



Research Article

Factors Associated with the Detectability of Owls in South American Temperate Forests: Implications for Nocturnal Raptor Monitoring

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ABSTRACT Owls occur at relatively low densities and are cryptic; thus, monitoring programs that estimate variation in detectability will improve inferences about their presence. We investigated temporal and abiotic sources of variation associated with detection probabilities of rufous-legged owls (*Strix rufipes*), a threatened forest specialist, and austral pygmy-owls (*Glaucidium nana*), a habitat generalist, in temperate forests of southern Chile. We also assessed whether detection of 1 species was related to the detection of the other species. During 2011–2013, we conducted 1,145 broadcast surveys at 101 sampling units established along an elevational gradient located inside and outside protected areas. We used a multi-season occupancy framework for modeling occupancy (ψ) and detection (p), and ranked models using an information-theoretic approach. We recorded 292 detections of rufous-legged owls and 334 detections of austral pygmy-owls. Occupancy was positively associated with elevation for rufous-legged owls but constant (i.e., did not vary with covariates) for pygmy-owls. Detectability for both owls increased with greater moonlight and decreased with environmental noise, and for pygmy-owls greater wind speed decreased detectability. The probability of detecting pygmy-owls increased nonlinearly with number of days since the start of surveys and peaked during the latest surveys of the season (23 Jan–7 Feb). Detection of both species was positively correlated with the detection of the other species. We suggest both species should be surveyed simultaneously for a minimum of 3–4 times during a season, survey stations should be located away from noise, and observers should record the moon phase and weather conditions for each survey. © 2014 The Wildlife Society.

KEY WORDS austral pygmy-owl, Chile, *Glaucidium nana*, moonlight, occupancy, Patagonia, rufous-legged owl, *Strix rufipes*.

Compared with other avian groups, owls are difficult to study and are typically not covered by land-bird monitoring programs because of their low densities, elusive behavior, and nocturnal habits (Fuller and Mosher 1987). As a result, inferences about the spatial and temporal variation in owl occurrence could be misleading if researchers do not account for incomplete detectability or false absences (Wintle et al. 2005, MacKenzie et al. 2006). Detectability of owls may be affected by several temporal, abiotic, and biotic factors (Andersen 2007). For example, intraseasonal breeding phenology and social status, which are commonly correlated with prey availability, can affect calling rates of owls (Morrell

et al. 1991, Hardy and Morrison 2000, Kissling et al. 2010). Unfavorable detection conditions such as wind speed, environmental noise, and cloud cover can influence the ability of researchers to detect owls (Fisher et al. 2004, Andersen 2007) and lunar cycles appear to influence communication and activity patterns of owls and their prey (Clarke 1983, Penteriani et al. 2010). Furthermore, the calling rates of owls may be affected by the risk of being detected by an intraguild predator (Lourenço et al. 2013), or by the presence of a dominant owl in the area (Olson et al. 2005). Thus the number of sampling units occupied by an owl species of interest and their detection probabilities can be underestimated if environmental or social factors are not considered.

Few studies have investigated habitat use and abundance of owls in the temperate forests of South America and none have examined occupancy and detectability (but see Martínez and Jaksic 1996, Ibarra et al. 2012). Two species, the rufous-legged

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owls (*Strix rufipes*) and austral pygmy-owls (*Glaucidium nana*), inhabit an eco-region that is among the most threatened on earth because nearly 60% of forest cover has been lost because of large-scale farming and plantation forestry (Lara 1996, Myers et al. 2000). In Chile, the great majority of remaining forests inhabited by these owls are located in high-elevation protected areas, whereas forests in lowland areas have varying levels of degradation and fragmentation (Armesto et al. 1998).

We examined factors associated with the probability of detecting rufous-legged and austral pygmy-owls in southern Chile to improve monitoring protocols for these raptors. Rufous-legged owls and austral pygmy-owls are the most abundant of the 5 species of owls occurring in the Andean portion of temperate forests; therefore, we anticipated we could obtain a sufficient number of detections to model detectability for these 2 species. Rufous-legged owls are medium-sized forest specialists that hunt and nest only within forests (Trejo et al. 2006). They also are one of the least known owls in South America and are declining because of increased habitat alteration (Martínez 2005). Austral pygmy-owls are small habitat generalists that hunt and/or nest within forests, shrublands, and around human habitation (Jiménez and Jaksic 1989, Trejo et al. 2006). They are abundant and common throughout their distribution in Chile (Jiménez and Jaksic 1989). Despite their wide distribution and local abundance, the ecology of austral pygmy-owls is still poorly known. We estimated owl detectability as a function of survey-specific temporal, abiotic, and biotic conditions (MacKenzie et al. 2006). Quantifying sources of variation in detection rates can provide more reliable

estimates for addressing research questions and may improve monitoring programs for owls in the region (e.g., Andersen 2007, Manning 2011).

STUDY AREA

We conducted our fieldwork within the Araucarias Biosphere Reserve (UNESCO 2010). Specifically, we studied owls in the Villarrica watershed in the Andean zone of the Araucanía Region (39°15'S 71°W), northern Patagonia, Chile (Fig. 1). We chose this watershed because accessibility was good and its landscapes were representative of Andean temperate forests. The climate was temperate with a short dry season (<4 months) and a mean annual precipitation of 1,945 mm (Di Castri and Hajek 1976). Forests in the area ranged from 200 m to 1,500 m in elevation and were dominated by deciduous *Nothofagus* species at lower altitudes and mixed deciduous with coniferous *Araucaria araucana* at higher elevations (Gajardo 1993). Most public protected areas at high elevations (>700 m) were forested, whereas lowlands (<700 m) were dominated by agriculture and human settlement. However, several private protected areas were established during recent decades in the lowland areas.

METHODS

Nocturnal Raptor Surveys

We assessed detectability of owls during 2 nesting seasons (mid-Oct to early Feb) at 95 sampling units during

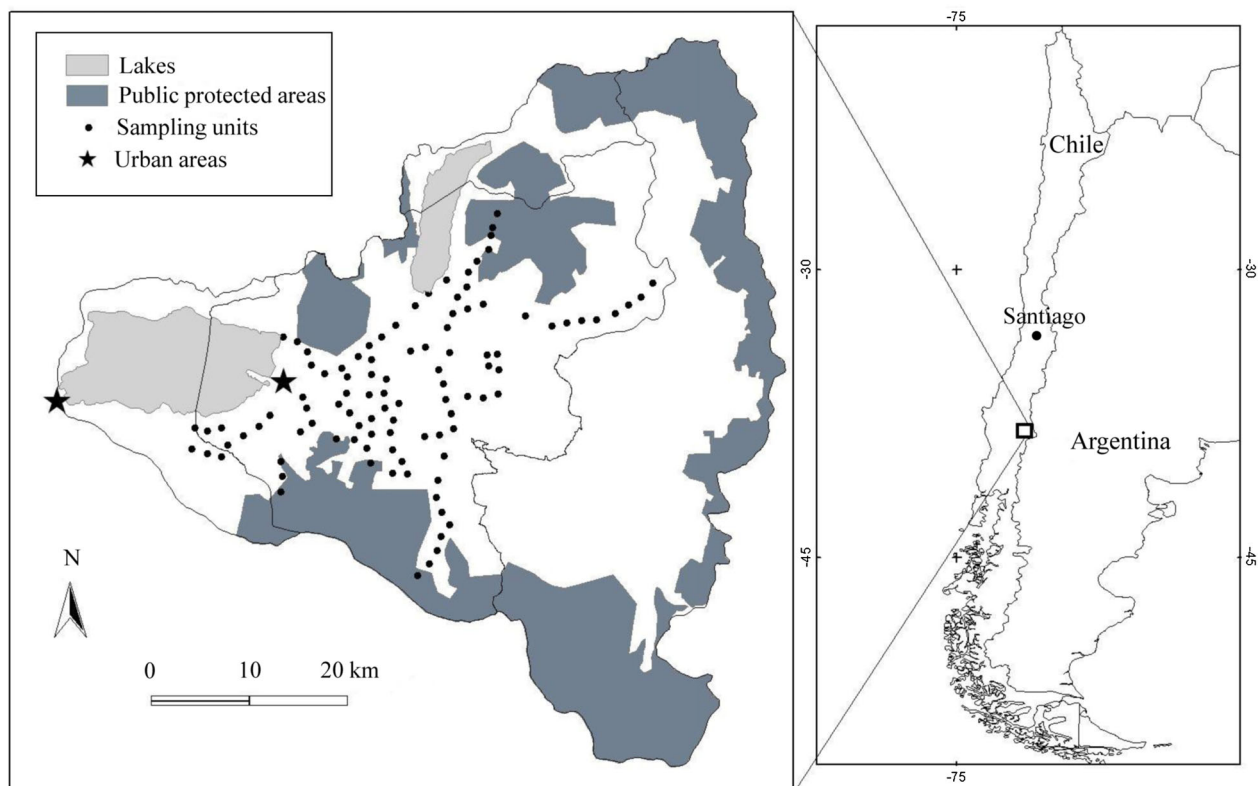


Figure 1. Distribution of 101 sampling units in the Villarrica watershed used to survey rufous-legged owls and austral pygmy-owls in a mountainous landscape in Andean temperate forests of the Araucanía Region (39°S), Chile.

2011–2012 and 101 units during 2012–2013 (i.e., 6 new units) in an area of 2,585 km² (Fig. 1). Sampling units spanned the gradient of the forest elevational range from 221 m to 1,361 m (near the tree line). This gradient represented a variety of habitat conditions from degraded and patchy forests to zones comprising continuous forests at higher elevations (Ibarra et al. 2012). We defined the sampling unit as the area within a 500-m detection radius of the sampling point, which corresponded to the area within which an owl could have heard a vocal lure during a survey (Sutherland et al. 2010). Using ArcGIS 10.1 (Environmental Systems Research Institute, Inc., Redlands, CA), we identified all the headwaters of smaller basins that were accessible by rural roads or hiking trails within the Villarrica watershed. We randomly selected 13 of these 19 basins and placed the first sampling unit within all basins near the headwater (within 1 km of the tree line). We systematically established the remaining sampling units at every 1.5 km within drainages descending from the headwaters.

We conducted surveys along rural roads and trails. Because playbacks of vocalizations improve detection rates of the owls we studied (Trejo et al. 2011, Ibarra et al. 2012), we broadcasted calls of both species beginning approximately 15 minutes after sunset until 0345 hours. We used a portable amplifier (Mipro MA-101C, Mipro, Chiayi, Taiwan; 27W) for broadcasting owl calls with a volume adjusted to 100 db at 1 m in front of the speaker measured using a digital sound-level meter (Extech 407730, Extech Instruments, Nashua, NH; Fuller and Mosher 1987). Each survey started with a 1-minute passive listening period, followed by playback of calls of both species played in a random sequence. For each species, we broadcasted vocalizations for 30 seconds while rotating the amplifier 360°, then listened for 1 minute so that we broadcasted calls for each species twice and followed each time with 1 minute of listening (Kissling et al. 2010). At the end of each survey, we took 2 minutes to record time, temperature (°C), relative humidity (%), and wind speed (m/s) at a height of 2 m using a hand-held weather monitor (Kestrel 4,200, Kestrelmeters, Birmingham, MI). We measured cloud cover using okta units (i.e., eighths of sky covered by clouds) and assessed the presence (1) or absence (0) of considerable environmental noise (e.g., stream or river sound, barking dogs).

We obtained the moon phase (%), where full moon = 100% for each night surveyed (<http://kwathabeng.co.za/travel/moon/moon-phase-calendar.html?country=Chile>). Because the amount of ambient light was affected negatively by the presence of clouds, we quantified moonlight (MI) as the proportion of illumination relative to the maximum possible at full moon, reduced by that obscured by clouds and computed as $MI = (1 - \text{cloud cover}) \times (\text{moon phase}/100)$ (Kissling et al. 2010). We repeated surveys of each sampling unit at intervals of approximately 10 days, and broadcasted owl calls always from the same location at the center of the sampling unit.

Statistical Analysis

We used a multi-season occupancy framework for open populations using detection histories of the owls during the

study period (MacKenzie et al. 2003). We modeled the data for each owl species independently (i.e., single-species occupancy models; MacKenzie et al. 2006). We estimated probabilities of occupancy (ψ) and detection (p) using the program unmarked, which allowed the response variables to be functions of covariates (Fiske and Chandler 2011). For ψ , we considered 2 covariates across the altitudinal gradient: mean elevation of the unit (meters above sea level/1,000), and Pa, a binary covariate indicating the sampling unit was located within 500 m of a protected area (1) or not (0). To identify potential covariates that may be associated with detectability, we used covariates that were correlated with owl detection in other studies (Morrell et al. 1991; Clark and Anderson 1997; Hardy and Morrison 2000; Crozier et al. 2005, 2006; Wintle et al. 2005). We modeled the probability of detection (p) assessing 9 temporal, abiotic, and biotic covariates (Table 1). We also included quadratic terms for number of days since the start of surveys and moonlight because the influence of these covariates on calling behavior of owls might not be linear throughout the breeding season (Ganey 1990, Kissling et al. 2010). We considered that pairs of collinear variables ($r > 0.7$) were estimates of a single underlying factor; therefore, we did not use collinear variables in the same model. We retained only the covariate that was expected to be more influential to owls in the analysis (Table 1).

To obtain the best model for each owl species, we first fit models using each covariate singly to predict ψ or p . We also fit a model with ψ constant across sampling units and p constant across surveys (i.e., null models). We ranked models using an information-theoretic approach (Akaike's Information Criterion [AIC], Burnham and Anderson 2002). After we fit the single-covariate models, we assessed more complex models containing different combinations of the best-supported covariates, on the basis of model weights and the precision of the estimated coefficients (from the single-covariate model). From this base model, we added extra covariates and evaluated each model's weight following every addition. We continued to add covariates until all supported covariates not in the base model had been considered. We considered models within 2 AIC units of the top model as the competitive set of best-supported models. We computed model weights (w_i), reflecting the relative weight of evidence for model i , and considered the best model to be that with the highest weight and lowest AIC value (Burnham and Anderson 2002).

RESULTS

We conducted 1,145 broadcast surveys over 2 years of sampling. In 2011–2012, we conducted 3 surveys at 2 sampling units, 4 at 4 units, and 6 at 89 units ($\bar{x} = 5.85$ surveys per sampling unit). In 2012–2013, we conducted 3 surveys at 1 sampling unit, 4 at 7 units, and 6 at 93 units ($\bar{x} = 5.83$ surveys per sampling unit). We obtained 292 detections (148 for 2011–2012 and 144 for 2012–2013) of rufous-legged owls and 334 (173 for 2011–2012 and 161 for 2012–2013) of austral pygmy-owls. From 493 surveys where at least 1 owl was detected during both seasons, 133 (27%)

Table 1. Candidate predictors of detectability for forest owls in the temperate forests of Chile

| Covariate | Type of variable (code) | Description | Reason for consideration |
|-----------|-------------------------------------|---|--|
| Temporal | Days (day) | Number of days since start of surveys | Owl calling behavior may change throughout the nesting season ^{a,b,c,d,j} |
| | Time (time) | Number of minutes after 21 hours | Owl calling behavior may change during the night ^{a,c,d,j} |
| | Year (year) | Nesting season 2011–2012 or 2012–2013 | Owl calling behavior may change between years ^{d,k} |
| Abiotic | Temperature (temp) ^o | ° C | Owl behavior ^{b,d,h,j,m} |
| | Wind (wind) | m/s | Owl behavior, visibility, sound carry ^{b,c,h,j} |
| | Relative humidity (Hu) ^o | % | Owl behavior ⁿ |
| | Moonlight (MI) | Amount of light available reduced for that obscured by clouds. MI = [(1 – cloud) × (moon phase/100)]. Moon phase refers to % where full moon = 100% | Owl and prey behavior ^{a,b,d,e,j,l,n} |
| | Environmental noise (noise) | 0 = quiet, 1 = substantial (dogs barking, and/or river and stream noise) | Sound carry ^c |
| Biotic | Other owl species detected (owl) | 0 = none, 1 = other owl detected | Owl behavior ^{f,g,i,k} |

^a Ganey (1990).

^b Hardy and Morrison (2000).

^c Kissling et al. (2010).

^d Clark and Anderson (1997).

^e Clarke (1983).

^f Crozier et al. (2005).

^g Crozier et al. (2006).

^h Fisher et al. (2004).

ⁱ Lourenço et al. (2013).

^j Morrell et al. (1991).

^k Olson et al. (2005).

^l Penteriani et al. (2010).

^m Wintle et al. (2005).

ⁿ O'Donnell (2004).

^o Pairs of strongly inter-correlated (Pearson's $r > 0.7$) covariates.

were co-detections (i.e., both species recorded during a survey), 159 (32%) were rufous-legged owls alone, and 201 (41%) were austral pygmy-owls alone. Rufous-legged owls were detected at 59 (62%) of 95 sampling units in 2011–2012 and 56 (55%) of 101 units in 2012–2013. Austral pygmy-owls were detected at 68 (72%) of 95 sampling units in 2011–2012 and 78 (77%) of 101 units in 2012–2013.

Occupancy and Detectability of Rufous-Legged Owls

We assessed 24 models for rufous-legged owls (Appendix S1, available online at www.onlinelibrary.wiley.com). Probabilities of occupancy for rufous-legged owls were positively associated with elevation and with sampling units located within 500 m of a protected area (Pa; Table 2, Fig. 2). Probability of occupancy varied among sampling units located either inside or outside protected areas (Pa = 1:

Table 2. Model selection results for estimating probability of occupancy (ψ) and detection (p) of rufous-legged owls and austral pygmy-owls in the temperate forests of Chile, 2011–2013. Sampling unit-specific covariates consisted of elevation in meters/1,000 (elev), and whether the sampling unit was 500 m within a protected area or not (Pa). Survey specific covariates consisted of moonlight (MI), environmental noise (noise), whether the other owl species was detected at the unit for the specific survey (owl), wind speed (wind), and number of days since start of surveys (day).

| Species | Model | K^a | ΔAIC^b | w_i^c |
|-------------------|--|-------|----------------|---------|
| Rufous-legged owl | $\psi(\text{elev} + \text{Pa}), p(\text{MI} + \text{noise} + \text{owl})$ | 9 | 0 | 0.58 |
| | $\psi(\text{elev}), p(\text{MI} + \text{noise} + \text{owl})$ | 8 | 1.43 | 0.28 |
| | $\psi(\text{Pa}), p(\text{MI} + \text{noise} + \text{owl})$ | 8 | 3.02 | 0.13 |
| Austral pygmy-owl | $\psi(\cdot), p(\text{wind} + \text{MI} + \text{noise} + \text{day}^2 + \text{owl})$ | 9 | 0 | 0.43 |
| | $\psi(\cdot), p(\text{MI} + \text{noise} + \text{day}^2 + \text{owl})$ | 8 | 0.88 | 0.28 |
| | $\psi(\cdot), p(\text{MI} + \text{noise} + \text{day} + \text{owl})$ | 8 | 2.69 | 0.11 |

^a Number of parameters estimated.

^b ΔAIC is the difference in AIC values between each model and the lowest AIC model.

^c AIC model weight.

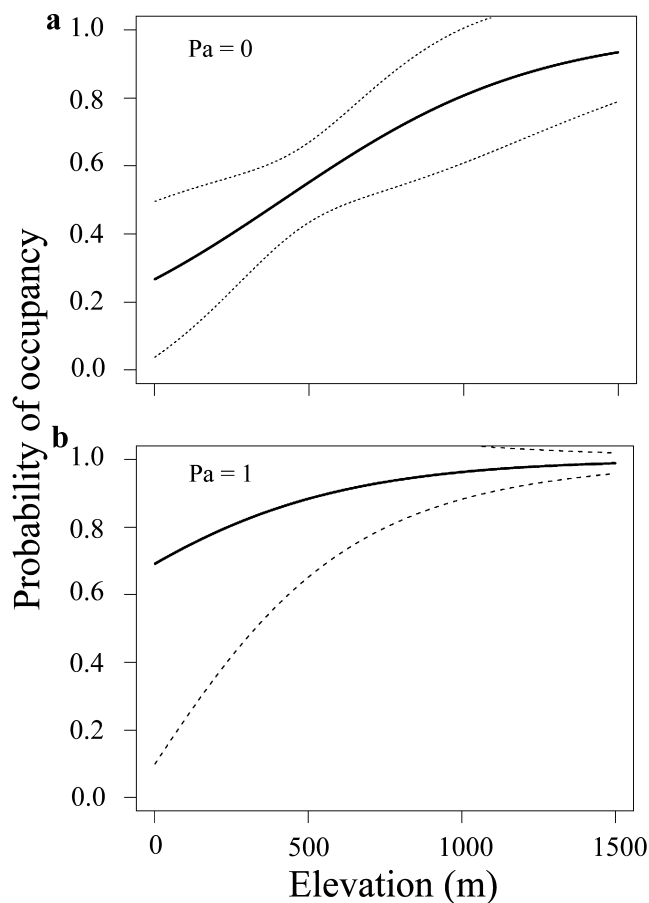


Figure 2. Predicted probabilities of occupancy (ψ) and 95% confidence intervals for rufous-legged owls in temperate forests of Chile (2011–2013), in relation to elevation (meters above sea level) when (a) $P_a = 0$ (sampling units located outside of a protected area) and when (b) $P_a = 1$ (sampling units located at least 500 m within a protected area), using the best model for this owl species.

$\psi = 0.69\text{--}0.99$, $P_a = 0$: $\psi = 0.27\text{--}0.93$). However, protected area status explained little variation given the 95% confidence intervals of the coefficient included 0 (Table 3). The best-approximating models indicated that the probability of detecting a rufous-legged owl increased with moonlight (i.e., brighter nights with waxing moon and little cloud) and was negatively associated with environmental noise (Table 3, Fig. 3). Furthermore, the detectability of rufous-legged owls increased when an austral pygmy-owl was detected at the same sampling unit during the same survey (Table 3). The detection probability ranged from 0.39 to 0.52 when an austral pygmy-owl was not detected; it increased to 0.52 to 0.65 when the latter owl was detected.

Occupancy and Detectability of Austral Pygmy-Owls

We assessed 20 models for austral pygmy-owls (Appendix S1, available online at www.onlinelibrary.wiley.com). Probabilities of occupancy were not associated with elevation and did not vary among sampling units located either inside or outside protected areas. In contrast, detectability increased with moonlight, decreased with both environmental noise and wind speed (Tables 2 and 3, Fig. 3), and increased

throughout the season from a minimum detectability ($p = 0.36 \pm 0.04$) at the beginning of the sampling season to a peak ($p = 0.47 \pm 0.08$) during the surveys from 23 January to 7 February (Fig. 3). Further, probability of detecting an austral pygmy-owl increased when a rufous-legged owl was detected at the same sampling unit during the same survey (Table 3). The probability of detecting an austral pygmy-owl ranged from 0.17 to 0.40 when a rufous-legged owl was not detected; it increased to 0.34 to 0.62 when the latter owl was detected.

DISCUSSION

We identified sources of variation associated with detection probabilities for the 2 most common owls in Andean temperate forests, and the patterns were similar between species; moonlight intensity increased and environmental noise decreased detectability of both rufous-legged and austral pygmy-owls, and the detection of both species was positively correlated with the detection of the other species. Although these 2 owl species have different broad habitat associations (Trejo et al. 2006, Ibarra et al. 2012), similarity in both nocturnal prey base and tree cavities used for nesting (Figueroa et al. 2006, Beaudoin and Ojeda 2011, Ibarra et al. 2014) may be potential causal mechanisms explaining similar patterns of calling activity, responses to covariates, and resultant probabilities of detection.

We used moonlight rather than moon phase per se to depict nocturnal illumination because it corrects ambient light estimates, derived from moon phase, and adjusts for the reducing effect of clouds on light intensity (Kissling et al. 2010). We found that owl calling rates were positively associated with clear nights as reported by Morrell et al. (1991) for great horned owls (*Bubo virginianus*) when cloud cover was less than 50%, but unlike saw-whet owls (*Aegolius acadicus*) whose calling rates increased when cloud cover was $>50\%$ (Clark and Anderson 1997). Likewise, some studies have reported either moon phase or moonlight were positively correlated with owl calling (Clarke 1983, Morrell et al. 1991, Clark and Anderson 1997, Kissling et al. 2010, Penteriani et al. 2010), but other studies have not (Ganey 1990, Hardy and Morrison 2000). The fact that brighter moonlight was positively correlated with detection rates for our study species suggests a general preference to be active during more illuminated nights. The efficiency of owl hunting may increase as moonlight waxes to full moon cycle, because predators need less time to capture prey (Clarke 1983). However, prey may reduce their activity in full moonlight as an anti-predatory response (Ylonen and Brown 2007). Little is known about nocturnal activity periods of owl prey in South American temperate forests. However, as most small-mammal prey (e.g., *Dromiciops gliroides*, *Irenomys tarsalis*, *Abrothrix olivaceus*, *Abrothrix longipilis*, *Oligoryzomys longicaudatus*) of the 2 owls we studied are chiefly nocturnal (Murúa 1995, Franco et al. 2011), we expect the amount of moonlight available during night-time to be a primary driver of owl and prey activity patterns in temperate forests.

Table 3. Competing models (Δ Akaike's Information Criterion ≤ 2.0) predicting probability of occupancy (ψ) and detection (p) of rufous-legged owls and austral pygmy-owls in temperate forests of Chile, 2011–2013. The estimated model coefficients and the lower and upper confidence intervals (LCI and UCI) are also shown.

| Species | Response | Variables | Coefficients | LCI | UCI | |
|-------------------|----------|-----------|-------------------|-----------|-----------|---------|
| Rufous-legged owl | Model 1 | ψ | Intercept | -1.012 | -2.182 | 0.159 |
| | | | Elevation | 2.441 | 0.190 | 4.692 |
| | | | Protected area | 1.818 | -0.498 | 4.134 |
| | | p | Intercept | -0.441 | -0.744 | -0.139 |
| | | | Moonlight | 0.006 | 0.0009 | 0.010 |
| | | | Noise | -0.508 | -0.837 | -0.180 |
| | | | Other owl | 0.513 | 0.178 | 0.848 |
| | Model 2 | ψ | Intercept | -1.276 | -2.379 | -0.172 |
| | | | Elevation | 3.285 | 1.251 | 5.319 |
| | | p | Intercept | -0.449 | -0.752 | -0.147 |
| Moonlight | | | 0.006 | 0.0009 | 0.010 | |
| Noise | | | -0.503 | -0.832 | -0.175 | |
| Austral pygmy-owl | Model 1 | ψ | Intercept | 1.415 | 0.772 | 2.058 |
| | | | p | Intercept | -1.04 | -1.350 |
| | | p | Wind | -0.46 | -0.873 | -0.046 |
| | | | Moonlight | 0.011 | 0.007 | 0.015 |
| | | | Noise | -0.579 | -0.885 | -0.273 |
| | | | Days ² | 0.00005 | -0.00001 | 0.00011 |
| | | | Other owl | 0.749 | 0.426 | 1.07 |
| | | | Model 2 | ψ | Intercept | 1.338 |
| | p | Intercept | -1.082 | | -1.374 | -0.790 |
| | | Moonlight | 0.112 | | 0.007 | 0.016 |
| Noise | | -0.604 | -0.909 | | -0.299 | |
| Days ² | | 0.00005 | -0.00002 | 0.0001 | | |
| | | Other owl | 0.870 | 0.540 | 1.190 | |

Environmental noise decreased detectability of both owls, and wind speed decreased pygmy-owl detection rates. Similar effects of both covariates were found for western-screech owls (*Megascops kennicottii*) and saw-whet owls in southeastern Alaska; detection rates for these species decreased by nearly 66% under considerable noise and also under moderate winds (< 3 km per hour; Kissling et al. 2010). Noise and wind speed can affect the range of vocal broadcasts, the capacity of researchers to detect responding owls, the rates of owls calling, or all of these (Morrell et al. 1991, Hardy and Morrison 2000). Because we systematically established sampling units 1.5 km apart, several were located near streams, rivers, and human habitation (where frequently dogs barked during our nocturnal surveys); the considerable noise produced by these factors reduced detectability for the 2 owls.

The peak period for detecting austral pygmy-owls was the end of the survey season in February when, according to the breeding phenology for the species, chicks had already fledged (Ibarra et al. 2014). Owls call more when they are territorial (e.g., they are searching for suitable sites for reproduction or have established pair bonds) and seldom vocalize when eggs are in the nest (e.g., long-eared [*Asio otus*], boreal [*Aegolius funereus*], and saw-whet owls; Clark and Anderson 1997). For example, Morrell et al. (1991) reported that great horned owls were more likely to respond earlier in the breeding season than later as a function of the chronology of the breeding activity. One explanation for our result is that adult austral pygmy-owls frequently emit territorial calls after fledging to

stimulate juveniles to disperse from their natal sites (Norambuena and Muñoz-Pedreros 2012).

The best-supported models for detectability of both species indicated that calling rates of each species was positively correlated with the other species although the effect was stronger for austral pygmy-owls. Previous studies have inferred that detection probabilities of spotted owls (*Strix occidentalis*) were lower at sites where the more aggressive barred owls (*Strix varia*) are undergoing expansion into spotted owl habitat (Olson et al. 2005, Crozier et al. 2006, Bailey et al. 2009). Furthermore, Lourenço et al. (2013) suggested that the detectability of tawny owls (*Strix aluco*) decreased at sites where eagle owls (*Bubo bubo*), their predators, were present. In contrast, the few studies that have reported higher calling rates in response to the calls of another owl species have been associated with mobbing behavior or inter-specific territoriality (Ganey 1990, Boal and Bibles 2001, Crozier et al. 2005). Our results did not support the hypotheses that either austral pygmy-owls constrain the calling rate of rufous-legged owls (Martínez 2005) or rufous-legged owls negatively influence calling by pygmy-owls because of predation risk. However, we explored only the association of interspecific calls on the probabilities of detecting the other owl species, not the spatial patterns of species co-occurrence. The latter may have been influenced by factors other than antagonistic behavior or intraguild predation, such as common environmental (e.g., habitat) choices (Brambilla et al. 2010).

We found that the occupancy rates of the forest specialist rufous-legged owl were positively associated with elevation.

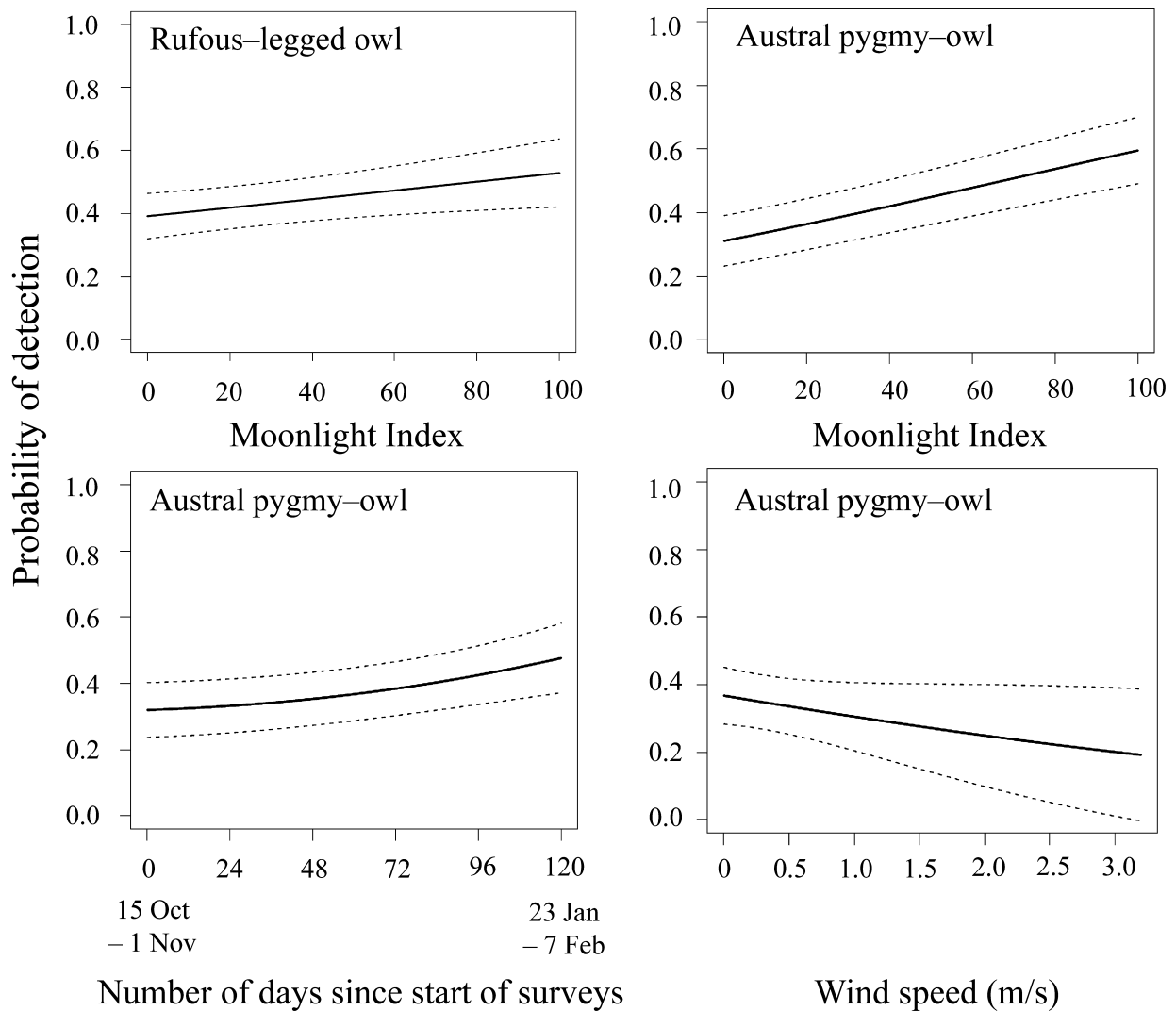


Figure 3. Predicted probabilities of detection (p) and 95% confidence intervals for rufous-legged owls and austral pygmy-owls in the temperate forests of Chile (2011–2013), in relation to moonlight index, number of days since start of surveys, and wind speed (m/s) using the best model for each species. Moonlight index refers to the amount of light available reduced by the proportion of sky obscured by clouds. $MI = (1 - \text{cloud cover}) \times \text{moon phase}/100$.

In our study area and in Chile generally, some of the last remaining continuous and structurally complex forests (e.g., stands maintaining a multi-storied vertical structure dominated by old shade-tolerant large trees with emergent pioneers) were restricted to high elevations in the Andes. At lower elevations, forests were mostly degraded and patchy (Armesto et al. 1998). The gradient of decreasing forest disturbance and increasing forest cover and complexity with higher elevation may have partially explained our results on the distribution and occupancy patterns of rufous-legged owls. Future occupancy studies and spatial assessments, incorporating detection probabilities into the analyses, need to include species-specific site and landscape-level covariates if they are available.

MANAGEMENT IMPLICATIONS

Developing efficient wildlife monitoring protocols is critical in regions subject to rapid habitat change such as South American temperate forests. For future owl monitoring

programs in this eco-region, we recommend broadcast surveys with a multi-species design. This has the advantage of being economically efficient as well as increasing detection rates of each species. To obtain reliable estimates of occupancy (i.e., $SE[\psi] \sim 0.05$) and allow modeling detection probabilities of owls in temperate forests, we recommend 3–4 surveys per season at a minimum number of 86 sampling units (MacKenzie and Royle 2005; J. T. Ibarra, University of British Columbia, unpublished data). We also recommend that survey designers avoid sampling noisy areas (e.g., human habitation with barking dogs, near streams and rivers) and conduct surveys under favorable weather conditions (e.g., low wind speeds <5 km per hour, relatively cloudless sky, no precipitation). In addition, observers should conduct surveys across several moon phases but record the moon phase for each survey (easily obtained from moon phase calendars available online). With data on cloud cover and moon phase, researchers will be able to calculate moonlight to depict illumination available for nocturnal owls and use this variable

to model detectability. These recommendations could be implemented in other areas of temperate forests where surveys for more than 1 species of owls are desirable.

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