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ORIGINAL ARTICLE

Rufous-legged Owl (*Strix rufipes*) and Austral Pygmy Owl (*Glaucidium nanum*) stand use in a gradient of disrupted and old growth Andean temperate forests, Chile

José Tomás Ibarra^{a,b,c,*}, Nicolás Gálvez^{a,d}, Alessandro Gimona^e, Tomás A. Altamirano^a, Isabel Rojas^a, Alison Hester^e, Jerry Laker^a & Cristián Bonacic^a

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We studied how human induced structural changes in forests affect stand use of the Rufous-legged Owl (forest-specialist) and the Austral Pygmy Owl (forest-facultative), in a gradient from lowland disrupted forests to protected Andean forests in Chile. We also tested if the calls of one species influenced the calling behaviour of the other. We detected a total of 34 Rufous-legged Owls and 21 Austral Pygmy Owls during the four seasons. Rufous-legged Owls were found principally in old growth *Araucaria-Nothofagus* stands (32.4%), and Pygmy Owls in old growth evergreen stands (52.4%). For both species there was a seasonal effect on call response, with a drop in responses in autumn and winter. Our models suggested that Rufous-legged Owls inhabit a more specific range of habitat characteristics than Pygmy Owls. The former selected stands with tall trees, relatively low tree density, and high bamboo density. Pygmy Owls selected stands with tall trees and relatively high tree density. There was no evidence that either species influenced the calling behaviour of the other, suggesting no negative association between use of a territory by the two species. Our results emphasize the importance of structural components of old growth forests for both species, but also the relevance of stands surrounding protected areas.

Estudiamos cómo los cambios estructurales en el bosque, inducidos por el ser humano, afectan el uso de hábitat del concón (especialista de bosque) y del chuncho (facultativo de bosque), en un gradiente desde bosques perturbados en zonas bajas hasta bosques andinos protegidos de Chile. También evaluamos si los llamados de una especie influyen el comportamiento de vocalización de la otra. Detectamos un total de 34 concónes y 21 chunchos para las cuatro estaciones del año. Los concónes fueron registrados principalmente en bosques antiguos de *Araucaria-Nothofagus* (32.4%), y los chunchos en bosques antiguos siempre-verdes (52.4%). Para ambas especies hubo una disminución de la actividad en otoño e invierno. Nuestros modelos sugirieron que el concón tiene requerimientos de hábitat más específicos que el chuncho. El concón seleccionó bosques con árboles altos y en baja densidad relativa, y una alta densidad de quila. Por su parte, el chuncho seleccionó bosques con árboles altos y en alta densidad relativa. No hubo evidencia de que los llamados de una especie afectaran las respuestas de la otra, sugiriendo que no existe una asociación negativa en el uso de un mismo territorio por ellas. Los resultados enfatizan la importancia de los elementos estructurales de los bosques antiguos para ambas especies pero, a su vez, la relevancia de los bosques periféricos a áreas protegidas.

Keywords: Akaike's Information Criterion; bird habitat use; Chile; forest structural components; interspecific competition; owls; temperate forests

Introduction

The distribution of Chilean temperate forests has been greatly disrupted by several human land-use practices such as logging, land clearance for intensive agriculture, sub-urbanizations and replacement of native stands by exotic plantations (Armesto et al. 1998). Land-use practices can alter stand-level distribution and density of structural components present in old-growth forests such as the volume of coarse woody

debris (CWD), large snags, understory vegetation and large canopy trees, especially affecting species with specific forest habitat requirements (Martínez & Jaksic 1996; Reid et al. 2004; Díaz et al. 2005).

There is widespread concern in Chile that the protection afforded to native species by the National System of Parks and Reserves (hereafter, SNASPE) is inadequate to secure long-term conservation of biodiversity (Armesto et al. 1998). Over 90% of forests

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in the SNASPE are at high Andean mountain locations. Therefore, lowland forest habitats adjacent to protected areas are considered to be a conservation priority in temperate ecosystems, especially during winter when protected forests at high elevations are subjects of severe climatic conditions such as snow cover remaining for months (Armesto et al. 1998; Pauchard & Villarroel 2002; Ibarra et al. 2010).

We selected for study two contrasting owl species which use temperate forests in Chile. The Rufous-legged Owl (*Strix rufipes*, King 1827), a forest specialist, depends strictly on forests for nesting, whereas the Austral Pygmy Owl (*Glaucidium nanum*, King 1828) is a forest facultative that may hunt and/or nest within the forest (Trejo et al. 2006). The former is one of the least known nocturnal raptors of South America (Martínez & Jaksic 1996), and populations are considered to be declining because of increasing habitat loss (Jaksic & Jiménez 1986; Pincheira-Ulbrich et al. 2008). Only Martínez & Jaksic (1996) have studied Rufous-legged Owl population relative abundances and associations with different habitat components, in the evergreen Valdivian rainforests of southern Chile, suggesting that this species preferred multi-stratified stands > 100 years old. However, stand use and critical components of forests for this owl have never been researched in other vegetation types within its geographical range, which extends from central Chile to southern Patagonia (Trejo et al. 2006).

In contrast, the Austral Pygmy Owl is considered the most abundant Strigidae in Chile, ranging from the northern limit of the country to the Cape Horn archipelago (Jiménez & Jaksic 1989). It inhabits forests and thickets, and sometimes it is also found in city parks (Goodall et al. 1957; Johnson 1967; Jiménez & Jaksic 1989). Jiménez & Jaksic (1989) suggested that the status of the Austral Pygmy Owl populations is 'stationary' over the entire country. However, as with the Rufous-legged Owl, no studies have explored its relative abundance and stand use in disrupted and old growth Andean forests of south-central Chile.

Furthermore, little is known about whether the occurrence of one species affects the stand use or activity of the other. Interspecific territoriality and agonistic behaviour among owls has been extensively documented (Janes 1985). Forest-specialist owls may be negatively affected by forest-facultative ones when the latter, more able to colonize recently disturbed and secondary forests, dominantly compete with the former for habitat and prey (Olson et al. 2005; Crozier et al. 2006). Although our focal species vary in body size, activity patterns and food habits (see Jiménez & Jaksic 1989; Martínez 2005); Martínez (2005) has hypothesized that increasing abundances of forest-facultative owls, coupled with loss of suitable habitat, may be

a factor influencing local extinction of the Rufous-legged Owl in the short term. There is no evidence, however, documenting the outcome of encounters between Rufous-legged Owls and Austral Pygmy Owls in those sites where they co-occur.

Here, we examined how structural stand-level changes in forests affect the seasonal stand use and relative abundances of these two owl species in a gradient from lowland disrupted (under logging, fire and livestock raising activities) and secondary forests, to protected high Andean old growth forest sites, using a modeling approach. We also explored interspecific interactions between the two species testing the hypothesis that the occurrence of one species influences the other's response, developing models predicting detections of one species as a function of both habitat variables and detections of the other owl species (MacKenzie et al. 2006).

Materials and methods

Study area

From January 2008 to February 2009 we conducted owl surveys in three different areas of the Villarrica Catchment, Araucanía District (39°15' S, 71° W). These areas were either in the surroundings or inside protected areas (Table 1). Elevations ranged from 627 to 1268 m asl in mountainous topography. The area has a temperate climate with a short dry season (< 4 months). The closest and most representative meteorological station (i.e. Lonquimay, roughly 100 km from the study area) has a mean annual precipitation of 1945 mm, falling as snow in higher altitudes (> 750 m) (Di Castri & Hajek 1976). The mean temperature is 15.1°C for the warmest month (January) and 1.9°C for the coolest month (July) (Di Castri & Hajek 1976). The vegetation comprises deciduous forest dominated by species of *Nothofagus* at lower altitudes and mixed deciduous with conifer forest at higher altitudes (Gajardo 1993). In higher elevations, high-Andean deciduous forests are dominated by *Araucaria araucana* (Gajardo 1993).

Although a relationship between abundances of our focal owl species and land-use practices may exist at the landscape level (Martínez 2005), we explored whether this relationship exists at the smaller stand-level, where forest management activities take place. We systematically surveyed eight forest stands, separated from each other by at least 5 km, representing a gradient of altitude and disturbance. Each stand had an area of at least 500 ha. Stands were: (a, b) two old growth *Araucaria–Nothofagus* stands: *Araucaria araucana–Nothofagus pumilio* association, >200 years old, one in Huerquehue National Park (HNP) and the other in El Cañi Private

Table 1. Mean \pm SE habitat structural elements available for owls in forests in Huerquehue National Park (HNP), El Cañi Private Park (CPP), Kawellucó Private Park (KPP) and its surrounding private lands in the Araucanía District, southern Chile.

Stand	Site	Altitude (m asl)	Canopy cover (%)	Bamboo density		Tree height (m)	Tree density (trees ha ⁻¹)	Snag density (snags ha ⁻¹)
				CN/3 m	DBH (cm)			
a) Old growth (<i>Araucaria–Nothofagus</i>)	HNP	1250.2 \pm 14.8	54.7 \pm 40.7	3.4 \pm 0.7	52.5 \pm 33.5	20.8 \pm 8.9	207.9	46.0
b. Old growth (<i>Araucaria–Nothofagus</i>)	CPP	1280.6 \pm 9.7	81.3 \pm 21.7	2.1 \pm 1.1	48.9 \pm 36.6	18.91 \pm 9.9	616.3	14.0
c. Old growth (evergreen)	HNP	921 \pm 15.1	56.3 \pm 34.7	2.6 \pm 0.5	67.7 \pm 44.9	23.3 \pm 10.1	170.6	13.0
d. Old growth (evergreen)	KPP	878 \pm 12.0	57.3 \pm 41.5	1.0 \pm 0.3	44.1 \pm 25.7	19.3 \pm 5.2	193.3	15.0
e. Secondary	HNP	865.2 \pm 18.3	96.3 \pm 10.6	1.7 \pm 0.5	24.0 \pm 13.5	16.8 \pm 6.0	900.5	11.0
f. Secondary	Adjacent to CPP	852.2 \pm 23.0	95.6 \pm 8.6	0.3 \pm 0.1	34.2 \pm 15.0	26.2 \pm 3.7	869.8	7.0
g. Disturbed	Adjacent to HNP	753.4 \pm 65.2	15.0 \pm 33.5	0.8 \pm 1.2	19.4 \pm 12.9	9.2 \pm 3.4	152.3	0.0
h. Disturbed	Adjacent to CPP	627.4 \pm 16.7	28.1 \pm 42.1	0.5 \pm 0.2	30.5 \pm 17.6	13.1 \pm 5.7	180.6	0.0

Park (CPP); (c, d) two old growth evergreen stands: *Saxegothaea conspicua–Laureliopsis philipiana* association, > 200 years old; one in HNP and the second in Kawellucó Private Park (KPP); (e, f) two secondary forests: *N. dombeyi–N. obliqua* association, 35–70 years old, one in HNP and the other in the surroundings of CPP; (g, h) two disrupted sites: multi-species forest stands, both under livestock pressure and logging use, one in the surrounding areas of HNP and the second in the surrounding areas of CPP (Table 1).

Habitat structure

We used the only previous study of Rufous-legged Owl stand use (Martínez & Jaksic 1996) to identify potential structural components of forests that may be important as a habitat for this owl. As far as we know, there are no studies on stand use by Austral Pygmy Owls. Thus, habitat surveys for this species considered the measurement of habitat components suggested as predictors for the Rufous-legged Owl and they were tested as covariates for the Austral Pygmy Owl as well. Therefore, for each of the eight forest stands we evaluated: (i) canopy cover (%); (ii) density of bamboo vegetation (understory) up to 3 m high, expressed as the number of contacts (CN) using the method described in Díaz et al. (2006); (iii) diameter at breast height (DBH, in cm); (iv) tree height (m); (v) density of all trees larger than 10 cm in DBH, using the point-quarter method described in Mueller-Dombois & Ellenberg (1974); and (vi) number of snags (snags ha⁻¹). We established eight sampling points per stand along a 140-m transect, with each point 20 m away from the next.

Owl surveys

We recorded individual call response as a proxy for relative abundance, associating it to the above

habitat-related variables across all stands (Andersen 2007; Trejo et al. 2011). Counts of responses to calls were collected along paths through the forest using the calling survey method, broadcasting recordings of calls of the two species available from Egli (2002). We called owls over 32 nights, starting approximately 30 min after sunset. Each call lasted 30 s, followed by a 30–60 s listening period after which the sequence was repeated twice (Martínez & Jaksic 1996; Trejo et al. 2011). To prevent double counting of individuals, orientation of the responses was identified, locations were approximately determined by compass triangulation, and surveys were restricted to 12–14 min at each survey station (Kochert 1986; Enríquez & Rangel-Salazar 2001). We recorded all individual owls that we heard during this period and if a bird responded to our call this was considered one response and all further responses from that bird were ignored for that immediate time period. Calls were conducted under relatively calm conditions with no precipitation or fog (Forsman et al. 1977). Each station was separated by at least 2 km from the nearest one and these were not surveyed again the following season (i.e. stations were randomized every season in each stand: Fuller & Mosher 1981). Owl surveys were carried out during eight nights per season: summer (January–February), autumn (April), winter (August) and spring (December). We estimated relative abundances as the number of individual birds per night survey and stand (Enríquez & Rangel-Salazar 2001; Andersen 2007). The species call orders were randomized at every calling station.

Data analysis

The data were clustered both within areas and stands. Since each stand was surveyed in four different seasons, within-stand counts were likely non-independent across time. We tested and accounted

for the possible interaction between stand effect and season effect, which could be expected from our exploratory analysis. To account for such data structure, we used generalized linear mixed models with a Poisson error and a random slope (stand) and intercept (season). We used habitat structural components (see Table 1 for details) as fixed effects in the models. Because detectable changes in calling behaviour can improve our understanding of interference competition between sympatric owls (Crozier et al. 2006), we also included Austral Pygmy Owl responses as a fixed effect that might affect Rufous-legged Owl responses in a given survey, and vice versa (MacKenzie et al. 2006).

For each species, we identified the most parsimonious model using the Akaike's Information Criterion (AIC) (Zabel et al. 2003; Richards 2005). We first compared AIC and BIC (Bayesian Information Criterion) of models without a random structure versus a model with only random intercept and one with random slope and intercept. We then searched for the model with the best fixed structure, given the random structure identified in the previous stage. We first fitted the full model (i.e. the model with all the independent variables as fixed effects), and then reduced each full model to the model with the lowest AIC value, by eliminating variables whose retention caused a higher AIC value than their deletion.

For both species we also compared the second best model and the best models using AIC weights calculated as $w = \exp(-\Delta\text{AIC}/2)$, where ΔAIC is the difference between the AIC of the second and of the best model. Data analysis and models were fitted using R[®] library `lm4` (R Development Core Team 2008).

Results

Structural characteristics of the eight forest stands surveyed are presented in Table 1. Both species were detected in old growth, secondary and disrupted forests along the gradient, although this varied between seasons and stands (Figure 1). We detected a total of 34 Rufous-legged Owls and 21 Austral Pygmy Owls by their individual response calls during the four seasons. From total calls, Rufous-legged Owls were found principally in old growth *Araucaria–Nothofagus* stands (32.4%), followed by secondary stands (29.4%), then old growth evergreen stands (26.5%), and least in the disrupted multi-species stands (11.8%). Austral Pygmy Owls were found principally in old growth evergreen stands (52.4%), followed by old growth *Araucaria–Nothofagus* stands (19.1%), with the same number of records for the secondary and the disrupted multi-species stands (both 14.3%). For both species

there was a seasonal effect on call response, with a drop in responses in autumn and winter (Tables 2, 3, Figure 1).

Rufous-legged Owl

The random structure model with lowest AIC was the one with “stand” as random slope and “season” as intercept. A model with non-random structure had an AIC = 76.5 versus 49.6 for a model with only “season” as random intercept, and 48.6 for a model with both random slope and intercept. The “between seasons” variance was 2.9 while the “between stands” variance was 0.25. The most parsimonious model for this species was one in which the environmental variables (fixed effect) included were “density of trees”, inversely related to owl responses, and “tree height” (see Table 2 for details). The second best model also included “bamboo density” and had a likelihood weight of 0.39 versus 0.61 of the best model.

Austral Pygmy Owl

The AIC for models with non-random structure had AIC = 92.3, with random slope and intercept yielded AIC = 44.7, and a model with only “season” as random intercept yielded AIC = 35.03, hence the latter was preferred. Among fixed effect variables, only “tree height” was significant in the most parsimonious model for this species (see Table 3 for details). The second best model also included “density of trees.” As in the case of the first species, the likelihood weight of this model was 0.39 versus 0.61 of the best model.

There was no evidence that the occurrence of either species affected the responses of the other (Austral Pygmy Owl $p = 0.946$; Rufous-legged Owl $p = 0.743$).

Discussion

Owl–habitat relationships

This study shows that in the Andean forests of south-central Chile, the Rufous-legged Owl inhabits a more specific arrangement of habitat characteristics than the Austral Pygmy Owl. We found that the Rufous-legged Owl selected forest stands with tall trees, relatively low tree density and high bamboo density. In our study area, tall trees are found mainly in protected old growth forests where the dominant tree species is the conifer *A. araucana*. Here, tall trees are correlated with those with higher DBH (i.e. old growth living trees) and could perform several important functions in owl habitat, providing thermally suitable roosting and breeding sites (i.e. cavities) (Ripple et al. 1997; Thome et al. 1999).

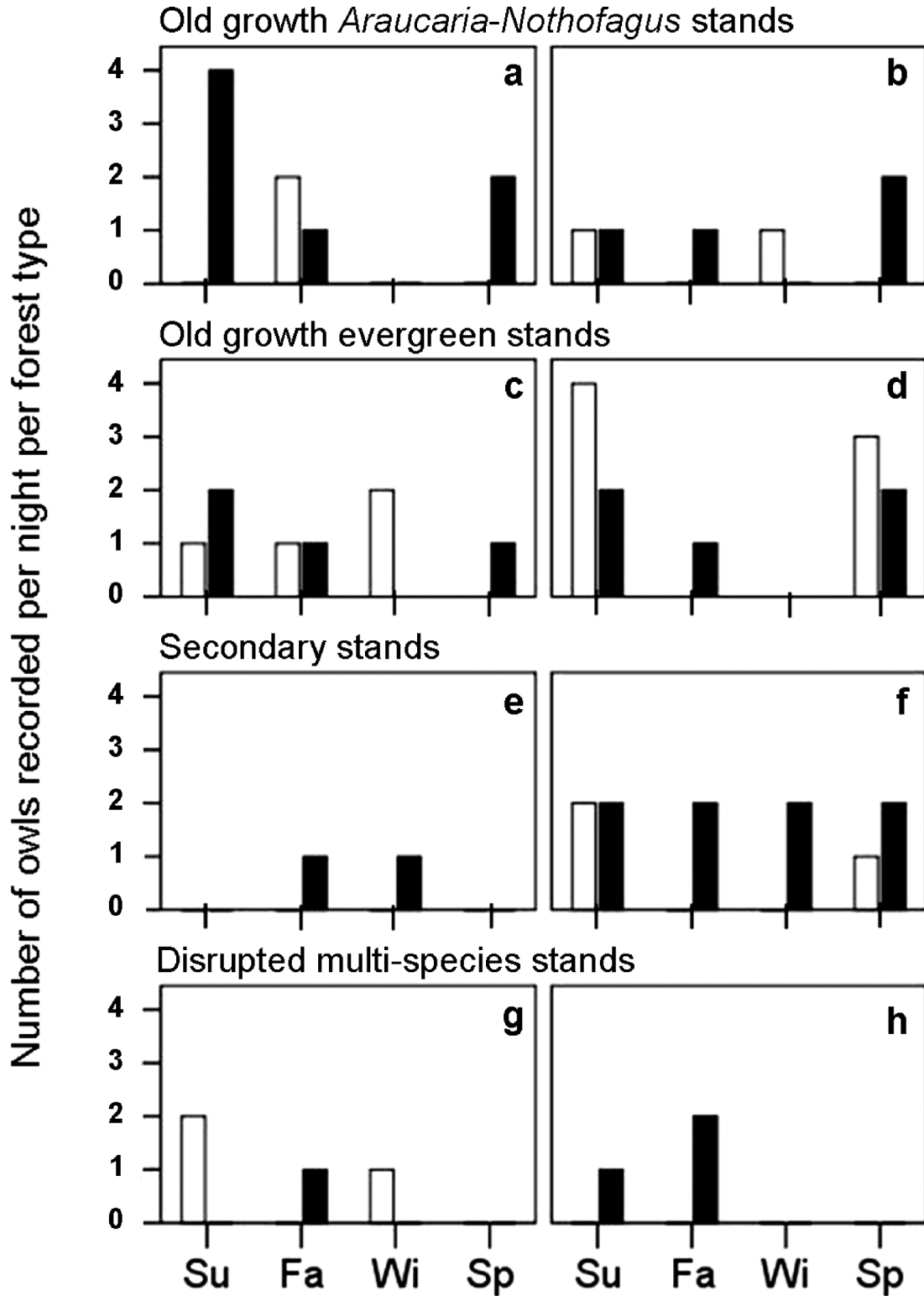


Figure 1. Number of Rufous-legged Owls (black bars) and Austral Pygmy Owls (white bars), recorded per night survey detected by season: summer (Su), fall (Fa), winter (Wi), and spring (Sp), in south-central Chile. (a, b) two old growth *Araucaria-Nothofagus* stands; (c, d) two old growth evergreen stands; (e, f) two secondary forests; (g, h) two disrupted sites: multi-species forest stands.

Table 2. Best model for Rufous-legged Owl, using Akaike's Information Criterion.

Variables	Estimate	S. E.	z value	p-value
Intercept	-2.314	1.245	-1.857	0.0632
Density of trees	-0.004	0.001	-3.344	0.0008
Tree height	0.136	0.066	2.042	0.0411
Random terms (variance)				
Season	2.912			
Stand	0.253			

Table 3. Best model for Austral Pygmy Owl, using Akaike's Information Criterion.

Variables	Estimate	S. E.	z value	p-value
Intercept	-1.602	0.795	-2.015	0.0439
Tree height	0.084	0.037	2.239	0.0252
Random terms (variance)				
Season	0.04			

Rufous-legged Owls have recently been reported to use large trees for nesting (92–170 cm of DBH and 18–32.5 m high) in Andean temperate forests, selecting cavities excavated by Magellanic woodpeckers (*Campephilus magellanicus*) (Beaudoin & Ojeda 2011). In our study area, the highest abundance of these excavator woodpeckers is in old growth *A. araucaria*–*N. pumilio* forests at high elevations (Ibarra, Gálvez, Altamirano, Rojas & Bonacic, unpublished data). Our observation that Rufous-legged Owls are strongly associated with the same vegetation type suggests that the presence of Magellanic woodpeckers may be a factor in nest site selection by Rufous-legged Owls. This may be important to investigate if we are to fully understand spatial co-occurrence of these two forest-specialist species.

In the Valdivian rainforest, south of our study area, Martínez & Jaksic (1996) found that the canopy cover alone was the best predictor of Rufous-legged Owl abundances. This variable was not significant in our study area, but the structural characteristics of our old growth forests differ from the southern Valdivian rainforests. In our old growth stands, *A. araucana* forms an overstory of scattered trees ca. 25–30 m tall above a 10–20 m tall stratum of *N. pumilio* (Veblen 1982), with relatively open canopies reaching covers between 54% and 81%. However, these stands are also characterized by a dense understory dominated by *Chusquea* bamboo and other small shrubs (Veblen 1982). We found that bamboo density was an important additional variable in the second best model, and we stress the importance of including this habitat structural component in all analyses. The main preys (arboreal and scansorial small mammals) of the Rufous-legged Owl in *A. araucaria* forests of

south-central Chile are strongly associated with dense bamboo thickets as well as old trees (Figueroa et al. 2006). Although our data showed that Rufous-legged Owls were also present in the disrupted multi-species forest under livestock pressure and logging use, the lower number of records in such stands suggests that these forests provide marginal habitat at best. In fact, within these disturbed areas, we observed that residual or remnant old growth trees were always the ones being used by the responding owls.

Our results suggest that the Austral Pygmy Owl is a more generalist species than the Rufous-legged Owl, in terms of the specific structural components of forests accounting for its relative abundances. Yet, and analogously to the Rufous-legged Owl, it was more strongly associated with old growth stands. These forests offer a higher number of cavities and a higher diversity and abundance of potential diurnal passerines and mammalian prey to this opportunistic predator, than disrupted forests at lower altitudes (Ibarra, Gálvez, Altamirano, Rojas & Bonacic, unpublished data). Its abundance also showed positive relationships to tree height. As mentioned above, tree height is a structural element correlated to DBH and both together are an indicator of old growth forests (Call et al. 1992). Previous descriptions of Austral Pygmy Owl habitat suggested that this species can be found in habitats with a variety of structural components and degrees of complexity (Jiménez & Jaksic 1989). Nevertheless, our findings indicate that, although this species was also found in disrupted and secondary stands, old growth forests, especially evergreen stands, can support higher numbers of individuals.

On the other hand, the lack of effect of response calls between species suggests non-avoidance between these sympatric forest owls (e.g., Hayward & Garton 1988; Crozier et al. 2006). However, further experimental studies and observations of direct interactions are necessary in order to elucidate factors responsible for this possible non-negative association.

Influence of seasons on call response and stand use

Both species showed a significant seasonal effect on call responses that could be due to habitat selection and/or detectability (the latter could be affected by environmental or weather conditions and behaviour). If we assume perfect detection (i.e. detecting the species if present), seasonal changes in habitat selection may be due to changing prey availability, predation vulnerability, and thermoregulation needs (Barrows & Barrows 1978; Forsman et al. 1984; Call et al. 1992). The absence of the Rufous-legged Owl from higher altitude sites (i.e. old growth *Araucaria*–*Nothofagus* and evergreen) during winter may be

associated with local altitudinal migrations. Such altitudinal movements have been described for other *Strix* species (e.g., Laymon 1989). For the Rufous-legged Owl, these seasonal movements would need further assessment because the connectivity between higher and lower forest habitats might be a key issue for its conservation. The understory of the *Araucaria–Nothofagus* stands is completely covered by snow during winter months (Ibarra et al. 2010), which may affect prey availability and induce owls to leave the area.

On the other hand, perfect detection of the birds by the researcher is not likely to be met due to the elusive nature of owls, although detection probabilities for other *Strix* species in a temperate forest environment of North America are high (e.g., 0.53–0.76; Olson et al. 2005). In any case, it could be a mixed habitat selection/detectability effect which we cannot differentiate with our data and sampling scheme. It would be relevant to carry out studies that account for imperfect detection using repeated surveys, to further explore temporal variation in site occupancy (Olson et al. 2005; MacKenzie et al. 2002).

Implications for owl conservation

Our results highlight the importance of structural components of old growth forests for both owl species. Old growth stands are mainly located at higher altitudes in both private and public protected areas. Nevertheless, both species are present in lowland forest habitats adjacent to or surrounding protected areas. Our work suggests that the maintenance of large trees and understory vegetation in buffer areas is indispensable to assure appropriate balance of owl conservation and productive activities (e.g., forestry, agriculture, livestock raising). With appropriate management, production areas can play an important role in nocturnal raptor conservation and contemporary management planning in the Andean temperate forests of south-central Chile.

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