error bars represent standard error of mean birds' abundance per point count station.

Figures

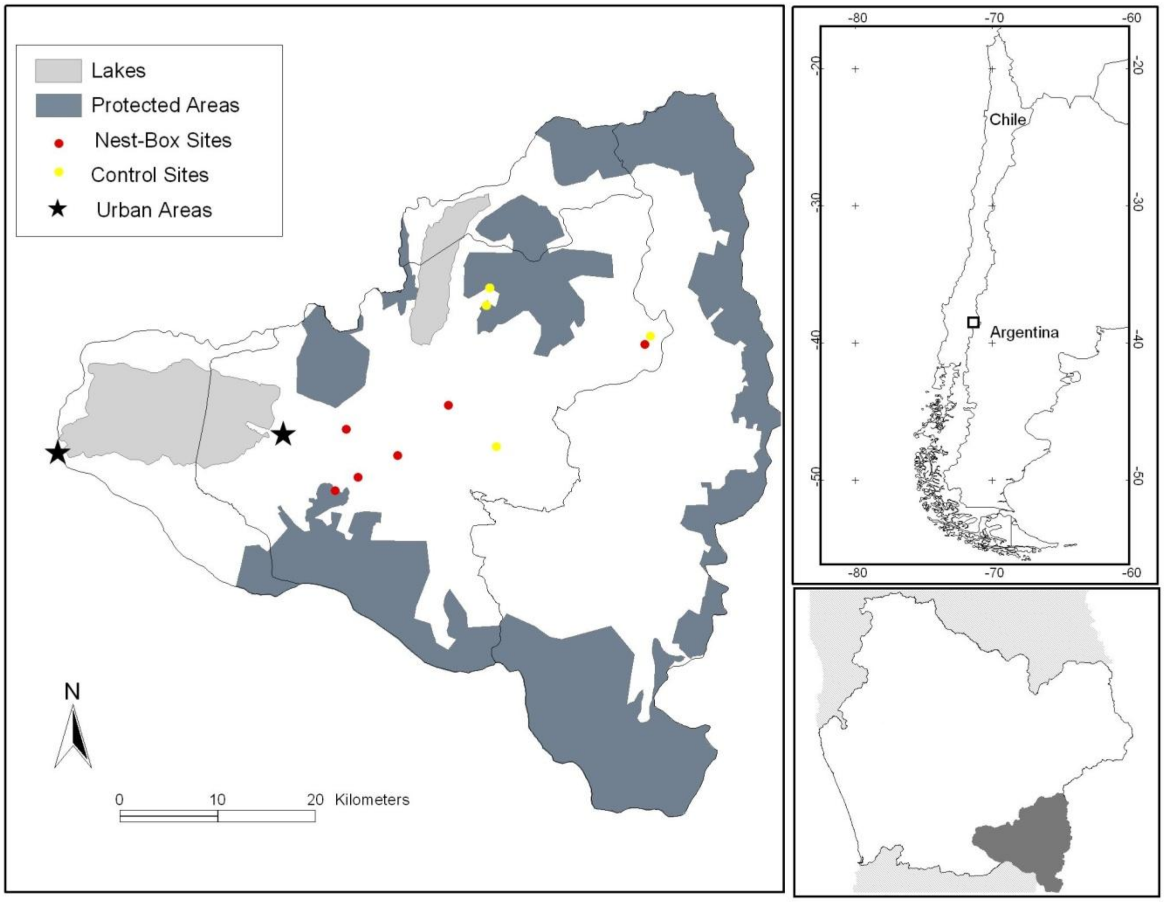

Figure 1

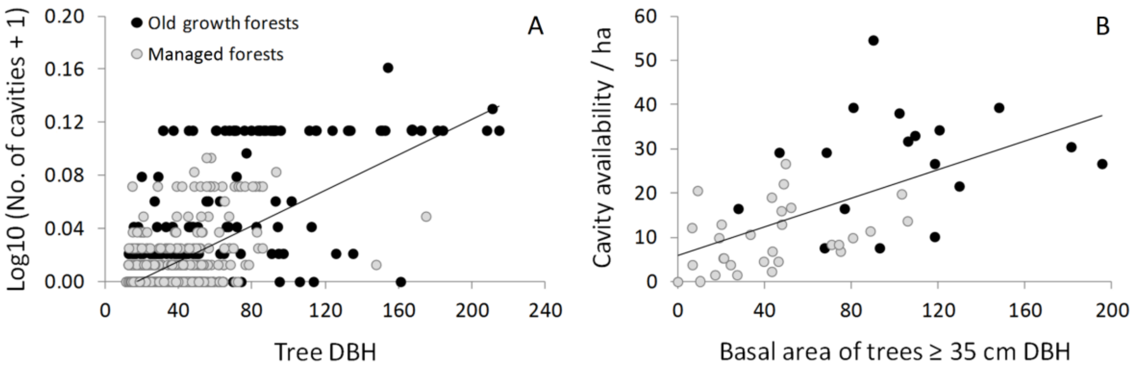
A
Log10 (No. of cavities + 1)
0.20
0.16
0.12
0.08
0.04
0.00
● Old growth forests
● Managed forests
0
40
80
120
160
200
240
Tree DBH
B
Cavity availability / ha
60
50
40
30
20
10
0
0
40
80
120
160
200
Basal area of trees ≥ 35 cm DBH

Figure 2

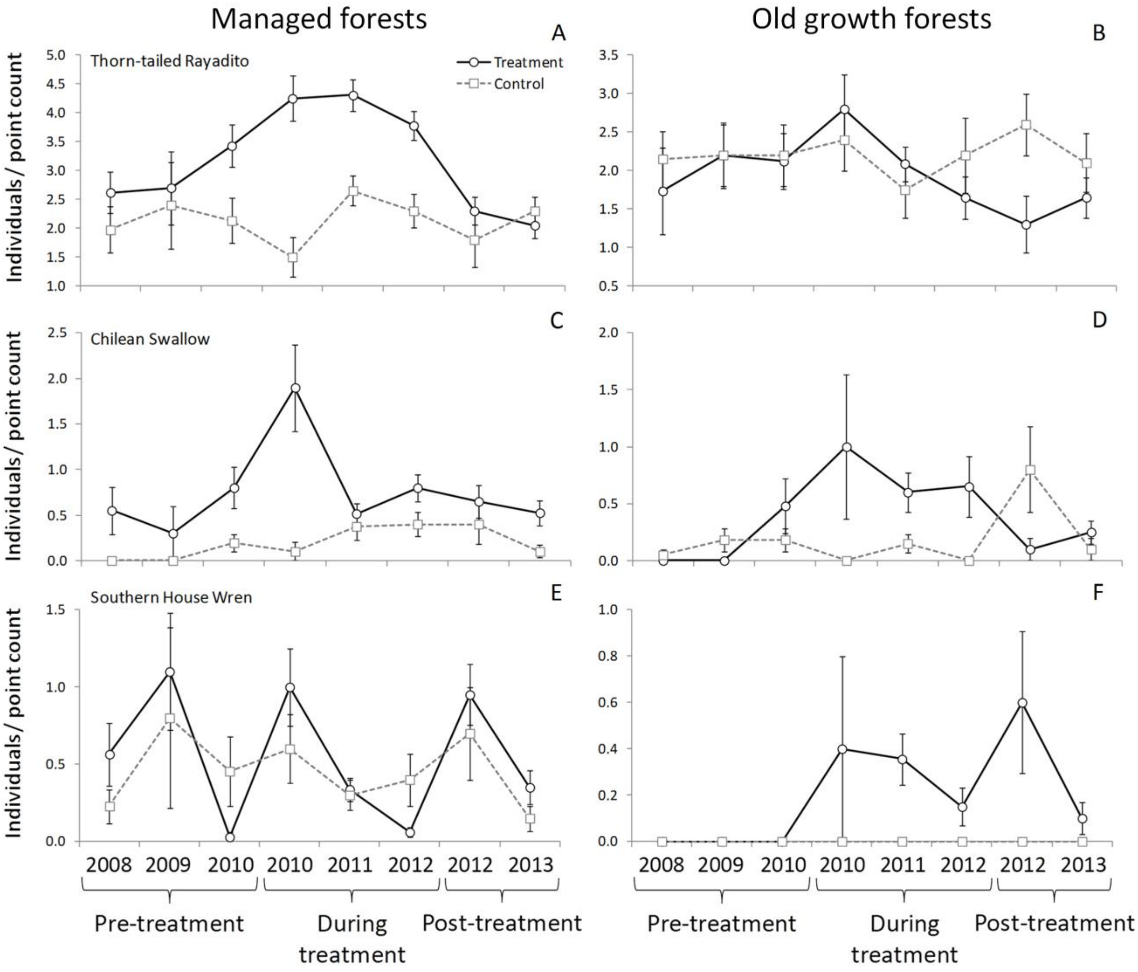
Managed forests
Old growth forests
A
B
C
D
E
F
Thorn-tailed Rayadito
Chilean Swallow
Southern House Wren
Treatment
Control
Individuals / point count
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0.2
0.4
0.6
0.8
2008
2009
2010
2010
2011
2012
2012
2013
Pre-treatment
During treatment
Post-treatment

Figure 3

Chapter 3

Cavity-nest web in the southern temperate rainforest of Chile: implications for forest bird conservation

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Abstract. Cavity-nesting communities exist within “cavity-nest webs” arranged hierarchically in nesting guilds in forest ecosystems, where community composition and nidic structure are imposed by cavity availability and by intra- and interspecific interactions. During three breeding seasons (2010-2013), we examined the components and structure of the cavity-nesting community in the Andean temperate rainforest of Chile, complementing our research with literature review. Cavity-nesting avian species (n=28) comprised a major component of the southern temperate forest bird community (55% of the avian community). Most cavity-using avian species (n=24) are secondary cavity nesters and only four are primary cavity nesters (excavators). We found a total of 263 nests belonging to 19 bird species, including nine species endemic to Southern temperate rainforest. Seventy five percent of nests were in tree-cavities created by natural processes (e.g. crevices, decay wood, broken branches), and the remaining 25% were cavities excavated mainly by the white-throated tree runners (*Pygarrhichas albogularis*) and Magellanic woodpeckers (*Campephilus magellanicus*). Cavity-nest web structure had a low dominance and evenness, with most of the network interactions were between non-excavators and trees, depending strongly of larger trees and advanced stages of decay. Similar to another cavity using community in northern Argentina, we found that tree decay and physical damage processes were much more important for tree cavity formation compared to excavators in Andean temperate rainforests. Our findings stress the importance of maintaining all stages of tree decay, in order to conserve an enough and long-term supply of the critical resource for cavity-nesting community, especially in timber production areas.

Keywords: Cavity-nesters, community structure, forest conservation, temperate rainforests, South America.

1. Introduction

In the world, many vertebrates depend on cavities for nesting (Newton, 1998, 1994). Cavity-nesting bird assemblages are arranged in hierarchical structures, analogous to food webs, within cavity-nest webs (Martin and Eadie, 1999). In cavity-nest webs, tree cavities are a vital resource around which birds interact, and two guilds exist depending on how cavities are obtained (Martin et al., 2004): “cavity-producers” or primary cavity nesters (PCNs; excavators), and “cavity-consumers” or secondary cavity nesters (SCNs; non-excavators) (Fig. 1). SCNs can nest in either excavated cavities (e.g. Beaudoin and Ojeda, 2011; Robles and Martin, 2013), or in those created by decay processes (Cockle et al., 2012). In food webs, top-down and bottom-up regulatory mechanisms are not mutually exclusive (Hunter and Price, 1992; Power, 1992). However, in terrestrial ecosystems the relative importance of these mechanisms change depending on productivity (Oksanen and Oksanen, 2000), with a bottom-up regulation being stronger when the key resource is limiting (Jaksic and Marone, 2006). Several studies have reported that cavity availability is the most significant limiting factor for cavity-nesting populations (Aitken and Martin, 2012; Brawn and Balda, 1988; Cockle et al., 2010; Newton, 1994; Tomasevic and Estades, 2006). Furthermore, competition can modulate densities of cavity-nesting birds in forests with low number of cavities

(Strubbe and Matthysen, 2009). Thus, cavity-nest webs could be a case where bottom-up regulations drive the diversity and abundance of cavity-nesting species.

Descriptions of the composition and structure of cavity-nest webs can provide us a strong evidence of the magnitude of the relationship between cavity-nesting birds and forest structure (Blanc and Walters, 2008a; Cockle et al., 2012; A. Koch et al., 2008; Martin et al., 2004). For example, in northern temperate forests of British Columbia, Martin et al. (2004) founded 20 cavity-nesting bird species strongly structured in a cavity-nest web through cavities excavated by Northern Flickers (*Colaptes auratus*) in Aspen trees (*Populus tremuloides*; 95% of nests in this tree species) (Fig. 1, scenario D). Furthermore, this cavity-nesting community showed a strong preference for excavated cavities (90%, Aitken and Martin, 2007; Cockle et al., 2011a) and unhealthy living trees (Martin et al., 2004). These results allowed identifying a key role of one PCN and one tree species in structuring a cavity-nest web in North America, with resulting specific recommendations for forestry schemes for the retention of Aspen in order to positively benefit most cavity-nesting species (Drever and Martin, 2010). In longlife pine forest in Florida State, 14 avian species compose the cavity-nest web, with eight PCNs and six SCNs (Blanc and Walters, 2008a). Here, more than 99% of nests used by SCNs were in excavated cavities chiefly by Northern Flickers and Red-cockaded Woodpeckers (*Picoides borealis*), with 73% of nests available in dead-standing trees or snags (Blanc and Walters, 2008; Fig. 1, scenario C). In contrast, in mega diverse Atlantic forests of South America, Cockle et al. (2011) found 69 cavity-nesting birds (12 excavators and 57 non-excavator), which mostly used cavities created by decay processes

(80%; Fig. 1, scenario B). In Australia, Gibbons and Lindenmayer (2002) reported 114 cavity-nesting birds in a system that lacks excavators (Mikusiński, 2006). Regarding to selected trees for nesting, cavity-users did not differ between tree species, but other structural variables were important to determine where bird are nesting, as diameter at breast height (DBH), and number of cavities and dead branches per tree (Gibbons et al., 2002). Thus, the management of key resource, could be a strong human driver for conservation of cavity-nester communities (Drever and Martin, 2010; Walter and Maguire, 2005).

Cavity nester species are strongly related to forests structure, and most of them can be very forest specialist, depending strictly on forest for nesting. These species has been reported to be highly sensitive to forest degradations (Cockle et al., 2011; Franzreb and Ohmart, 1978); thus, forestry practices play a strong role in structuring cavity-nest webs (Drever et al., 2008; Gibbons et al., 2002; Zarnowitz and Manuwal, 1985) (Fig. 1). This may be especially true in forest ecosystems with exceptional rates of endemism and subject to high rates of anthropogenic degradation such as temperate rainforests of South America (TRSA, Armesto et al., 1998). TRSA support a relatively low bird richness (nearly 44 species, Rozzi et al., 1996), but host large number of endemic avian species (41%, Vuilleumier, 1985, 1972). Similar to other forest ecosystems in the world (Bednarz et al., 2004), most studies of cavity-nesting birds in TRSA have been focused at the species level (e.g. Ibarra et al., 2014, 2012, Carneiro et al., 2013; Peña-Foxon et al., 2011; Ippi et al., 2012; Moreno et al., 2005; Vergara and Schlatter, 2004; Vergara and Marquet, 2007) and only a few have explored cavity-nesting birds at the community level (e.g. Díaz et al., 2005; Ippi and Trejo, 2003). Furthermore, it is not clear how many species actually rely on tree-cavities for nesting in TRSA, which is the degree of dependence for cavities (i.e. obligate, facultative, marginal, and accidental cavity nesters), and even less information is available on the tree characteristics selected for nesting.

Conservation of cavity-nesting communities requires a deep understanding of how tree-cavities are created and used (Cockle et al., 2012). However, no studies have assessed the interaction between PCNs and SCNs in temperate rainforests of South America. The aims of this study were to: (i) describe the cavity-nest web composition and structure, and assess the degree of dependence for cavities of the cavity-nesting community, (ii) compare the role of tree decay and excavation processes in structuring this cavity-nest web and contrast our results with other cavity-nest webs across the Americas, and (iii) determine characteristics of nest-trees selected and preferred, and the implications for conservation management of cavity-nesting communities in South America.

2. Methods

2.1 *Study area*

We conducted our study across an altitudinal and disturbance gradient of temperate rainforests in La Araucanía region, Chile (Fig. 2). Temperate rainforests of South America (TRSA) occurs in both sides of the Andean range, forming a narrow but latitudinally extensive strip of land between 35° and 55° S (Armesto et al., 1998). TRSA cover more than 40 000 km^2 along the south-western margin of continent, mainly in Chile and a small adjacent area of Argentina (CONAF et al., 1999; Donoso, 1993). These forests are isolated by more than 1 000 km from other forests areas in the continent, and are one of the seven of these forest types in the world (Alaback, 1991). The main weather characteristics are cool summers, precipitations distributed throughout the year, and relatively absence of natural fire events. These ecosystems are classified among the 200 biologically most valuable and critically endangered eco-regions in the world (Olson and Dinerstein, 1998). However, they have been widely disturbed, and only 30% of the original vegetation remains (Myers et al., 2000). Land use change and resulting habitat loss is the main threat to biodiversity inhabiting TRSA (Sala et al., 2000; Simonetti and Armesto, 1991). In coastal areas, 67% of native forests had been replaced by other land use types from 1975 (Echeverria et al., 2006), whereas in Andean locations native forests have been reduced in 44% in the last two decades (Altamirano and Lara, 2010).

We studied the cavity-nest web composition and structure in twenty forest stands (Fig. 2). We surveyed a gradient of stands from second-growth forests (< 60 years) which were burned 60 years ago and were subject to selective logging, to old-growth forests (> 150 years) within protected areas. Old-growth stands were defined as those stands with a core area where edge effect was minimal, maintain a complex vertical structure, and the plant species composition has not been significantly modified (Armesto et al., 2009). Nine of the second-growth stands were dominated by broadleaf species such as *Nothofagus obliqua*, *Nothofagus dombeyi* and *Laurelia sempervirens*. The remaining eleven were old-growth stands, conifer-broadleaf mixed forests, were dominated by *Saxegothaea conspicua*, *Araucaria araucana*, *Laureliopsis philippiana*, *Nothofagus pumilio* and *N. dombeyi*. The understory, in both second- and old-growth stands, was dominated by bamboo species (*Chusquea spp.*), *Rhaphithamnus spinosus*, different species of *Azara*, and tree saplings.

2.2 *Nest searching and monitoring*

We searched for all occupied cavities in our sites over three breeding seasons, from 1 October to 28 February of 2010-2011, 2011-2012, and 2012-2013. We followed the protocol for localization and monitoring of natural nests of Martin and Geupel (1993), observing the adults behaviour and look for evidence of recent wear around cavity entrance (Cockle et al., 2011b). When a cavity apparently had been used for nesting, we checked the interior of these. For lower cavities (< 2 m of high) we checked directly using flashlight with a mirror, and for higher cavities we used a wireless monitoring systems with a telescopic pole that reached up to 15 m of high (Cockle et al., 2011b; Huebner and Hurteau, 2007; Martin et al., 2004). When cavities were up to 15 m, we determined if the cavity contained an active nest from the ground, looking for breeding signals (e.g. feeding nestlings or extracting fecal bags) displayed by the adults. We considered a nest when one or more eggs or nestlings were present inside the cavity. For each nest we recorded: breeding species, origin of the cavity (decay or excavated), excavator species (if the cavity was excavated), and tree species. We then assigned a unique nest, cavity, and nest-tree numbers for monitoring the cavity use across the three breeding seasons. The status of each cavity (adult activity and fecundity data) was checked every 3-4 days, to detect the fate of the nests (i.e. depredated, number of hatched eggs, number of fledged nestlings), and determine when cavities were available again to other nesting attempt.

Complementary, we conducted a literature review to have nesting information of other cavity-nesting bird species for which we did not find nests in our study area. We considered only published works (e.g. thesis and papers) conducted in either the central valley or Andean location areas of TRSA.

2.3 *Cavity-nest web structure*

We classified each cavity-nesting bird as PCNs or SCNs, to construct a hierarchical cavity-nest web (*sensu* Martin and Eadie, 1999). We quantified the frequency of interactions between different species of trees, PCNs, and SCNs. A cavity-nest web is a quantitative interspecific network in which species that create cavities (trees and PCNs) are linked to species that use these cavities (SCNs; Cockle et al., 2012). Lines in the network represent the couple species interactions. For example, for any species A and B, where A is a cavity consumer and B is a cavity producer (tree or excavator), an interaction occurs when an individual of species A uses a cavity created by species B. In addition, we included the tree decay classes in the cavity-nest web diagram, in order to depict the tree decay stages that were selected for nesting in relation to tree species.

2.4 *Tree-nest selected and resource availability*

When the nesting season was over, we quantified nest-tree characteristics for each nest: species, diameter at breast height (DBH in cm), and decay class of the nest-tree (1: live and healthy tree; 2: live and unhealthy tree, from trees with few signs of boring arthropods and/or fungal decay, until trees with advanced decay signals such as broken top and many dead branches; 3: recently dead tree, from trees with minor dead branches intact until only with major branches and hard wood; 4: dead standing tree, from trees with dead remnants of major branches and with spongy wood, until trees without branches and soft wood; and 5: fallen tree by natural processes, adapted after Thomas et al. 1979). To quantify resource availability, we systematically established 40 vegetation plots in each forest stand (0.04 ha, radius = 11.2 m). For each tree with DBH ≥ 12.5 cm, we recorded: species, DBH, and decay class.

2.5 Data analysis

We considered each nesting attempt as an independent data point, including cases where a single cavity was used more than once in a breeding season and in more than one year, in order to generate a general picture of the nesting niches for each species. We assessed the cavity-nest web dominance and evenness to describe the diversity of interactions between bird species and tree species, and between bird species (e.g. a SCN using a cavity excavated by a PCN). Dominance was calculated as the total number of interactions between the two species that interacted most often, divided by the total number of interactions counted for all species (Cockle et al., 2012; Sabatino et al., 2010). The network evenness was calculated using the PIE index (Probability of Interspecific Encounter) (Hurlbert, 1971):

$$\mathrm{PIE} = \sum_{i=1}^{S} \left(\frac{N_i}{N}\right)\left(\frac{N - N_i}{N - 1}\right)$$

Where S is the total number of links in the network, N is the total number of interactions in the network, and N_i is the interaction frequency of the link i. PIE values close to 0 indicate a particular dominant link (almost all interactions occur between one pair of species), and a PIE value of 1 indicates equal partitioning of interactions frequencies in the network (each pair of species interacts the same number of times as each other pair of species) (Hurlbert, 1971; Sabatino et al., 2010).

All tree characteristics, excluding decay class, are presented as mean ± standard deviation (SD). Decay class is a categorical and rank variable; thus, we present the median and range of its values. Chi-square was employed to examine the significance of the selection of tree characteristics (tree species and decay class) in contrast to their availability. One-way ANOVA was used to compare the tree

DBH of nesting vs. non-nesting trees. All analysis were conducted with JMP® 9 statistical package (SAS software).

3. Results

3.1 Cavity-nest web richness and composition

We found 28 bird species nesting in tree cavities, belonging to six orders and fifteen families. Furnariidae was the most represented family with five species. Cavity-nesting bird species comprised a major component (55%) of the TRSA avian community. Seventeen (61%) were obligate, 5 (18%) facultative, 4 (14%) marginal, and 2 (7%) accidental cavity nesters (Table 1). Twenty four (85.7%) species were secondary cavity nesters and four (14.3%) were primary cavity nesters. From the total species, nine (32%) were endemic to TRSA. One song bird (*Zonotrichia capensis*) was not previously described as cavity nester. We recorded four small-mammals (*Dromiciops gliroides, Oligorizomys longicaudatus, Irenomis tarzalis* and *Rattus rattus*) and three reptiles (*Liolaemus chilensis, Liolaemus tenuis* and *Liolaemus pictus*) using tree cavities.

3.2 Cavity-nest web structure

We found 263 nests belonging to 19 bird species. Nests were located in 172 different trees and 215 different cavities. Ten tree species were used for nesting, including: *Dasyphyllum diacanthoides* (DASDIA), *Eucryphia cordifolia* (EUCCOR), *Gevuina avellana* (GEVAVE), *Lomatia hirsuta* (LOMHIR), *Luma apiculata* (LUMAPI), *Nothofagus dombeyi* (NOTDOM), *Nothofagus obliqua* (NOTOBL), *Nothofagus pumilio* (NOTPUM), *Persea lingue* (PERLIN), and *Saxegothaea conspicua* (SAXCON). From literature review, we added 156 nests into the analysis, and two tree species *Araucaria araucana* (ARAARA) and *Laurelia sempervirens* (LAUSEM) (Fig. 3A).

One hundred seventy two (71%) nests were located in trees belonging to the *Nothofagus* genus. One hundred two (42%) nests were located in *N. dombeyi*, 40 (16%) in *N. obliqua*, 34 (14%) in *G. avellana*, 30 (12%) in *N. pumilio*, and 13 (5%) in *E. Cordifolia* (Fig. 3A). All PCNs produced cavities that were used later by SCNs; however, only three species of SCNs used excavated cavities as their main (>50%) nesting substrate. *Campephilus magellanicus* and *Pygarrychas albogularis* were the main cavity producers. Three nests (60%) of *Strix rufipes* and 31 nests (57%) of *Enicognathus ferrugineus* were located in cavities excavated by *C. Magellanicus*. Twenty one (68%) cavities used by breeding *Tachycineta meyeni* were produced by PCNs. From this, 18 (86%) nests were in cavities created by *P. Albogularis*. From the 71 links and 427 interactions recorded, the most frequent were between *C. magellanicus* and *N. pumilio* (54 interactions), and between *A. Spinicauda* and *N. dombeyi* (39 interactions). The network dominance was low (0.124) and the PIE index indicated a high evenness (0.952).

3.3 Cavity selection: tree decay versus excavation processes

Seventy five percent of cavities used by breeding SCNs were produced by decay processes (e.g. crevices, decay wood, broken branches). The remaining 25% were excavated cavities. Eleven out of a total 18 SCNs (61%) found breeding in study area never nested in excavated cavities. Furthermore, none SCNs nested exclusively in excavated cavities. These results on the origin of cavities used by SCNs are similar to those reported for the Atlantic forests of South America (80% used by SCNs were produced by decay processes; Cockle et al., 2012, 2011a) (Fig. 4). These results contrast with the cavity-nesting community in North America, where only 10% in temperate forests of British Columbia (Aitken and Martin, 2007) and < 1% in longlife pine forests of United States (Blanc and Walters, 2008a), were cavities produced by decay processes (Fig. 4).

3.4 Tree selection and preferences

Nothofagus dombeyi was the main tree species selected to nesting. However, we did not find a preference for its selection (X^2 = 0.46; p = 0.50). The same pattern was found for *E. cordifolia* (X^2 = 0.07; p = 0.79). In contrast, *N. obliqua* was selected disproportionally less in relation to its availability (X^2 = 19.28; p < 0.01). We found a preference for *N. pumilio* (X^2 = 8.65; p < 0.01) and *G. avellana* (X^2 = 7.48; p < 0.01), as they were selected disproportionally more than their availability (Fig. 5A). Seventy nine percent of nests present in *G. avellana* belonged to either *Troglodytes musculus* (16 nests) or *Aphrastura spinicauda* (11 nests).

Mean DBH of nest-trees differed significantly between bird species ($F = 4.40$; $p < 0.001$; Table 2). Birds selected trees ranging from 11.6 to 193.8 cm DBH. *Colaptes pitius*, *P. tarnii*, and *Glaucidium nana* used the largest trees, while *Veniliornis lignarius*, *P. albogularis*, and *T. musculus* used the smallest trees (Table 2). Furthermore, tree DBH differed strongly ($F = 350.80$; $p < 0.01$) between nest-trees (mean ± SD = 57.26 ± 34.88 cm) and available trees (mean ± SD = 26.11 ± 19.99 cm). We found that DBH for all trees selected for nesting were larger than those available in the site: *N. dombeyi* (mean DBH = 79.4 vs. 29.4 cm; $F = 325.49$; $p < 0.01$), *N. obliqua* (mean DBH = 39.9 vs. 25.9 cm; $F = 29.38$; $p < 0.001$), *G. avellana* (mean DBH = 21.4 vs. 14.8 cm; $F = 75.56$; $p < 0.001$), *N. pumilio* (mean DBH = 60.2 vs. 46.5 cm; $F = 9.33$; $p < 0.01$), and *E. cordifolia* (mean DBH = 42.8 vs. 21.5 cm; $F = 34.73$; $p < 0.001$) (Fig. 5B).

Both standing and fallen dead trees were the most common nest substrate (58%; Fig. 5C), and were strongly preferred over living trees ($X^2 = 327.97$; $p < 0.0001$). Live and healthy trees were barely used for nesting (only 1 out of 263 nests), despite being the most abundant tree decay class in the area ($X^2 = 204.70$; $p < 0.0001$). Live and unhealthy trees were highly selected by cavity-nesting birds, but in similar proportion to their availability ($X^2 = 0.71$; $p = 0.40$). Recently dead trees also showed a proportional selection in relation to their availability ($X^2 = 0.45$; $p = 0.50$). Birds showed a strong preference for the two most advanced stages of tree decay: long dead trees ($X^2 = 539.47$; $p < 0.0001$) and fallen trees ($X^2 = 33.82$; $p < 0.0001$) (Fig. 5C and see Fig. 3B for specific details). For example, *Scelorchylus* *rubecula* and *Scytalopus magellanicus* nested in cavities available almost entirely in fallen trees (91%). On the other hand, *Pteroptochos tarnii* nested in cavities available mostly in large living unhealthy trees (86%). However, most birds breeding in living trees used a dead section of the main trunk or dead branch as nest substrate.

4. Discussion

4.1 Cavity-nest web in the southern temperate rainforest

We provide the first community level study of cavity-nesting birds in the temperate rainforest of South America, and the second cavity-nest web research in the southern hemisphere (after Cockle et al., 2012). The forest bird community shows one of the highest association with tree cavities (55%), compared to other cavity-nesting communities as those of the Pacific northwest (25-30%, Bunnell et al., 1999), southeastern Oregon (50%, Dobkin et al., 1995), northeaster Colorado (32-43%, Sedgwick and Knopf, 1986), central Venezuela (15%, Gibbs et al., 1993), and central Costa Rica and northern Belize (both with 33%, Gibbs et al., 1993). Cavity-nest web in southern temperate rainforests shows a B scenario (Fig. 1), with higher number of species in both extremes of the pyramid (trees and SCNs). Contrary to what was reported by Gibbs et al. (1993) for temperate forests in the northern hemisphere, we found half of the number of PCNs in the TRSA at the same latitude (39° LS; 29% vs. 14% of the cavity-nesting bird community for the northern and the southern hemispheres, respectively).

Our findings are similar to cavity-nest web structures found in Atlantic forests (Cockle et al., 2012). However, in the TRSA the network depends in 71% of three tree species from the same genus (*Nothofagus spp*), and birds nest directly in a total of 12 tree species, a relatively few number of tree species used for nesting in comparison to the 27 tree species and one palm recorded for Atlantic forest (Cockle et al., 2012). This result suggests a potentially stronger effect of intensive forest management schemes on the cavity-nesting bird community, and lower resilience to breeding habitat disturbance in TRSA. Moreover, despite the lower species richness in our cavity-nesting community, there was comparable functional diversity to other cavity nesting community studies with two to three times more species (e.g. Cockle et al., 2011; Gibbons and Lindenmayer, 2002). For example, we found two small body size excavators (*P. albogularis* and *V. lignarius*), one middle body size excavator (*C. pitius*) and one large body size excavator (*C. magellanicus*). This condition makes our cavity-nest web a good representative network but very vulnerable for the three SCNs that nest most often in excavated cavities, if one of these species lack, all of a cavity size spectrum would be lost. In contrast to North American forests (Blanc and Walters, 2008b; Martin et al., 2004), our findings suggest a relatively high level of functional evenness between trees, SCNs, and PCNs, where the wide distribution of links generates a lower dominance index (0.124 in the TRSA versus 0.24 for northern temperate forests, and 0.43 for longlife pine forests; cited in Cockle et al., 2012). However, the cavity-nest web in TRSA also differed from the one in Atlantic forests (0.028; Cockle et al., 2012), having 4.5 times higher dominance index, likely related to a high network dependence on only three tree species (i.e. *Nothofagus spp*).

4.2 Cavities produced by tree decay: key driver structuring the network

Similar to another cavity-nesting community in Northern Argentina (Cockle et al., 2012), we found that tree decay and physical damage processes were much more important for tree cavity formation compared to excavators in the temperate rainforests of South America. The great majority of SCNs most often used cavities formed by tree decay processes. For example, 78% of nest from *A. spinicauda* were built in crevices or fissure cavities, agreeing with the results reported for this species in Chiloé island (Cornelius, 2008). Our findings contrast strongly with cavity selection in North America (Aitken and Martin, 2004; Blanc and Walters, 2008a; Martin et al., 2004), where excavators play a key role as cavity facilitators for a large number of SCNs. Excavated cavities can be produced at higher rates (Cockle et al., 2011a), and have higher persistence in northern temperate forests (Edworthy et al., 2012). In contrast, cavities created by tree decay are formed over long-term processes that eventually produce a high quality cavity for cavity-nesting birds (A. J. Koch et al., 2008; Lindenmayer et al., 1993). For example, in Australia, more than 100 years are necessary to form a non-excavated cavity, and even more than 200 years for large cavities (entrance diameter > 10 cm and minimum depth of 15 cm) (Gibbons et al., 2002; A. J. Koch et al., 2008). Therefore, forest harvest activities reducing the number of large old decaying trees can be very detrimental for cavity-nesting communities (Drever and Martin, 2010; Politi et al., 2010), as they directly decrease the availability of tree cavities and their persistence (Edworthy and Martin, 2013).

4.3 Nest-tree characteristics and preferences

We found a strong selection for trees belonging to the *Nothofagus* genus. This could be due to the ecology of these tree species, forest dynamics in Andean locations (gaps dynamic), and the high dominance of this genus in TRSA (Veblen and Alaback, 1996). *Nothofagus* species are shadow-intolerant and pioneer trees, which are favored by periodical disturbances such as volvanic eruptions, gap releases, and landslides, in Andean TRSA (Donoso, 1993). The strong selection for *Nothofagus* species matches the few studies at the cavity-nesting species level in other locations of TRSA. These studies, have reported similar occurrences of nests on *Nothofagus* species at coastal locations for *A. spinicauda* (Cornelius, 2008) and *Enicognathus leptothynchus* (Peña-Foxon et al., 2011), in the central valley for *Anas flavirostris* (Jiménez and White, 2011) and *E. Leptothynchus* (Carneiro et al., 2013), and in Andean locations for *G. nana* (Ibarra et al., 2014), *Enicognathus ferrugineus* (Díaz and Kitzberger, 2013), *C. magellanicus* (Ojeda et al., 2007), and *Strix rufipes* (Beaudoin and Ojeda, 2011). Thus, our results at the community level confirm patterns observed by single species studies, suggesting that *Nothofagus* species play a key role (along all latitudinal and altitudinal distribution of TRSA) in the community ecology of cavity-nesting birds. This result has implications for forest management, because this tree genus has been the most impacted by human activities (Bustamante and Castor, 1998) and forest harvest (selective logging; Veblen and Alaback, 1996) across its distribution.

Our findings support the idea that large trees are exceptionally important forest structures for cavity-nesting birds (Cockle et al., 2011b; Díaz et al., 2005; Gibbons et al., 2002; Robles and Ciudad, 2012; Schlatter and Vergara, 2005), and they can determine whether bird species breed or not in some areas (Politi et al., 2009). Cavity-nesting species showed a strong preference for larger tree DBH in all tree species selected for nesting. As our system is highly dependent of non-excavated cavities, similar to forest bird community in New Zealand, tree DBH would strongly explain the increase in number of cavities per tree and cavity volume in these forests (Blakely et al., 2008). On the other hand, our findings highlight the importance of dead standing and fallen trees. Contrasting with northern temperate forest (Canada; Martin et al., 2004), where 55% of the cavity-nesting birds nest in living trees, and similar to longlife pine forest (USA; Blanc and Walters, 2008), where 73% of cavity-nesting bird community nest in dead standing trees. TRSA contain a high density of dead standing trees (Carmona et al., 2002; Díaz et al., 2005), even more than reported for temperate forests of North America (Gibbs et al., 1993), probably explaining the high selection and preference for advanced stages of decays by cavity-nesting birds.

In a specific decay class analysis, similar to Atlantic forests, birds in TRSA show high selection of live unhealthy trees (Cockle et al., 2012), commonly using a dead section of these trees or dead branches suppressed under the highest canopy of the forest. Cavity-nesting birds breed widely in trees at advanced stage of decay, despite that these kinds of trees are in very low density in the area. Trees in advanced stage of decay are more unstable and more likely to fall down than less decayed trees (Martin et al., 2004). Therefore, when a forest only has live trees and trees in advanced stages of decay, this can be an ecological trap for cavity-nesting birds. Birds could concentrate their focus strongly in these advanced decay trees for nesting, and the complete -or a section of- these trees can collapse and/or fall down to the ground. Thus, it is very important for the forest management not only to consider the presence of dead standing trees, but also to ensure the presence of all stages of tree decay (Cockle et al., 2011a), maintaining a continuous from “less cavity trees” (future resource available) to “many cavity trees” (current resource available). Finally, flightless birds (as Rhinocryptids: *S. rubecula* and *S. magellanicus*) depend almost exclusively of cavities in fallen trees for nesting, which adds another factor of specialization for this group of birds (bamboo specialist; Reid et al., 2004).

4.4 Implications for forest bird conservation

Understanding the critical processes determining community structure can be extremely difficult (Martin et al., 2004). Construct cavity-nest webs can be very useful to understand that, and to give us tools to predict the effects of disturbs on this communities (Blanc and Walters, 2007; Cockle et al., 2012). Our findings underscore the importance of key forest structures (e.g. the presence of larger tree DBH and advanced tree decay) for the cavity-nesting bird community maintenance and conservation in the TRSA. Fifty five percent of the birds inhabiting this forest, nine of which are endemic, strongly depend on large tree DBH and dead trees. However, the majority of forest policies in the world specify a diameter limit of trees to be harvested (Cockle et al., 2011a), many times protecting younger trees and discouraging the presence of larger trees and dead trees. In the TRSA, national forestry policy only superficially mentions tree DBH and does not mention anything about dead trees (standing and fallen) (Law number 20 283; CONAF, 2014). We tightly suggest incorporating these findings in both native forest and plantation management (in governments as in private enterprises and certification agencies), establishing limits to logging old living trees, dead standing trees, and removing fallen trees. This would ensure a good density of each decay classes, as dead trees with many obvious cavities commonly indicate past rather than present or future resource availability (Aitken and Martin, 2004). Thus, conserving a sufficient and long-term supply of key resource for cavity-nesting bird communities in timber production areas.

Finally, as the majority of birds inhabit and breed the TRSA across wide elevational gradients (Vuilleumier, 1985), it would be important assess the cavity-nest web differentially within this gradient and forest composition and structure. On the other hand, including forest management pressures in cavity-nest web studies, describing harvest selection trees in terms of species, tree DBH, and decay class, could give us an accurate picture of the effects of human beings on cavity nesters, quantifying the magnitude and directionality of these effects.

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Figures captions

Figure 1. Hypothetical cavity-nest web structure, modified from Martin and Eadie (1999). The guilds include birds as: Secondary Cavity Nesters (SCN), Non-cavity Nesters (Non Cav) and Primary Cavity Nesters (PCN). Forest management is including because affect directly the base of the pyramid, and the resilience of the system will depend of the composition and structure of the network. The likely scenarios of cavity-nest web structures considering how many tree species and cavity-nesting birds (pyramid of numbers) interact in the web: (A) a typical structure of a terrestrial food web; (B) a lower species diversity at middle level, observed in Atlantic forests of Argentina (Cockle et al., 2012); (C) a higher species diversity in middle levels, observed in Florida State of USA (Blanc and Walters, 2008a); (D) an inverse pyramid structure, observed in northern temperate forests of Canada (Martin et al., 2004).

Figure 2. Twenty forest stands where cavity-nesting community was monitored. Pucón, Araucanía district, Chile.

Figure 3. Cavity-nest web structure in southern temperate rainforests. The diagram is divided in two parts: A) above the tree species level, showing the links between the cavity or tree with the specific cavity-nesting birds, and B) under the tree species level, showing the links between tree species and tree decays. The intensity of the relationship is indicated by three types of lines: thick lines (more

than 50% of the nests), thin lines (between 10% and 49% of the nests), and dashed lines (less than 10% of the nests). Sample size includes nests from literature review plus our total recorded nests. See Table 1 for bird species codes and see text for tree species codes.

Figure 4. Origin of nesting cavities (percentage) in different forest types across America. Black bars show decay formed cavities selected to nesting, and gray bars show excavated cavities selected to nesting by secondary cavity nesters.

Figure 5. Nest-tree characteristics selected by secondary cavity nesters in relation to their availability in the southern temperate rainforest of Chile. (A) Species, (B) diameter at breast height (DBH), and (C) decay class. Error bars indicate standard error. See text for tree species codes.

Tables

Table 1. Species, code, endemism, and dependence of forests and cavities by members of the cavity-nesting bird community in southern temperate rainforests.

Species		Species code	Endemic to TRSA[Δ]	Dependence of	
Scientific name	**Common english name**			**Forest[†]**	**Cavity[‡]**
Primary Cavity Nesters					
Veniliornis lignarius	Striped Woodpecker	VENLIG	Endemic	F	O
Colaptes pitus	Chilean Flicker	COLPIT	--	F	O
Campephilus magellanicus	Magellanic Woodpecker	CAMMAG	--	S	O
Pygarrhychas albogularis	White-throated Treerunner	PYGALB	Endemic	S	O
Secondary Cavity Nesters					
*Chloephaga poliocephala**	Ashy-headed goose	CHLPOL	--	F	M
*Anas flavirostris**	Speckled teal	ANAFLA	--	F	M
Milvago chimango	Chimango caracara	MILCHI	--	F	F
*Falco sparverius**	American kestrel	FALSPA	--	F	O
*Enicognathus ferrugineus**	Austral Parakeet	ENIFER	Endemic	S	O
*Enicognathus leptorhynchus**	Slender-billed Parakeet	ENILEP	Endemic	S	O
*Tyto alba**	Barn Owl	TYTALB	--	F	O
*Bubo magellanicus**	Magellanic Horned-Owl	BUBMAG	--	F	F
*Strix rufipes**	Rufous-legged Owl	STRRUF	Endemic	S	O
Glaucidium nana	Austral Pygmy-Owl	GLANAN	--	F	O
Cinclodes fuscus	Bar-winged Cinclodes	CINFUS	--	F	F
Cinclodes patagonicus	Dark-bellied Cinclodes	CINPAT	--	F	F
Aphrastura spinicauda	Thorn-tailed Rayadito	APHSPI	Endemic	S	O
Leptasthenura aegithaloides	Plain-mantled Tit-Spinetail	LEPAEG	--	M	O
Pteroptochos tarnii	Black-throated Huet-huet	PTETAR	Endemic	S	O
Scelorchilus rubecula	Chucao Tapaculo	SCERUB	Endemic	S	F
Scytalopus magellanicus	Magellanic Tapaculo	SCYMAG	--	F	O
*Elaenia albiceps**	White-crested Elaenia	ELAALB	--	S	A
Tachycineta meyenii	Chilean Swallow	TACMEY	--	F	O
Pygochelidon cyanoleuca	Blue-and-white Swallow	PYGCYA	--	F	O
Troglodytes musculus	Southern House Wren	TROMUS	--	M	O
Turdus falcklandii	Austral Thrush	TURFAL	--	F	M
Zonotrichia capensis	Rufous-collared Sparrow	ZONCAP	--	M	A
Phrygilus patagonicus	Patagonian sierra-finch	PHRPAT	Endemic	F	M

* Species classified as cavity-nester by literature review (Beaudoin and Ojeda, 2011; Carneiro et al., 2013; Jiménez and White, 2011; Ojeda and Trejo, 2002; Peña-Foxon et al., 2011).

[Δ] Rozzi et al. (1996); Vuilleumier (1985).

[†] S = Depends strictly on forests for nesting; F = Habitat-generalist that may forage and/or nest within the forests; M = Generally open habitat species, but may forage and/or nest in forest edges (adapted from Trejo et al., 2006).

[‡] O = Depends strictly on cavities for nesting (> 90% nests in cavities); F = Generalist of nesting substrate that may nest in cavities (between 10% and 90% of nests in cavities); M = Chiefly open nesters, but may nest in cavities (between 1% and 10% nests in cavities); A = Open nester, but accidentally may use cavities for nesting (< 1% nests in cavities) (T.A. Altamirano and J.T. Ibarra unpubl. data).

Table 2. Nest-tree characteristics for cavity-nesting birds in southern temperate rainforests. DBH = diameter at breast height; *n* is the number of occupied nests. Decay classes follow Thomas et al. (1979), where 1 represents live and healthy trees, 2 live and unhealthy trees, 3 recently dead trees, 4 long-dead trees, and 5 fallen trees.

Species	*Nothofagus dombeyi*			*Nothofagus obliqua*			*Gevuina avellana*			*Nothofagus pumilio*			*Eucryphia cordifolia*			All tree species		
	DBH	Decay class		DBH	Decay class		DBH	Decay class		DBH	Decay class		DBH	Decay class		DBH	Decay class	
	Mean ± SD	Median (range)	n	Mean ± SD	Median (range)	n	Mean ± SD	Median (range)	n	Mean ± SD	Median (range)	n	Mean ± SD	Median (range)	n	Mean ± SD	Median (range)	n
Primary Cavity Nesters																		
Veniliornis lignarius											2 (2)	1				26.9	3 (2-4)	2
Colaptes pitus	181.1	2 (2)	1													181.1	2 (2)	1
Campephilus magellanicus		2 (2)	1														2 (2)	1
Pygarrhychas albogularis	102.4	2 (2)	1	29.6 ± 14.6	4 (1-4)	10				51.4 ± 30.5	3 (2-4)	2	16.1 ± 1.2	4 (4)	3	35.9 ± 27.5	4 (1-4)	20
Secondary Cavity Nesters																		
Milvago chimango					4 (4)	1											4 (4)	1
Glaucidium nana	113.2	3 (3)	2	83.3	2 (2)	1										103.2 ± 17.5	3 (2-3)	3
Cinclodes fuscus										63.6 ± 7.9	2 (2)	2				63.6 ± 7.9	2 (2)	3
Aphrastura spinicauda	75.5 ± 25.9	4 (2-5)	49	35.1 ± 10.8	4 (2-4)	16	18.0 ± 4.4	2 (2-4)	11	60.9 ± 23.2	2 (2-4)	9	65.0 ± 43.4	2 (2-4)	5	58.5 ± 31.4	4 (2-5)	102
Leptasthenura aegithaloides	69.4 ± 2.7	4 (4)	2				23.5	2 (2)	1							54.1 ± 26.6	4 (2-4)	3
Pteroptochos tarnii	193.8	3 (2-4)	2							81.8 ± 38.5	2 (2)	2				104.4 ± 47.2	2 (2-4)	8
Scelorchilus rubecula	72.0 ± 34.7	5 (4-5)	6													72.0 ± 34.7	5 (4-5)	7
Scytalopus magellanicus	61.3 ± 51.1	5 (5)	4							63.9	5 (5)	1				62.0 ± 41.8	5 (5)	6
Tachycineta meyenii	106.1 ± 32.9	3 (2-4)	13	29.7 ± 13.6	4 (2-4)	6	26.2	2 (2)	1	60.6 ± 19.5	2 (2-3)	5	43.9 ± 45.7	4 (2-4)	3	71.9 ± 42.9	3 (2-4)	31
Pygochelidon cyanoleuca	126.4	5 (5)	1													126.4	5 (5)	3
Troglodytes musculus	60.5 ± 17.9	4 (2-4)	16	60.1 ± 23.3	2 (2-4)	5	22.7 ± 7.6	2 (2-3)	16	49.4 ± 17.6	2 (2-4)	5	25.8 ± 0.0	4 (4)	2	41.9 ± 21.9	2 (2-5)	54
Turdus falcklandii	42.4	4 (4)	1							69.3	3 (3)	1				55.9 ± 19.0	3.5 (3-4)	2
Zonotrichia capensis	75.3	2 (2)	1													75.3	2 (2)	1
Phrygilus patagonicus		3 (3)	1							61.3	3 (3)	1				61.3	3 (3)	3

Figures

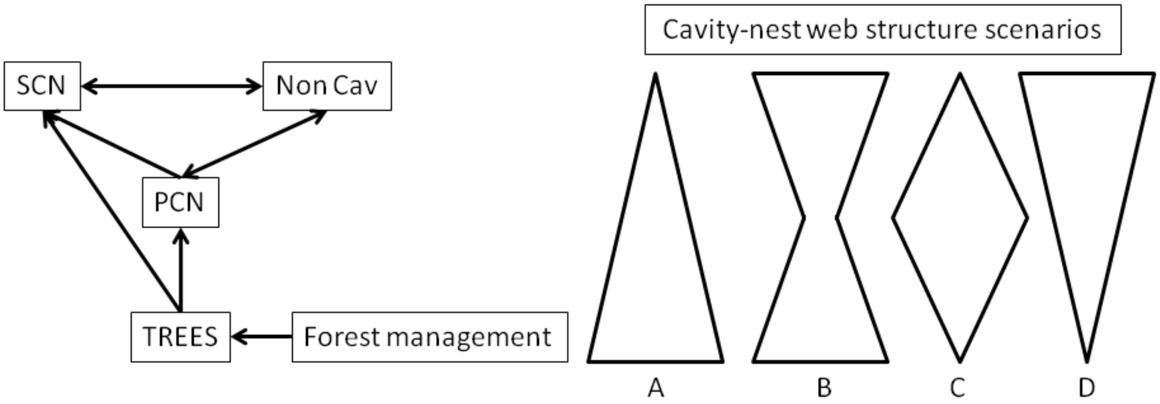
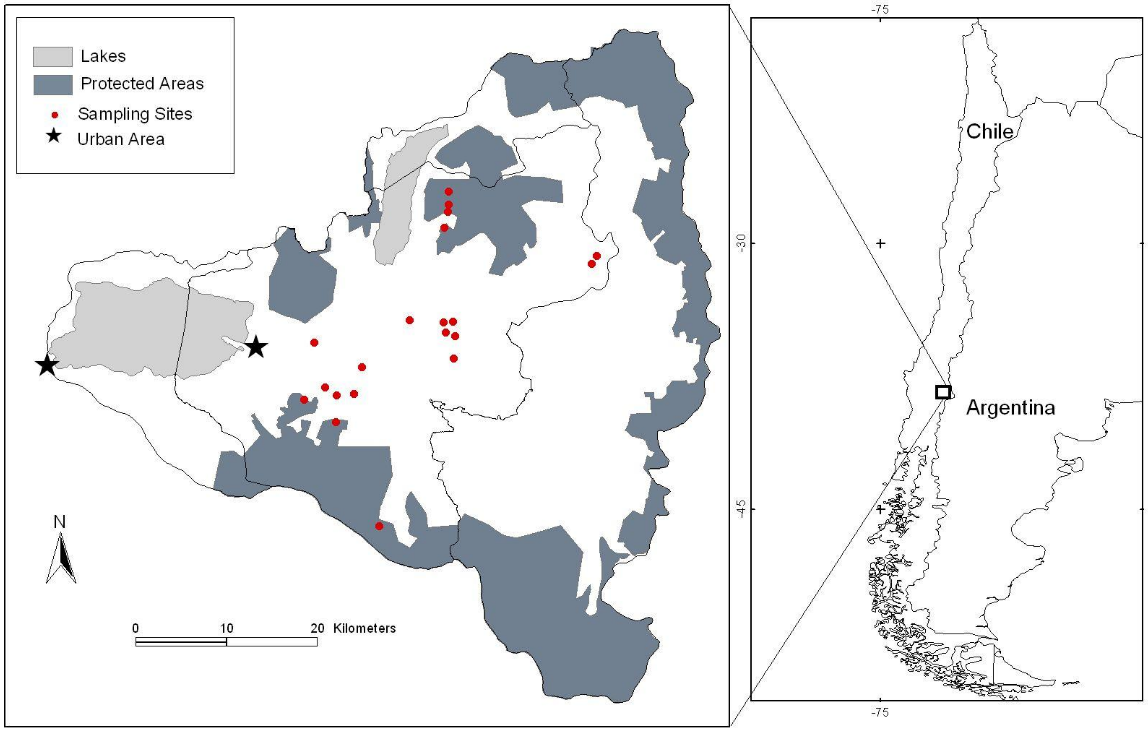


Figure 1


Lakes
Protected Areas
Sampling Sites
Urban Area
N
0
10
20 Kilometers
-75
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Chile
Argentina
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-30
-45

Figure 2

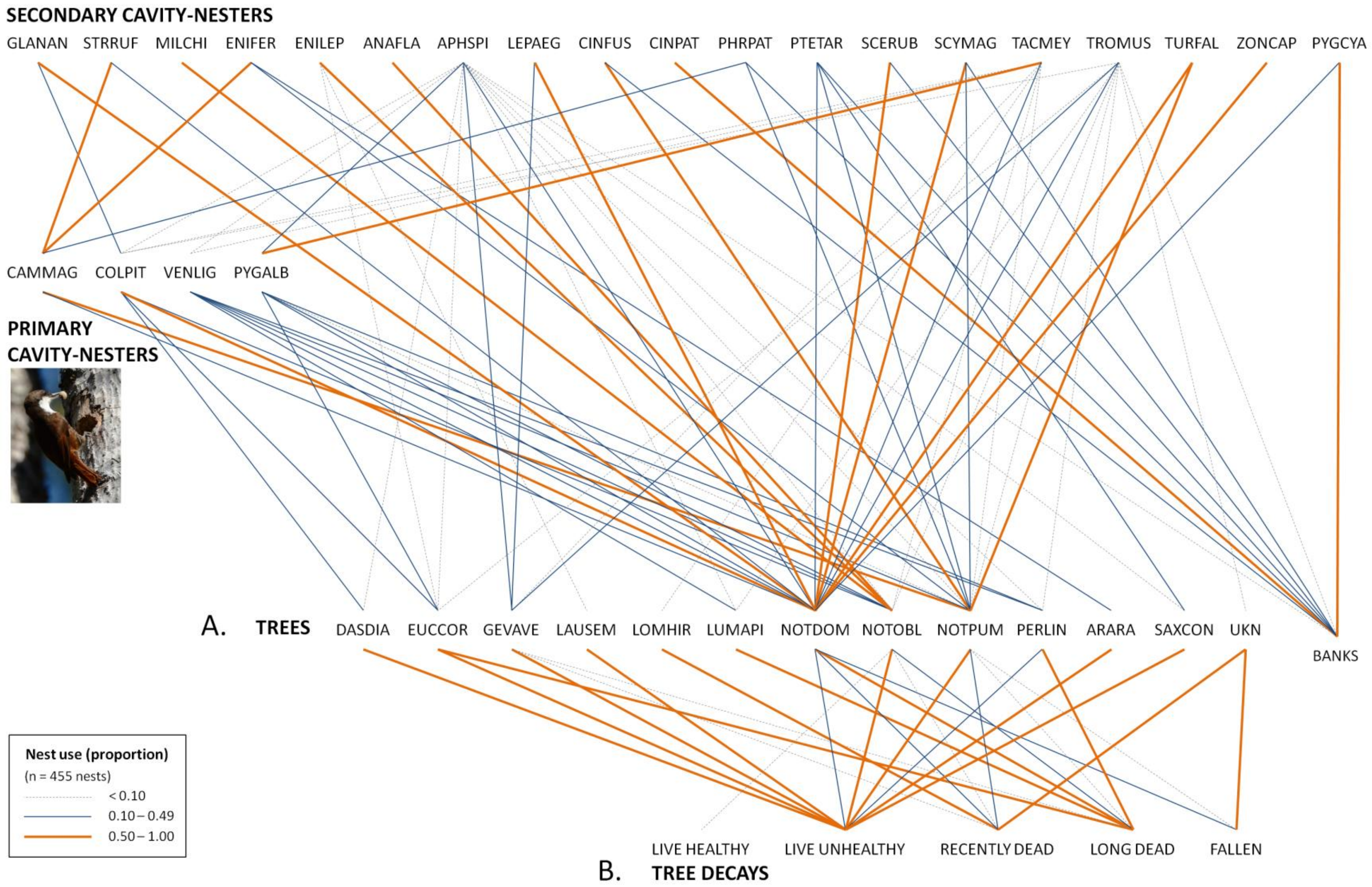
SECONDARY CAVITY-NESTERS
GLANAN
STRRUF
MILCHI
ENIFER
ENILEP
ANAFLA
APHSPI
LEPAEG
CINFUS
CINPAT
PHRPAT
PTETAR
SCERUB
SCYMAG
TACMEY
TROMUS
TURFAL
ZONCAP
PYGCYA
CAMMAG
COLPIT
VENLIG
PYGALB
PRIMARY CAVITY-NESTERS
A.
TREES
DASDIA
EUCCOR
GEVAVE
LAUSEM
LOMHIR
LUMAPI
NOTDOM
NOTOBL
NOTPUM
PERLIN
ARARA
SAXCON
UKN
BANKS
Nest use (proportion)
(n = 455 nests)
< 0.10
0.10 – 0.49
0.50 – 1.00
LIVE HEALTHY
LIVE UNHEALTHY
RECENTLY DEAD
LONG DEAD
FALLEN
B.
TREE DECAYS

Figure 3

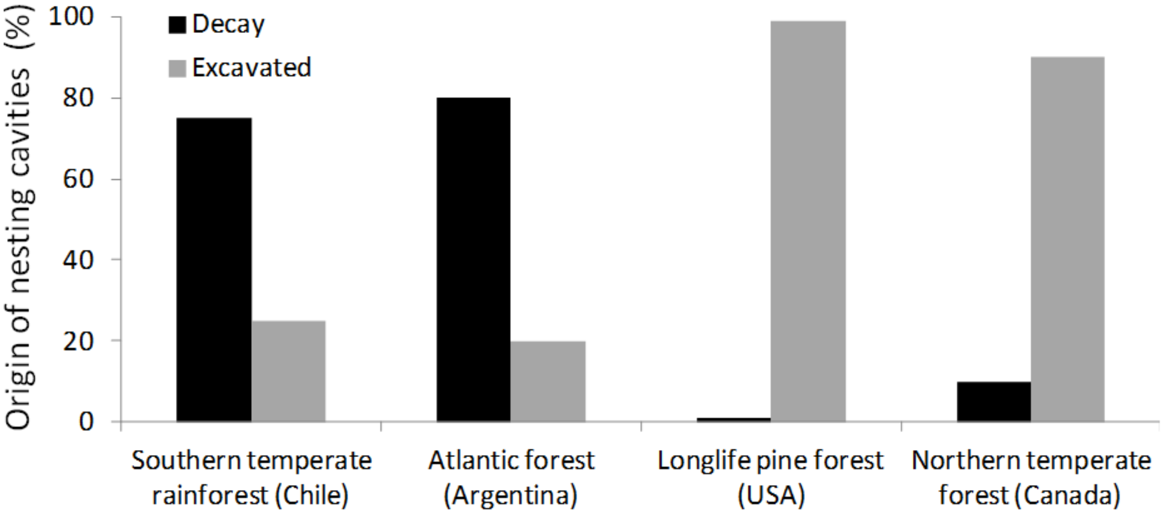
Origin of nesting cavities (%)
100
80
60
40
20
0
■ Decay
▨ Excavated
Southern temperate rainforest (Chile)
Atlantic forest (Argentina)
Longlife pine forest (USA)
Northern temperate forest (Canada)

Figure 4

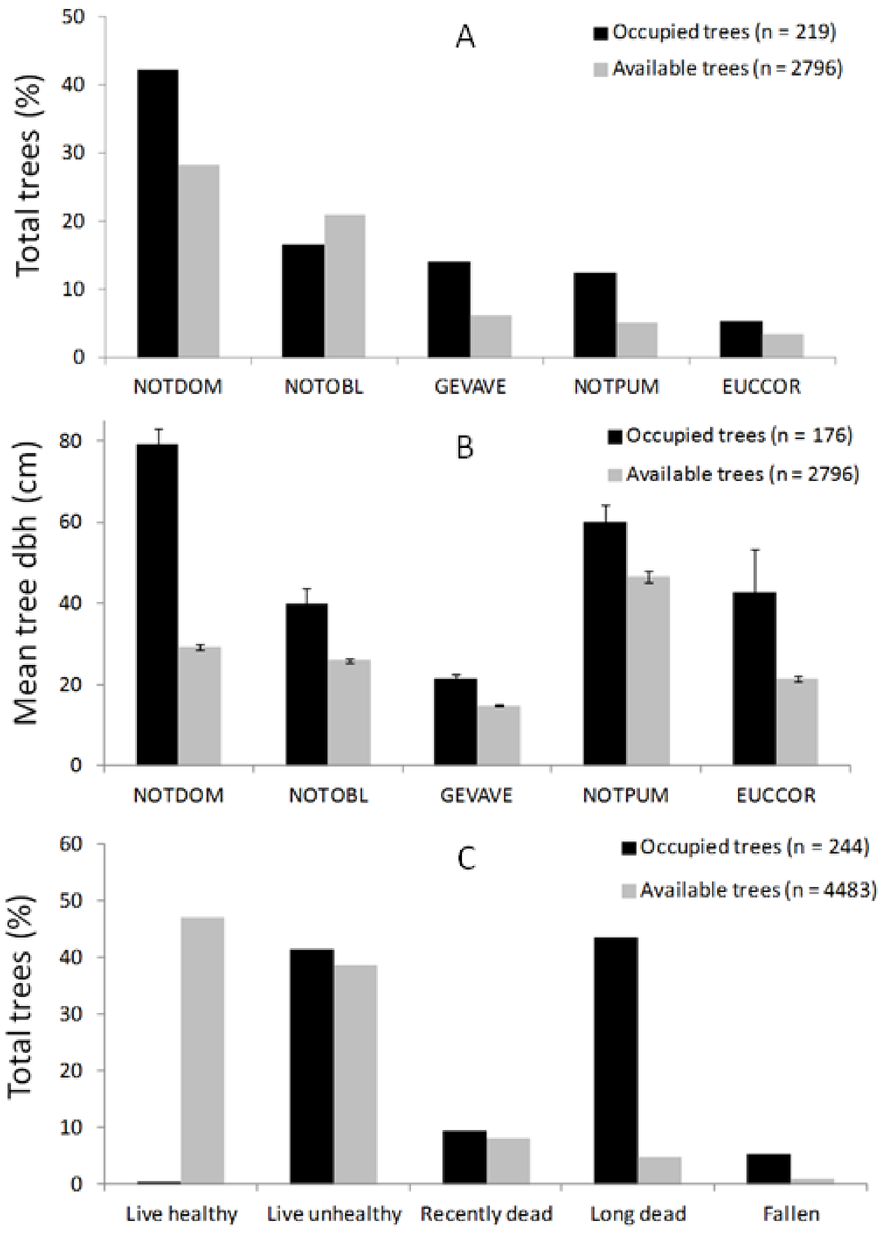
A
■ Occupied trees (n = 219)
▨ Available trees (n = 2796)
Total trees (%)
0
10
20
30
40
50
NOTDOM
NOTOBL
GEVAVE
NOTPUM
EUCCOR
B
■ Occupied trees (n = 176)
▨ Available trees (n = 2796)
Mean tree dbh (cm)
0
20
40
60
80
NOTDOM
NOTOBL
GEVAVE
NOTPUM
EUCCOR
C
■ Occupied trees (n = 244)
▨ Available trees (n = 4483)
Total trees (%)
0
10
20
30
40
50
60
Live healthy
Live unhealthy
Recently dead
Long dead
Fallen

Figure 5

General discussion

We conclude that thorn-tailed rayaditos (*Aphrastura spinicauda*) may have an adaptive response to shorter breeding seasons at higher elevations: they have smaller clutches sizes, lower number of broods, and invest more time taking care of nestlings (Badyaev and Ghalambor, 2001). However, these potential adaptations do not seem to compensate for the increased predation rates at higher elevations; this brings to question the adaptive significance of this strategy, and suggests that individuals at these higher elevations could make only a marginal contribution to overall population abundance. Reproductive life-history traits of rayaditos in Andean locations were different to those of coastal locations, resulting in a higher number of offspring per nest. Our results highlight the importance of studying the ecology of birds in southern Andean locations, and examining the effects of elevational gradients on bird communities in temperate forests of South America (TRSA).

On the other hand, we provide evidence of a consistent and strong population limitation on thorn-tailed rayaditos inhabiting in secondary and managed forests (Brawn and Balda, 1988; Cornelius *et al*., 2008; Tomasevic and Estades, 2006), but not in old growth forests. Chilean swallows (*Tachycineta meyeni*) and southern house wrens (*Troglodytes musculus*) did not show any significant response in either type of forest. Our findings suggest that the spatial differences associated to forest age in the responses to experimental cavities manipulation, are likely to be driven by specific forest structures (i.e. tree DBH and basal area) present in both kinds of forests.

This is the first study about cavity-nest web in the temperate rainforest of South America. The forest bird community shows one of the highest dependence on tree cavities (55%), compared to other cavity-nesting communities as those of the Pacific northwest (25-30%, Bunnell *et al*., 1999), southeastern Oregon (50%, Dobkin *et al*., 1995), northeaster Colorado (32-43%, Sedgwick and Knopf, 1986), central Venezuela (15%, Gibbs *et al.*, 1993), and central Costa Rica and northern Belize (both with 33%, Gibbs *et al.*, 1993). Our findings are similar to cavity-nest web structures found in Atlantic forests (Cockle *et al.*, 2012). However, in the TRSA the cavity-nest web depends in 71% of three tree species (*Nothofagus spp*), and birds interact directly with a total of 12 tree species, opposite to the 27 tree species and one palm found in Atlantic forest. This result suggests a higher effect of forest management on the cavity-nesting bird community. We found that tree decay and physical damage processes were much more important for tree cavity formation compared to excavated processes. Regarding to nest-tree selection, our findings support the idea that tree DBH is a very important forest structure for cavity-nesting birds (Cockle *et al.*, 2011b; Díaz *et al.*, 2005; Gibbons *et al.*, 2002; Robles and Ciudad, 2012; Schlatter and Vergara, 2005), and it can determine whether bird species breeding or not in some areas (Politi *et al.*, 2009). Cavity-nesting species showed a strong preference for larger tree DBH and advanced stages of decay (standing and fallen trees), despite that these kinds of trees were in very low density in the area.

Forest management implications

Understanding the ecology of cavity-nesting birds may influence biodiversity conservation strategies. Our findings highlight the importance of maintaining forest attributes that supply suitable cavities to SCNs in managed areas. Thus, maintaining large and dead trees in managed forests could improve habitat conditions for cavity-nesting birds, and be a real contribution from silviculture to the conservation of forest specialist birds inhabiting managed areas.

Cavity-nest webs can give us tools to predict the effects of disturbs on this communities (Blanc and Walters, 2007; Cockle *et al.*, 2012). Our findings underscore the importance of key forest structures (e.g. the presence of larger tree DBH and advanced tree decay) for the cavity-nesting bird community conservation in the TRSA. On the other hand, including forest management pressures in future cavity-nest web studies, describing harvest selection trees in terms of species, DBH, and decay class, could help us to generate an accurate picture of the effects of human beings on cavity nesters, quantifying the magnitude and directionality of these effects.

In summary, fifty five percent of the birds inhabiting this forest, nine of which are endemic, strongly depend on large tree DBH and dead trees. However, most of forest policies specify a tree diameter limit to be harvested, many times protected younger trees more than large and old trees (Cockle *et al.*, 2011a). National forestry policy of Chile only superficially mentions tree diameter in the authorization for tree logging, and does not mention anything about dead trees (standing and fallen) (Law number 20,283; CONAF, 2014). We strongly suggest limiting the maximum diameter of trees for harvest 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 size trees (future resource availability; Aitken and Martin 2004), and of each tree decay classes, would be very useful to allow breeding of cavity-nesting birds in managed forests. Thus, maintain a sufficient and long-term supply of key resource for cavity-nesting bird communities in timber production areas.

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Appendices

Appendix 1. Forest structure effects on nest-box occupation rates and nesting success by thorn-tailed rayaditos in Andean temperate forests of Chile.

Vegetation survey. In order to quantify micro-site forest structure around nest-boxes (which could influence a bird's preference to nest, as well as nesting success), we established 240 vegetation plots with center in each nest-box, and 0.04 ha (radius = 11.2 m) surface area. After the nesting season, we quantified site characteristics within these plots: successional stage (early 4-20, mid 35-80, late >100 years old), slope, signs of recent human impact (presence or absence of tree cut, livestock or fire), canopy cover, understory cover, coarse woody debris volume, tree density, tree diameter at breast height (DBH), tree decays (decay class: 1: live, healthy tree; 2a: live tree with few signs of boring arthropods and/or fungal decay; 2b: live tree with advances decay signals and with broken top, 21-80% of dead branches; 2c: nearly dead tree with broken top and advanced levels of decay, with less than 20% of living branches; 3: recently dead trees with major and minor branches intact; 4: standing dead tree with major branches and hard wood; 5: standing dead tree with remnants of major branches and spongy wood; 6: standing dead tree without branches and soft wood; and 7: fall down tree by natural processes, adapted after Thomas *et al*., 1979), vine and epiphytes cover per tree (categorical variable; 0: no cover, 1: 1-25%, 2: 26-50%, 3: 51-75%, and 4: 76-100%), and number of small and large cavity per tree (separated by origin, created by decay or excavation processes). All tree variables were recorded only for trees with DBH ≥ 12.5 cm.

Data analysis. We assessed habitat effects on nest-box occupation rates by conducting Generalized Linear Models, with an ordinal multinomial distribution and *logit link function*, suitable for logistic regression (Quinn and Keough, 2002). The dependent multinomial variable is 0 if the nest-box was not used any breeding season, 1 if it was used only one year, 2 for two years-used and 3 if a nest-box was used every breeding season (2010-2011, 2011-2012, and 2012-2013). To analyse whether forest structure had effects on nesting success, we used Generalized Linear Models (Multiple Logistic Regression), considering nesting success as an ordinal multinomial variable (values between 0 successful and 2 unsuccessful). Before these analyses, to reduce the number of explanatory variables and prevent excessive colinearity, we examined correlations among all variables using Pearson linear correlations and visually examining bivariate plots. When variables were strongly correlated, we eliminated one and retained the one that could most easily be interpreted.

Results. In low land forests, understory density was negatively associated with nest-box occupation rates (chi-square = 12.41; $p < 0.01$), whereas coarse woody debris volume shows the opposite effects (chi-square = 5.46; $p = 0.02$). In high land forests, we found that thorn-tailed rayaditos occupied nest-boxes with higher canopy cover (chi-square = 8.26; $p < 0.01$) and tree decay (chi-square = 10.23; $p < 0.01$) (Table 1). Generalized linear models indicated that nesting success was negatively associated with both tree decay (chi-square = 6.49; p = 0.01), and epiphyte and vine cover (chi-square = 4.55; p = 0.03) at low land forests. Whereas at high land forests, nesting success was negatively associated with high canopy cover (chi-square = 5.55; p = 0.02), and tree DBH (chi-square = 17.34; p < 0.01), and positively associated with tree decay (chi-square = 7.01; p < 0.01) (Table 2).

Discussion. Tree decay, and epiphyte and vine cover were the structural components of forests that showed negative association with nesting success at low land elevations. We suggest that forest stands with a higher number of old-growth trees or snags, may have a greater number of predators, mainly Austral Opossums, who is also a cavity-nesting species and select snags for roosting, hibernation and nesting (Celis-Diez *et al.*, 2012). Our results go in the same direction than those of Cornelius (2008), who found higher survival rates of Rayaditos' nests in trees with lower epiphyte cover. Cornelius (2008) suggested that predators can climb up easier in trees with higher epiphyte cover, and also adults have a worse view of predators near to nest (Li and Martin, 1991). At high elevations, our models indicated that Rayaditos' nests were more successful when the nest-site had lower canopy cover, lower tree DBH, and higher tree decay. Similar results for almost all cavity-nesting birds in Arizona (approximately at 2,300 m a.s.l.) were reported by Li and Martin (1991). They found a higher quantity of unsuccessful nests in sites with higher density of large conifers and higher foliage cover. Li and Martin (1991) speculated that the main predators (Red Squirrels, *Tamiasciurus hudsonicus*) concentrate their activity in large conifers, and that foliage difficults the view of parents for defending their nests. In our study site, at high elevations, bigger DBHs are mainly of a long lifespan conifer (Prince Albert's Yew, *Saxegothaea conspicua*). This tree species forms many natural cavities in its trunk and probably is a very good habitat for predators, but this speculation should be tested. On the other hand, tree decay at high elevation plays an opposite effect on nesting success, compared to low land forests. This could be due to the influence of Prince Albert's Yew, tree with many cavities that could be relaxing the fauna focus on snags or trees in very advanced decays.

Table 1. Forest structure effects on nest-box occupation rates at low and high elevations in Andean temperate forests of Chile.

	LOW LAND FORESTS			HIGH LAND FORESTS		
Variable	*Chi-square*	*p value*	Effect	*Chi-square*	*p value*	Effect
High canopy cover	1.381	0.240		8.261	0.004	(+)
Litter depth	0.765	0.382		0.031	0.861	
Understory density	12.405	0.000	(-)	0.071	0.789	
Corse woody debris volume	5.462	0.019	(+)	0.152	0.697	
Tree DBH	0.090	0.764		0.359	0.549	
Tree decay	1.567	0.211		10.232	0.001	(+)
Epiphyte and vines cover	0.438	0.508		0.000	0.997	

Table 2. Influence of forest structure on Thorn-tailed Rayadito nesting success at low and high elevations in Andean temperate forests of Chile.

	LOW LAND FORESTS			HIGH LAND FORESTS		
Variable	*Chi-square*	*p value*	Effect	*Chi-square*	*p value*	Effect
High canopy cover	0.678	0.410		5.546	0.019	(-)
Litter depth	0.234	0.628		0.924	0.336	
Understory density	0.402	0.526		0.613	0.434	
Corse woody debris volume	1.677	0.195		0.996	0.318	
Tree DBH	0.004	0.952		17.341	0.000	(-)
Tree decay	6.493	0.011	(-)	7.012	0.008	(+)
Epiphyte and vines cover	4.553	0.033	(-)	0.000	1.000	

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Appendix 2. Güiña (*Leopardus guigna*) preys on cavity-nesting nestlings

Güiña (*Leopardus guigna*) depreda polluelos de aves que nidifican en cavidades

Running title: GÜIÑA PREYS ON CAVITY NESTERS

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Predation has been a leading cause of nesting failure among diverse species of birds, accounting for up to 90 % of nest failure in some endangered populations (e.g., Cain et al. 2003). Different types of predators, such as small/medium-sized mammals and birds, are able to impact the reproductive success of birds by preying on their nest contents (Rogers & Caro 1998, Söderström et al. 1998, Purcell & Verner 1999). Nevertheless, direct evidences of predation events has been poorly documented, highlighting the relevance to obtain original and reliable data about an ecological interaction that may strongly impact bird populations and community structure, particularly in highly perturbed ecosystems.

The vulnerable güiña (*Leopardus guigna* Molina 1782), or kodkod cat, is one of the smallest (1.2-2.2 kg) felids in the world (Nowell & Jackson 1996). It has a limited distribution, restricted to a narrow strip within the temperate forests in south-central Chile and Argentina (30-50° S, 70-75° W) (Redford & Eisenberg 1992), inhabiting continuous and fragmented forests (Gálvez et al. 2013). The güiña has been described as a nocturnal carnivore (Hernández et al. Unpublished data), suggesting daily activity synchronization with small rodents, its primary prey item (up to 82 %; Dunstone et al. 2002, Correa & Roa 2005). Flightless (e.g., Chucao tapaculo *Scelorchilus rubecola* Kittlitz 1830, Huet-huet *Pteroptochos tarnii* King 1831) and occasionally flying birds (e.g., Austral thrush *Turdus falklandii* Quoy & Gaimard 1824, Thorn-tailed rayadito *Aphrastura spinicauda* Gmelin 1789) have been documented as secondary prey items within güiña's diet (24 %, Sanderson et al. 2002, Freer 2004). Even though güiña has been suggested as primarily terrestrial, its ability to prey on birds inhabiting the overstory or large-trees coincides with the well-developed tree climbing abilities displayed by the species (Sanderson et al. 2002). Previous güiña diet studies have been focused mainly on the identification of bird remains to species level (Sanderson et al. 2002, Freer 2004), not differentiating between age classes (e.g., adults/nestlings birds). The latter could shed light into the effects of predation on the reproductive biology of temperate forest bird assemblages.

In this article, we report the first records of güiña attempting to prey upon cavity-nesting bird nestlings in the temperate forest of South America. The study was conducted in an Andean landscape in the Araucanía district, South-Central Chile (39º16’ S, 71º48’ W). We identified study sites in six independent forests across an elevation gradient, from 271 meters above sea level (masl) to 1.063 masl. Sites were separated by a minimum linear distance of 1.6 km. Four sites represent early successional stages of forests at lowlands dominated by broadleaf species such as Roble beech *Nothofagus obliqua* (Mirb.) Oerst., Coigüe *Nothofagus dombeyi* (Mirb.) Oerst., and Chilean laurel *Laurelia sempervirens* (Ruiz & Pav.) Tul. The remaining two sites are old-growth, conifer-broadleaf mixed forests at higher altitudes dominated by Prince Albert’s yew *Saxegothaea conspicua* Lindl., Chilean Tepa *Laureliopsis philippiana* (Looser) Schodde, and Coigüe.

In winter 2010, 240 nest boxes (40 per site) were installed in order to assess nest box use by small cavity-nesting birds and mammals (i.e., depth 17.1 cm; entrance hole diameter 3.1 cm). The nest boxes were systematically placed in a grid, by hanging them from a tree branch 1.5 meters above ground and 25 meters apart. During two breeding seasons (2010-2011 and 2011-2012), nest boxes were monitored by direct observation and through the use of camera traps to monitor the activity of cavity users and identify potential nest predators. Passive digital camera traps (i.e., Reconyx®) were used to monitor activity at the 49 nest boxes. Cameras were placed at each box for 22 days resulting in 1,078 camera-trap days. Cameras were set in front or beside each box, programmed to operate 24 hours a day, and visited for maintenance every 10 days. An independent predation attempt at a site was defined as a photo capturing the presence of a predator with at least one hour interval between sequences (Di Bitetti et al. 2006).

Two secondary cavity nesting bird species used the nest boxes, mainly Thorn-tailed Rayadito and occasionally Southern House Wren (*Troglodytes aedon* Vieillot 1809). Additionally, three small mammal species were recorded as nest box users: Monito del monte (*Dromiciops gliroides* Thomas 1894), Chilean Arboreal-rat (*Irenomys tarsalis* Philippi 1900), and Long-tailed Rice Mice (*Oligoryzomys longicaudatus* Bennett 1832). Monito del monte also was registered as a cavity-nesting bird predator, along with *Milvago chimango* Vieillot 1816, *Glaucidium nana* King 1828, *Rattus rattus* Linnaeus 1758 among others[1]. We registered güiña activity in three of the study sites, with predation attempts only on Thorn-tailed

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[1] ALTAMIRANO TA, M DE LA MAZA & C BONACIC (2011) Depredación de nidos de rayadito (*Aphrastura spinicauda*) en el bosque templado andino de Chile. X Congreso Chileno de Ornitología, Santiago, Chile. Boletín Chileno de Ornitología 17: 26.

Rayadito nestlings. We detected at least three different individuals of güiña within seven independent photo sequences, two of them involving spotted güiñas (black-spots over buff or gray-brown coat) and a single melanistic individual (black coat) (Fig. 1). Seventy one percent of the predation attempts were concentrated at night (i.e., 2100 to 0600 h), whereas only 29 % were registered at dawn and dusk periods. This behaviour parallels the species' activity pattern described in other studies (Hernández et al. Unpublished data), which may correspond with the heightened activity of smalls mammals.

Previous studies investigating güiña diet suggest the species' preference to depredate flightless avian species that predominantly nest and forage close to the ground (e.g., *S. rubecula*) (Sanderson et al. 2002, Freer 2004). However, we show evidence for güiña preying on nestlings of a "large-tree user" birds (as Thorn-tailed Rayadito, Díaz et al. 2005), supporting an opportunistic felid behaviour. Trees climbed by individual güiñas within this study had a diameter at breast height (dbh) ranging from 5.4 to 7.5 cm. This differs from previous observations that report güiñas easily climbing trees with dbh > 8 cm (Sanderson et al. 2002).

Most predation attempts lasted less than two minutes (86 %, mean ± SD = 00:47 ± 0:41 minutes, n = 6), except one (36:11 minutes). These attempts mainly affected nests in nestling stages, and only one occurred in the post fledging stage (empty nest box), possibly attracted by the fecal odor. Only the longest güiña predation attempt was successful (14 %), resulting in the capture of a single nestling from the box (Fig. 1). The individual güiña then attempted to capture another Rayadito nestling from the same nest box but was unsuccessful.

The limited predation success and time allocated to güiña predation attempts could be explained by the depth dimension of nest boxes and their restricted entrance holes, which likely hampered the nestling captures. In fact, the entrances of natural cavities used for nesting -excluding fissures- in temperate forest are normally larger and/or less deep than nest boxes (TA Altamirano & JT Ibarra unpublished data), suggesting that real güiña predation success may be underestimated as a result of the restricted artificial cavity/nest box dimensions. To estimate the real cavity-nesting predation success, it would be necessary to conduct experimental nest box designs comparing different entrance size and box depth, or even better, assessing directly the predation success of natural cavities showing different dimensions. Finally, as güiña predation events do not leave any distinct sign on the nest box, at least with these dimension and entrance diameter, studies using this technique in temperate forest of South America should be cautious as not to overestimate breeding success when counting missing nestlings without predation evidence.

Our data provide the first evidences of güiña predation behaviour on cavity-nesting birds of the temperate forest of South-Central Chile, contributing to improve the natural history knowledge of this vulnerable felid. However, many interesting questions remain regarding the güiña diet and the influence of its predatory behaviour on different temperate forest bird populations. How does the predation success compare between open vs. cavity-nesting birds? Are nestlings more common prey than adult birds? How much does the güiña contribute to predation pressure on bird species? How are güiña impacting breeding site selection? What are the implications for avian reproductive biology and conservation?

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Figure legend

Fig. 1. Images of güiña predation attempts on nest boxes occupied by cavity-nesting birds. Spotted güiña trying to prey on a nest box (A); melanistic güiña attempting to capture a nestling (B); spotted güiña climbing a tree to approach a nest box; trying to catch a nestling; and capturing it (C-F).

Imágenes de intentos de depredación de güiña sobre aves que utilizan cajas-nido. Güiña moteada tratando de depredar una caja-nido (A); güiña melánica intentando capturar un polluelo (B); güiña moteada escalando el árbol de la caja-nido; tratando de capturar un polluelo; y capturándolo (C-F).

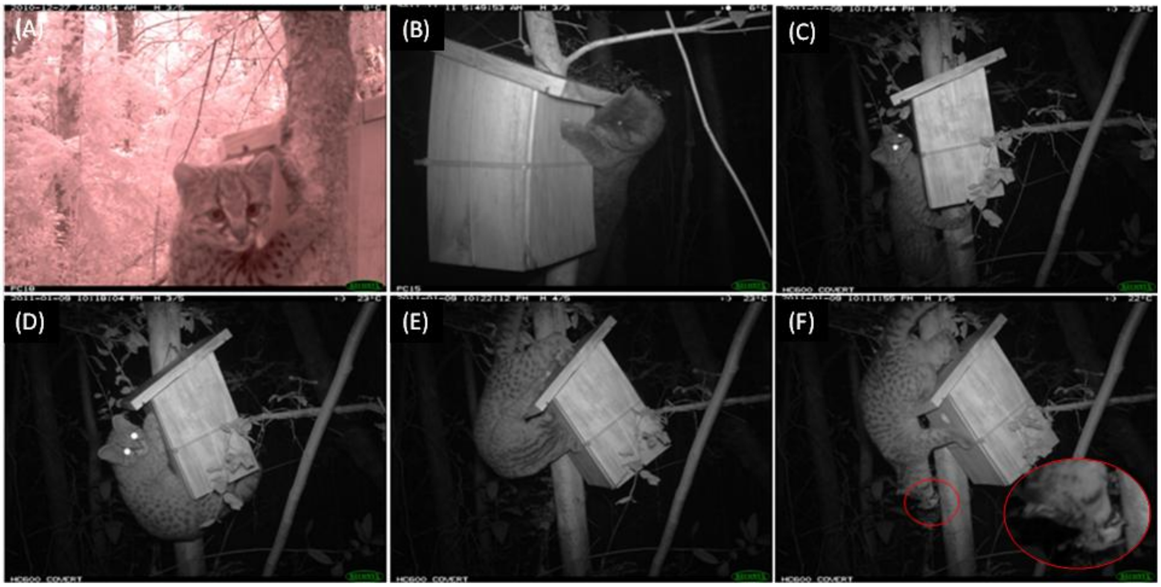

Fig. 1.