Nest habitat selection by the Austral parakeet in north-western Patagonia

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Abstract   Identifying habitat or nesting microhabitat variables associated with high levels of nest success is important to understand nest site preferences and bird–habitat relationships. Little is known about cavity availability and nest site requirements of cavity nesters in southern hemisphere temperate forests, although nest site limitation is suggested. Here we ask which characteristics are selected by the Austral parakeet (*Enicognathus ferrugineus*) for nesting in *Araucaria araucana–Nothofagus pumilio* forest in Argentine Patagonia. We compared nest plot and tree characteristics with unused plots and trees among areas of different *A. araucana–N. pumilio* density. We also examine whether nest plot and tree use and selection, and the associated consequences for fitness of Austral parakeets are spatially related to forest composition. Austral parakeets showed selectivity for nests at different spatial scales, consistently choosing isolated live and large trees with particular nest features in a non-random way from available cavities. Mixed *A. araucana–N. pumilio* forests are ideal habitat for the Austral parakeets of northern Patagonia, offering numerous potential cavities, mainly in *N. pumilio*. We argue that Austral parakeet reproduction and fitness is currently very unlikely to be limited by cavity availability, although this situation may be rapidly changing. Natural and human disturbances are modifying south temperate forests with even-aged mid-successional stands replacing old growth forests. Cavity nesting species use and need old growth forests, due to the abundance of cavities in large trees and the abundance of larvae in old wood. Neither of the latter resources is sufficiently abundant in mid-successional forests, increasing the vulnerability and threatening the survival of the Austral.

Key words: *Araucaria araucana*, breeding, *Enicognathus ferrugineus*, nest site selection, *Nothofagus*.

INTRODUCTION

Nest-cavity selection may have important consequences for fitness, as cavity availability and distribution can influence life history traits in birds (Martin 1993; Martin *et al.* 2004; Aitken & Martin 2007). Secondary cavity nesters, by definition, depend on existing cavities as they cannot excavate them. Therefore, nest-site selection can be constrained by their intrinsic selectivity and nest requirements for specific cavity features, either provided naturally or through direct modification of existing cavities. Thus, cavity quality and availability are critical factors for secondary cavity nesters that directly influence their abundance (Newton 1994). Nest-site selection can also be constrained by features that have been previously selected by excavators (Aitken & Martin 2007). Although the origin of the cavities (natural or excavated) is something rarely registered in breeding biology studies, it may provide insight into nest site requirements of secondary cavity nesters and the importance of excavators

in forest communities. Furthermore, fitness may be affected by nest site characteristics and habitat structure around the nest, predator avoidance by concealment, and nest height or accessibility to predators (Martin 1995; Nalwanga *et al.* 2004; Chalfoun & Martin 2007). For most species, it remains unclear which essential resources are most limiting to populations. Identifying habitat or nesting microhabitat variables associated with high levels of nest success is important to understand the fitness consequences of nest site selection and to provide precise information for conservation plans.

Cavity abundance is a key factor for secondary cavity nesters and may vary depending on habitat structure (Newton 1994, 1998), the rate of cavity formation by natural decay and excavator selectivity and rates of cavity formation, minus cavity loss due to tree mortality and decomposition (Cockle *et al.* 2011a). Cavity availability will be determined by cavity abundance and the access to the cavity due to territorial or anti-predator behaviour (Cornelius *et al.* 2008). Forests with contrasting rates of cavity formation and availability will provide a heterogeneous habitat for secondary cavity nesters. Furthermore, cavity availability is directly affected by anthropogenic disturbances such as logging, which can reduce the

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abundance and availability of snags and large trees that bear the majority of cavities (Newton 1994) and thus can limit cavity-nester populations (Holt & Martin 1997; Newton 1998; Cornelius 2008; Cornelius *et al.* 2008). This has been recorded in cavity nester populations worldwide but with only a few studies in Neotropical forests (Cockle *et al.* 2010; Politi *et al.* 2010), and hardly at all in the south temperate forests of South America (Cornelius *et al.* 2008).

Studies about cavities as a limiting habitat factor are mainly from the northern hemisphere (Newton 1998), and while some studies suggest that cavities are not a limiting resource for most cavity-nesting birds (review in Wesolowski 2007), others find the opposite (see review in Newton 1994 and Cockle *et al.* 2011b). Little is known about cavity availability and nest-site requirements of cavity nesters in the Neotropics (Cornelius *et al.* 2008) with the recent exception of the Atlantic and the subtropical montane forest cavity nesters (see Politi *et al.* 2009, 2010 and Cockle *et al.* 2008, 2010, 2011b). Even less is known about south temperate forest species, although nest-site limitation is suggested (Tomasevic & Estades 2006; Cornelius 2008) and there is also some evidence of keystone tree species being important (Ojeda *et al.* 2007; Cornelius 2008).

The south temperate forest has a high proportion of endemic bird species (Armesto *et al.* 1996) and cavity nesters (Díaz *et al.* 2005). One of them is the Austral parakeet (*Enicognathus ferrugineus*), a secondary cavity nester that uses natural and excavated cavities for nesting (Forshaw 2010; Díaz in press). The Austral parakeet is abundant in the *Nothofagus pumilio* and *Araucaria araucana* forests which dominate the northern temperate forests of Chile and Argentina, where it is known to use cavities extensively during the breeding season (Forshaw 2010). *Nothofagus pumilio* and *A. araucaria* have distinctive characteristics important for cavity nesters, such as different rates of wood decay (Gonzalez *et al.* 2006; Ojeda 2006) and the absence of excavated cavities in *A. araucana* (Gonzalez *et al.* 2006; Díaz in press). Thus, mixed forests of these two species provide heterogeneous scenarios for cavity nesters, with less diversity and availability of cavities in *A. araucana*. Also, the specific characteristics of tree cavities and cavity selection for nesting in forests with *A. araucana* have not been studied before.

In this study, our objectives were to (i) describe for the first time nest cavity use by the Austral parakeet, (ii) determine the habitat characteristics that influence nest-site selection and nest reuse by the parakeets, and (iii) examine the influence of forest composition, tree species and cavity origin (natural or excavated) on the reproductive parameters of the Austral parakeet. We predicted that forests with *A. araucana* will contain fewer cavities than forests with *N. pumilio* due to intrinsic arboreal characteristics and the lack of exca-

vated cavities in *A. araucana*. Also, we expected the Austral parakeet to use cavities of different origin and from different species in relation to their availability.

METHODS

Study species

The Austral parakeet is a medium sized parakeet (38 cm, 180 g) endemic to western Patagonia in Chile and Argentina, with a distribution that ranges between 34°S and 54°S (Forshaw 2010). Austral parakeets depend on *A. araucana* seeds and pollen during their breeding season in mixed *N. Pumilio–A. araucana* forest of north-western Patagonia (Díaz & Kitzberger in press), but depend on *N. pumilio* pollen and seeds in monotypic forests (Díaz & Kitzberger 2006). In southern temperate forest, it is the last bird species to begin its breeding season, laying eggs only once a year synchronously throughout the population (Díaz *et al.*, unpubl. data, 2012). Laying occurs in mid December in the northern part of its distribution and in the first days of January in the south (Díaz & Kitzberger in press). They start cleaning and defending the cavity a few weeks before egg-laying begins. Austral parakeets make a bed in the rotten inner part of the nest cavity (Díaz in press) and they do not make a cup with branches or add extra material to the cavity, as suggested by Housse (1945).

Study area

We conducted this study in a temperate forest in north-western Argentine Patagonia (39°35′S, 71°25′W, 1050 m a.s. l.). The study area is a glacial valley of *A. araucana–N. pumilio* mixed forest, with an understorey of *Alstroemeria aurea* and *Ribes magellanicum*. The landscape has been shaped by fire events, mainly caused by lightning and volcanism, which have created a patchwork of stands of different ages.

The weather is characterized by marked seasons: dry summers (December to February) with average temperatures of 17–19°C, and intensive rain and snow periods between April and September with average temperatures of 7–8°C. Annual precipitation varies between 2000 and 3500 mm (Malalco meteorological station, Autoridad Interjurisdiccional de Cuencas).

The study area has a natural east–west gradient of tree composition. Three broad forest types were identified along this gradient according to tree species composition: pure *N. pumilio* forest (2.44 ha, hereafter LF), mixed *N. pumilio* and *A. araucana* forest (5.56 ha, with 15–40% of *A. araucana* trees in a *N. pumilio* matrix, hereafter MX) and forest dominated by *A. araucana* (4.01 ha, with 62–100% of *A. araucana* trees, hereafter PF). It was possible to distinguish between forest types with no error, as they were each separated by volcanic sand corridors of more than 200 m.

The two tree species present have distinctive characteristics important for cavity nesters. *Araucaria araucana* is a thick-barked conifer with low rot rates, high rates of fire and lightning scarring that eventually form natural cavities

(Gonzalez *et al*. 2006), and are highly resinous. South temperate forest woodpeckers (*Campephilus magellanicus*, *Picoides lignarius* or *Colaptes pitius*) avoid excavating live *A. araucana* trees and only rarely excavate in fire- or lightning-scarred trees (S. Díaz, pers. obs., 2010). On the other hand, *N. pumilio* has thin bark, a high rot rate, and little resin, thereby allowing frequent excavation by woodpeckers in live trees (Ojeda 2006).

Study design

Between 2007 and 2010 we located 54 nests and monitored them weekly during the breeding season (November–March). Nests were defined as cavities in which one or more nestlings reached the fledging stage. We measured characteristics of the nest plots, nest trees and nest cavities. Nest plots consisted of circular plots centred on the nest tree (12 m radius = 452.4 m^2, following Gibbons & Lindenmayer 2002). The total number of nest plots was 46 due to the lack of some measurements for 8 nests. We climbed the nest trees with ropes and aluminum ladders, and also used a wireless camera attached to a 12 m pole (home made non-commercial device) to measure each nest cavity and also to record breeding data. Nests were examined with a mirror and flashlight or by using the camera, to count the number of eggs or nestlings (between 1–4 min).

Control plots (with no nests) were the same size as nest plots, and were randomly located within each forest in numbers proportional to the total area of each forest type: 39 plots in LF, 89 plots in MX, and 64 plots in PF. All control plots were measured during the last breeding season of the study (2010) to ensure that these were sites that were not used by Austral parakeets during the study period. Cavity surveys were performed to count the number of potentially suitable cavities for Austral parakeet nesting. Based on a survey of 10 previously known successful nest cavities (observed since 2005) within our study area, we defined potentially suitable cavities by the following criteria: minimum entrance of 4 × 6 cm, but no bigger than 40 × 40 cm, minimum vertical depth of 10 cm, and minimum internal diameter of 15 cm. Cavity inspections were performed to corroborate that the minimum requirements were met, by climbing the trees, or by using a wireless camera attached to an extensible pole. The combination of these techniques limited the cavity inspection to those no higher than 15 m. In the case of very high or inaccessible cavities that could not be inspected with the camera, 4- to 6-h ground observations were made to determine their use (or lack thereof). In this way, we inspected all cavities in each control plot, recording 479 suitable cavities for the Austral parakeet.

In each control and nest plot we recorded the total number of trees by species, total number of *N. pumilio* and *A. araucana* trees with and without cavities (the latter was used only for habitat structure descriptions), the number of cavities per tree, and location (type of forest). For each nest and unused tree (not used for nesting but bearing cavities), we recorded diameter at breast height (DBH), species, location (type of forest), number of cavities, compass orientation of the cavity entrance (0–360°), cavity origin (natural: cracks and scars with uneven shape, or excavated: rounded or ellip-

tical shape or that researchers knew were created by an excavator, if in doubt then recorded as natural). In all trees within nest plots, we recorded also the percentage of dead canopy and the presence of *Misodendrum* spp. (*N. pumilio* hemi-parasite) as measures of tree decay. Only trees with DBH > 23 cm were measured, as this is the minimum required for nesting for this species (Díaz & Kitzberger in press). Each nest tree was climbed and for each nest cavity we recorded its forest type, tree species, nest height, nest tree height, tree diameter at the nest and breast height (1.4 m), height of the lowest branch of the tree, number of principal branches of the tree, origin of the cavity, presence of other entrances, cavity entrance width and height, compass orientation of the cavity entrance (0–360°), cavity depth and internal diameter. We did not measure cavity characteristics for unused cavities due to time constraints, which prevented an analysis of cavity selection.

To record nest reuse, nest inspections were performed in each subsequent year after they were found for 3 years. All nest cavities that were known to be used in previous years and all nests found during this study were inspected every year once in mid-October to determine if any other bird species was occupying the nest. Every 15 days from November to January Austral parakeet nesting attempts (eggs, nestlings, eggs shells or abandoned eggs) were monitored. Because new nests were found in each year, only nests with previous-year data were included in the re-use analysis (i.e. only second year nests were included in this analysis).

To test the consequences of nest selection on Austral parakeet fitness, clutch size and number of fledglings per nest were recorded over the three years of the study. There were no nest failures during the period of this study.

Data analysis

All variables were tested for normality using the Shapiro-Wilk test. We constructed simple correlation matrices to determine which independent variables measured in plots, trees or cavities were correlated with one another. To assess differences between nest cavity features, tree and plot variables, Mann–Whitney and Kruskal–Wallis with post hoc Dunn tests were performed while accounting for the origin of the cavity (natural or excavated), type of forest (LF, MX and PF) and nest tree species (*N. pumilio* or *A. araucana*).

We tested for habitat associations at the plot level using non-paired logistic regression, comparing differences between used (nests, $n = 46$) and unused (control plots with at least one cavity, $n = 154$). The predictive variables used in the model were: proportion of *N. pumilio*, proportion of *N. pumilio* and *A. araucana* with cavities, and proportion of snags. Other plot variables that were correlated with the above mentioned variables, were not used for modelling, including: mean diameter of *N. pumilio* and *A. araucana* bearing cavities ($r = 0.67$ and $r = 0.52$, correlated with the proportion of trees of the given species with cavities) and non-bearing cavities ($r = 0.55$ and $r = 0.98$ correlated with the proportion of trees of the given species).

Also, we tested for habitat associations at the tree level using conditional logistical regression. Case–control studies should be analysed using conditional logistic regression because the ratio of controls to cases in the sample is not the

same as the ratio of controls to cases in the population (Keating & Cherry 2004). For this analysis we compared differences between nest-trees ($n = 44$) and unused trees within the nest plots (with at least one cavity but not used as nests, $n = 44$). Our binary response variable was coded as either nest-used (1) or non-used (0), and the effect of explanatory variables was to increase or decrease the odds of a nest occurring. The variables tested for the model were: tree height, DBH, percentage of dead canopy, number of principal branches and presence of the parasitic *Misodendrum* sp.

We evaluated support for the candidate models with an information-theoretic approach (Burnham & Anderson 2002), by comparing Akaike's Information Criterion (AIC) corrected for small sample size (AIC_c) and Akaike weights (measure of the support for a given model relative to the other models in the set, Burnham & Anderson 2002). The AIC is composed of the model deviance and the number of estimated parameters and thus allows the ranking of different models according to the best compromise between precision and bias (Burnham & Anderson 2002). The candidate models were ranked according to their ΔAIC_c values (the difference in AIC_c value between each candidate model and the model with the lowest AIC_c value) to evaluate the strength of support for each model. We considered a model to be well supported by the data if it had an ΔAIC_c of <2 and an Akaike weight of >0.8.

We analysed cavity entrance orientation using Raleigh's test (z, Zar 1999) to evaluate whether nest and unused cavity entrances were randomly distributed with respect to azimuth angles.

To test if nest-site selection affected Austral parakeet fitness, we used Mann–Whitney tests when comparing reproductive parameters (clutch size and number of fledglings) between tree species and cavity origin, and Kruskal–Wallis tests with the post hoc Dunn test when comparing reproductive parameters between forests and years. We also tested for nest and fitness associations using non-paired logistic regression comparing cavities, trees and plots characteristics of reused and non-reused nests throughout the study period. Our binary response variable was coded as either reused (1) or non-reused (0). The variables tested for the cavity characteristics model were: nest height, cavity entrance width and height, type of cavity (natural or excavated), cavity location (main or secondary tree branches), internal diameter, depth, presence of other entrances to the nest cavity chamber, width of the nest wall (calculated by subtracting the internal diameter of the nest cavity from the diameter at nest height). The variables tested for the tree characteristics model were: tree species, height, lower canopy branch height, DBH, number of principal branches, percentage of dead canopy and presence of the parasitic *Misodendrum* sp. The variables tested for the plot characteristics model were: proportion of *N. pumilio*, DBH of *N. pumilio* bearing cavities, DBH of *A. araucana* bearing cavities, DBH of *N. pumilio* non-bearing cavities, proportion of *N. pumilio* with cavities, proportion of snags.

All statistical analyses were performed with R statistical software version 2.13.1. with function (clogit) for conditional logistic regression from the *survival* package to analyse Austral parakeet nest-plot selection, and with function (glm) for the analysis of nest tree selection and nest reuse (R Development Core Team, R Foundation for Statistical Computing, Vienna, Austria, http://www.R-project.org). Values are

reported as means $\pm$ SD, and tests of hypotheses were considered significant at $P < 0.05$.

RESULTS

Nest tree characteristics

A total of 54 different nest trees were identified over the course of the three breeding seasons. We found 39 nests cavities in living *N. pumilio*, 8 in dead *N. pumilio*, 7 in living *A. araucana* and none in dead *A. araucana*. Nests were placed mainly on the principal branches of the trees ($n = 47$), but the number of principal branches on nest trees did not vary significantly between forests (mean$_{LF}$ = 2.62 $\pm$ 1.4, mean$_{MX}$ = 2.1 $\pm$ 0.97 and mean$_{PF}$ = 1.81 $\pm$ 0.98) but did vary with cavity origin ($U = 9.331$, $P = 0.002$, mean$_{Nat}$ = 1.78 $\pm$ 1.12, median = 1, mean$_{Exc}$ = 2.62 $\pm$ 1.18, median = 2). Nest tree size (DBH) differed with tree species, with larger *A. araucana* trees than *N. pumilio* trees (Table 1), but did not vary between forest types (Kruskal–Wallis χ^2 = 4.761, d.f. = 2, $P = 0.092$). Similar to nest tree DBH, diameter at nest height was significantly greater for *A. araucana* than for *N. pumilio* (Table 1) but did not differ between forest types (Kruskal–Wallis χ^2 = 5.057, d.f. = 2, $P = 0.08$). Nest-tree DBH varied according to cavity origins, with natural nest-cavities in *N. pumilio* and *A. araucana* found on larger trees than excavated nest-cavities (only present in *N. pumilio*, Mann–Whitney $U = 3025$, $P < 0.001$). On the other hand, the diameter at nest height was significantly different between nest-trees bearing cavities of different origin ($U = 3020$, $P < 0.001$, mean$_{Nat}$ = 64.77 $\pm$ 31.71 cm, median = 54.3, mean$_{Exc}$ = 52.71 $\pm$ 13.82 cm, median = 52.25 cm). No statistically significant differences in DBH and diameter at nest height were found between natural or excavated nest-cavities for *N. pumilio* alone (Table 1).

Nest cavity characteristics

The internal diameter of nest cavities did not vary between tree species (Table 1), although the nest entrance dimensions of *N. pumilio* were larger than in *A. araucana* nests. Cavity internal dimensions differed according to cavity origin, with excavated nest-cavities being larger than natural nest-cavities (internal diameter: mean$_{Nat}$ = 26.46 $\pm$ 6.95, median = 28 and mean$_{Exc}$ = 30.43 $\pm$ 8.57, median = 28.65, $U = 3025$, $P < 0.001$; and cavity depth: mean$_{Nat}$ = 54.24 $\pm$ 47.62, median = 40, mean$_{Exc}$ = 41.29 $\pm$ 31.19, median = 31.5 cm, U_{Depth} = 3002, $P < 0.001$). However, these differences were not significant when comparing cavity internal dimensions by cavity origin for *N. pumilio* alone (Table 1). Finally, the wall width of the cavity

Table 1.   Austral parakeet nest and nest-tree characteristics

	Nothofagus pumilio (n = 47)	*Araucaria araucana* (n = 7)	Mann–Whitney	Natural (n = 16)	Excavated (n = 31)	Mann–Whitney
DBH (cm)	60.6 ± 16.4	113.7 ± 36.2	**U = 17, P < 0.001**	62.4 ± 19.2	59.8 ± 15.1	U = 271, P = 0.751
Diameter at nest height (cm)	52.8 ± 13.4	91.6 ± 45.3	**U = 60, P = 0.006**	53.0 ± 13.1	52.7 ± 13.8	U = 254.5, P = 0.965
Entrance width (cm)	6.6 ± 2.3	3.2 ± 2.4	**U = 294, P = 0.001**	6.9 ± 2.1	6.5 ± 2.4	U = 301, P = 0.330
Entrance height (cm)	10.8 ± 4.0	7.5 ± 5.7	**U = 217, P = 0.022**	9.6 ± 2.4	11.5 ± 4.6	U = 198, P = 0.208
Internal diameter (cm)	29.5 ± 8.3	23.7 ± 3.8	U = 241, P = 0.067	27.7 ± 7.8	30.4 ± 8.6	U = 218, P = 0.412
Depth (cm)	44.4 ± 35.2	62.8 ± 60.4	U = 148, P = 0.622	50.5 ± 42.7	41.3 ± 31.2	U = 219.5, P = 0.444
Wall (cm)	23.3 ± 13.1	67.9 ± 43.4	**U = 53, P = 0.003**	25.4 ± 15.9	22.3 ± 11.5	U = 273.5, P = 0.710

Number of nests is in parentheses. Also reported mean ± SD for each nest tree species. All nests in *A. araucana* were in natural cavities. Nests in *N. pumilio* are divided between natural and excavated. Significant results are shown in bold. *Wall* is showing the wall width of the cavities, calculated by subtracting the internal diameter from the diameter at nest height. DBH, diameter at breast height.

Table 2.   Characteristics of unused trees with suitable cavities for the Austral parakeet available in control plots

	Forest				
	LF (613 trees)	MX (2140 trees)		PF (615 trees)	
	Nothofagus pumilio	*N. pumilio*	*Araucaria araucana*	*N. pumilio*	*A. araucana*
Number of trees with cavities	71 (11.6%)	288 (13.5%)	5 (0.2%)	9 (1.5%)	5 (0.8%)
DBH (cm)	54.9 ± 17.7	45,1 ± 18.0	54,6 ± 29.0	50,4 ± 17.1	83,5 ± 24.8
Number of cavities per tree	1.2 ± 0.5	1.2 ± 0.5	1	1.1 ± 0.3	1.2 ± 0.4

The *number of trees with cavities* corresponds to the total number of trees with cavities in each respective type of forest, with the percentage it represents of the total number of trees present in that forest type in parentheses. Values are reported as mean ± SD for *DBH* (diameter at breast height) and *number of cavities per tree*. DBH, diameter at breast height; LF, pure *N. pumilio* forest; MX, mixed *N. pumilio* and *A. araucana* forest; PF, forest dominated by *A. araucana*.

(obtained by subtracting the internal diameter from the diameter at the nest height) only varied between tree species, not cavity origin, with nests in *A. araucana* having wider walls (Table 1).

Cavity availability and use

Cavity surveys were performed in 189 control plots and 3368 trees (2420 *N. pumilio* and 948 *A. araucana* trees). A total of 479 cavities potentially suitable for Austral parakeet nesting were found in 378 trees, indicating an average of 30 suitable cavities per hectare. Trees with cavities (Table 2) tended to have larger DBHs than the ones without cavities (mean$_{Arauc}$ = 59.79 ± 22.89 cm,   median = 42.25 cm,   n = 186, U = 35344, P < 0.001; mean$_{Noth}$ = 41.02 ± 14.95 cm, median = 36.8 cm,   n = 1017,   U = 1428025, P < 0.001). A notable difference in the percentage of suitable cavities in each forest and in each species was

found (Table 2). Clearly, *N. pumilio* is the more cavity rich species with an order of magnitude higher incidence of cavities. Thus in forest types where *N. pumilio* is present (LF and MF) 12% and 14% of *N. pumilio* trees provided cavities to Austral parakeets, respectively (Table 2), whereas *A. araucana* provided cavities in <1% of trees.

The number of cavities per tree was notably constant among forests (Table 2). Only 25.6% of the potential cavities found were excavated cavities, mainly by *Campephilus magellanicus*, and these were almost all on *N. pumilio*. Natural cavities represented 62% of the cavities in LF, 79% in MX and 57% in PF. Almost all natural cavities were located on the main bole of trees, broken branch nodes and crevices in the main bole or principal branches of the trees.

Within nest plots there were significant associations between cavity origin (natural or excavated) and occupancy of cavities (U = 28.94, P < 0.001). Although natural cavities were 3 times more abundant than
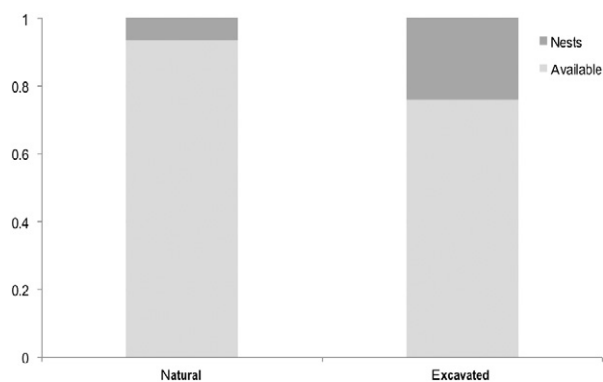
Fig. 1. Proportion of cavities by origin used as nest by the Austral parakeet in a mixed *Nothofagus pumilio* and *Araucaria araucana* forest in north-western Argentine Patagonia. Only 7.1% ($n = 23$) of natural cavities ($n = 326$) and the 30.6% ($n = 31$) of excavated cavities ($n = 101$) were used for nesting.

excavated cavities (326 and 101 respectively), only 23 (about 7.1%) were used for nesting (Fig. 1). In contrast, 31 woodpecker-excavated cavities (about 30.6%) were used for nesting by Austral parakeets (Fig. 1). Nest occupancy was dependent on azimuth orientation of entrance. Austral parakeet nest cavity entrances had non-random compass orientation (Raleigh's test $z = 3.1$, $n = 54$, $P < 0.05$), with most nests ($n = 42$) in non-west-facing cavities. Unused cavities had a non-random compass orientation (Raleigh's test $z = 4.6$, $n = 330$, $P < 0.05$), with most unused natural cavities mainly oriented to the north ($n = 122$) and unused excavated cavities mainly oriented to the north and west ($n = 30$ and 34 respectively).

Unused trees

Trees bearing cavities not used for nesting (unused trees) showed clear differences between nest plots and control plots. Unused trees in nest plots were larger than in control plots (Mann–Whitney, $U = 569535$, $P < 0.001$, $DBH_{nest-plot}$: 48.86 ± 16.1 cm, median = 45, $n = 482$ *vs.* $DBH_{control-plot}$: 42.36 ± 19.6 cm, median = 37.5, $n = 2886$). Differences in size also held true when considering tree species, with larger unused *A. araucana* ($U = 21408$, $P < 0.001$) and *N. pumilio* ($U = 331435.5$, $P < 0.001$) in nest plots (DBH_{Arauc}: 58.01 ± 23.79 cm and DBH_{Noth}: 47.50 ± 14.18 cm) than in control plots (DBH_{Arauc}: 47.68 ± 26.72 cm and DBH_{Noth}: 40.27 ± 14.49). Finally, for both nest and control plots, there was no difference in average tree size between forest types (nest plot trees: Kruskal–Wallis $\chi^2 = 1.81$, d.f. = 2, $P = 0.405$, control plot trees $\chi^2 = 4.731$, d.f. = 2, $P = 0.094$).

Model results: tree and plot -level nest selection

Nest-site selection at the plot level was explained by a low proportion of *N. pumilio* and snags and a low proportion of trees of both species bearing cavities ($w_i = 0.66$, Table 3), with limited support for the model including the variable 'Proportion of *A. araucana*' ($w_i = 0.22$, Table 3), highlighting that *A. araucaria* are not important for the Austral parakeets when selecting nest-sites. Nest-tree selection was explained by tree size and shape (short trees with large DBH and few principal branches), and also by tree decay status (low percentage of dead canopy and absence of parasitic *Misodendrum* spp., Table 3), although the performance of the models was weak ($w_i \leq 0.21$, Table 4).

Reproduction

Nest reuse was observed in 26% of the nest cavities (14 of 54). Twelve nests were reused twice and two reused in each of the 3 years of the study period. Nests tended to be reused if extra entrances to the cavity chamber were present, were excavated rather than natural and had wide walls, although the performance of the models was weak (Table 5). The tree species also weakly explained nest reuse (Table 5). *N. pumilio* nest trees with a high percentage of dead canopy and number of principal branches were more reused (Table 5). Finally, nests in plots with low numbers of *N. pumilio* bearing cavities, weakly explained nest reuse (Table 5).

Both reproductive parameters varied between nest tree species (Mann–Whitney, $U_{clutch\ size} = 2304$, $U_{fledglings} = 2204$, $P < 0.001$ for both), with higher values in *N. pumilio* nests ($n = 41$, 6.4 ± 1.7 for clutch size, 4.1 ± 2.0 for the number of fledglings) than in *A. araucana* nests ($n = 7$, 5.4 ± 1.9 for clutch size, 2.7 ± 1.7 for the number of fledglings). All recorded nests on *A. araucana* were located in PF. No differences were found in the reproductive parameters when analysed among forest (Kruskal–Wallis, $P > 0.05$ for both), although clutch size tended to be lower in PF (5.9 ± 2.3, $n = 11$) and higher in LF (6.3 ± 1.5, $n = 27$), and the number of fledglings recorded for MX (4.3 ± 2.3, $n = 10$) was higher when compared with LF (3.8 ± 1.7) and PF (3.9 ± 2.5). Also, nests in natural cavities ($n = 35$) had larger values of both reproductive parameters (clutch size = 6.5 ± 1.7, fledglings = 4.9 ± 1.9) than excavated cavities ($n = 13$, clutch size = 5.5 ± 1.6, fledglings = 3.5 ± 1.8, $U_{clutch\ size} = 2304$, $U_{fledglings} = 2201$, $P < 0.001$ for both). Finally, both reproductive parameters varied among years (Table 6). Clutch size and the number of fledglings in 2010 were notably lower than 2008 and 2009, with a more marked difference for the number of fledglings.

Table 3. Ranking of logistic regression models of plot selection by the Austral parakeet supported by Akaike's Information Criterion corrected for small sample size (AICc) (n = 200) in Lanin National Park, north-western Argentine Patagonia

Models	k	ΔAICc★	w_i	Model likelihood
Prop.*Noth* + Prop.*Noth*withC + Prop.*Arauc*withC + Prop.snags	**5**	**0**	**0.66**	**1.00**
Prop.*Noth* + Prop.*Noth*withC + Prop.snags	4	2.19	0.22	0.33
Prop.*Noth* + Prop.*Noth*withC + Prop.*Arauc*withC	4	3.39	0.12	0.18

Models predict presence/absence of nests at the plot level and are arranged according to fit, from highest to lowest weighted with top model in bold. Prop.*Noth* = proportion of *N. pumilio* in each plot; Prop*Noth*withC = proportion of *N. pumilio* bearing suitable cavities; Prop.*Arauc*withC = proportion of *A. araucana* bearing suitable cavities; Prop.snags = proportion of snags in each plot; ΔAICc = difference in AICc between this model and the model with the lowest AICc; w_i = Akaike weight. The model likelihood indicates the support of the model, given the data (★The AICc for the top model was 126.95).

Table 4. Ranking of paired logistic regression models of tree selection by the Austral parakeet supported by Akaike's Information Criterion corrected for small sample size (AICc) in Lanin National Park, north-western Argentine Patagonia

Models	k	ΔAICc★	w_i	Model likelihhod
Height + DBH + dead canopy + principal branches + *Misodendrum*	**6**	**0.00**	**0.21**	**1.00**
Height + DBH + principal branches + *Misodendrum*	5	0.02	0.21	0.99
DBH + dead canopy + principal branches + *Misodendrum*	5	0.32	0.18	0.85
DBH + principal branches + *Misodendrum*	4	0.35	0.18	0.84
Height + DBH + dead canopy + principal branches	5	1.22	0.12	0.54
Height + DBH + principal branches	4	1.22	0.12	0.54
DBH + principal branches + dead canopy	4	1.42	0.10	0.49

Models predict presence/absence of nests at the tree level and are arranged according to fit, from highest to lowest weighted with top model in bold. Height, DBH = measures of height and DBH of individual trees, dead canopy = % of dead canopy of each tree, principal branches = number of principal branches, *Misodendrum* = presence of the hemiparasite *Misodendrum* sp, ΔAICc = difference in AICc between this model and the minimun AICc model, w_i = Akaike weight. The model likelihood indicates the support of the model, given the data (★The AICc for the top model was 50.99).

None of the characteristics associated with each individual nest at the nest-, tree- or plot-level varied significantly between years (Kruskall–Wallis, $P > 0.05$ for all).

DISCUSSION

Austral parakeets showed selectivity for nest-sites at different spatial scales, consistently choosing particular nest-site characteristics in a non-random way from the ones available. Nests were located in plots with low numbers of extra suitable cavities nearby, and a low density of *N. pumilio* trees and snags. Nest trees were larger than surrounding trees in the nest plot, despite their relative scarcity, and trees within nest plots were larger than the trees available in random plots in the forests. Selection of these 'islands' in the forest is consistent with nest-site selection by other parrots, which also have been shown to prefer large isolated trees for nesting (Brightsmith & Bravo 2006; Renton & Brightsmith 2009). Tree size is important in these forest types, as described for another austral temperate forest cavity nester, the thorn-tailed rayadito (*Aphrastura spinicauda*, Cornelius 2008), which prefers to nest in large *Nothofagus nitida* snags in higher proportion

than their availability. The Austral parakeet, however, used a low number of snags for nesting, although snags have been reported to be commonly used by other psittacids for nesting (see review in Goldingay 2009 for Australian species, Renton & Brightsmith 2009 for several species of macaws). The low preference for snags by Austral parakeets is due to the low availability of suitable snags in the studied forest, consistent with surveys done in *Nothofagus* forests in New Zealand (Blakely *et al.* 2008).

The preference of secondary cavity nesters for large *N. pumilio* trees is likely due to the fact that larger trees are older (*N. pumilio* can live more than 350 years, Ojeda *et al.* 2007, see also Díaz *et al.* 2005) and are therefore more likely to exhibit decay and partial crown dieback (Ojeda *et al.* 2007) or defects due to other natural processes (e.g. fungal decay, branch breakage and insects attacks). Natural cavities used for nesting were in large trees, and commensurate with the findings of Goodall *et al.* (1946), Díaz *et al.* (2005) and Peña-Foxon *et al.* (2011) for its congeneric *E. leptorhynchus*, which was almost exclusively founded in old growth forest. However, natural cavities are the only nesting and refuge sites available in *A. araucana* trees, highlighting the critical conservation value of

Table 5. Ranking of logistic regression models evaluating the effects of nest cavity ($n = 54$), nest tree and nest plot ($n = 46$ for both) characteristics on Austral parakeet re-nesting behaviour in north-western Argentine Patagonia, only showing models that explained the data

Level of analysis	models	k	$\Delta AIC_c\star$	w_i	Model likelihood
Cavity	(★AIC_c of the top model = 61.84).				
	otherEntr	**2**	**0**	**0.29**	**1.00**
	TypeC. + otherEntr + wall	4	0.46	0.23	0.80
	otherEntr + wall	3	0.69	0.20	0.71
	otherEntr + wall + Nest Height	4	1.38	0.14	0.50
	TypeC. + otherEntr + wall + Nest Height	5	1.39	0.14	0.50
Tree	(★AIC_c of the top model = 55.39).				
	species + dead canopy	**3**	**0**	**0.44**	**1.00**
	species + dead canopy + principal branches	4	0.42	0.35	0.81
Plot	(★AIC_c of the top model = 67.19).				
	DBH*Noth*withC	**2**	**0**	**0.34**	**1.00**
	DBH*Noth*withC + DBH*Noth*w-outC	3	0.41	0.14	0.41
	DBH*Noth*withC +Prop.*Noth*withC	3	0.40	0.14	0.40
	DBH*Noth*w-outC	2	0.40	0.13	0.40
	Prop.*Noth*withC	2	0.39	0.13	0.39
	DBH*Arauc*withC	2	0.37	0.12	0.38

Models compare reused and not-reused nests during the study period, and are arranged according to fit from highest to lowest weighted, with the top models in bold. Cavity characteristics: otherEntr = other entrances to the nest-cavity chamber, TypeC. = type of cavity: natural or excavated, wall = width of the nest cavity (subtraction of the internal diameter of the cavity from the diameter at nest height), *Nest Height*. Tree characteristics: species = tree species, dead canopy = percentage of dead canopy, principal branches = number of principal branches. Plot characteristics: DBH*Noth*withC = DBH of *N. pumilio* bearing suitable cavities, DBH*Noth*w-outC = DBH of *N. pumilio* not bearing suitable cavities, Prop.*Noth*withC = proportion of *N. pumilio* bearing suitable cavities, DBH*Arauc*withC = DBH of *A. araucana* bearing suitable cavities. For all models: top model parameters estimated value, k = number of parameters, ΔAIC_c = difference in AIC_c between this model and the minimun AIC_c model, w_i = Akaike weight. The model likelihood indicates the support of the model, given the data. AIC_c, Akaike's Information Criterion corrected for small sample size.

Table 6. Austral parakeets reproductive parameters between years, with their corresponding mean ± SD and range (between parenthesis), and the Kruskal–Wallis and Dunn post hoc test values

	2008	2009	2010	Kruskal–Wallis	Dunn post hoc
Number of nests (nests in *N. pumilio*)	12 (11)	20 (18)	16 (12)		
Mean clutch size	6.6 ± 0.7 (6–8)	7.5 ± 1.4 (6–10)	4.4 ± 0.7 (3–6)	$\chi^2 = 33.21$, $P < 0.001$	8–9: Z = −1.977, P = 0.048 8–10: Z = 4.422, P < 0.001 9–10: Z = 5.154, P < 0.001
Mean number of fledglings	4.3 ± 1.3 (3–7)	6.0 ± 1.5 (4–9)	2.7 ± 1.2 (1–4)	$\chi^2 = 29.25$, $P < 0.001$	8–9: Z = −2.869, P = 0.004 8–10: Z = 2.971, P = 0.003 9–10: Z = 5.042, P < 0.001

large *A. araucana* individuals to Austral parakeets. This suggests that Austral parakeets, in the absence of excavators, use primarily old growth or mature forest patches. Additionally, *A. araucana* nests were located in *N. pumilio*-dominated patches, suggesting the importance of *N. pumilio* patches in *A. araucana* forest as nesting sites and the high habitat value of mixed, rather than monospecific forests.

The high abundance of potential suitable cavities available recorded in this study suggests that reproduction by Austral parakeets is not constrained by cavity availability, although the amount of suitable cavities (30 per hectare) may have been overestimated since detailed measurement of their characteristics were not made. Cavity availability as a constraint for cavity nesters has been previously suggested by other studies (Díaz *et al*. 2005; Cornelius *et al*. 2008; Ojeda 2009) from different Austral temperate forest locations in Argentina and Chile. The cavity density estimated in this study is similar to those for old growth forests in other regions of the world (Newton 1998), and much lower than in subtropical montane and the Neotropi-

cal Atlantic forests (Cockle *et al.* 2010; Politi *et al.* 2010). In our study area, *N. pumilio* trees bear most of the cavities, with a mean value of 1.2 cavities per tree > 23 cm DBH. This is lower than those reported for other species of *Nothofagus* in New Zealand (range 17.3–0.3, Blakely *et al.* 2008). This difference cannot be explained by the origin of the cavities as there are no excavators in New Zealand and the proportion of excavated cavities in this study was low, so cavity availability presumably can only be explained by species-specific decay rates. But, excavated cavities were used more than natural cavities with respect to their availability. This pattern was also recorded for parrots from the Brazilian Atlantic forest (Guix *et al.* 1999). In contrast, parrots in the Argentine Atlantic forest (Cockle *et al.* 2008, 2011b) and secondary cavity nesters in Canada (Aitken & Martin 2007) used excavated cavities in proportion to their availability, while secondary cavity nesters from Asia (Bai *et al.* 2005) and Europe (Remm *et al.* 2006; Wesolowski 2007) avoided excavated cavities. Characteristics of natural and excavated cavities measured in this study were not different within *N. pumilio*, although a sharp difference was found when comparing cavities from both arboreal species. This suggests that differences in cavity characteristics are due more to tree species than cavity origin. Additionally, *A. araucaria* cavities were rare and scattered, suggesting that this nesting resource should be treated as a separate and distinct unit in conservation plans, while *N. pumilio* cavities can be pooled without distinction of their origin.

Patterns of cavity orientation showed a clear avoidance of west-facing aspects, thereby avoiding direct exposure to the dominant winds and storms from the Andes. Also, cavity wall width was one of the nest-cavity features related to nest reuse, suggesting a selection of cavities with better insulation characteristics. This suggests a clear selection of nesting cavities that maintain uniform temperatures in the nests during the breeding season. Similar results have been observed in other psittacids (Saunders *et al.* 1982; Rodriguez Castillo & Eberhard 2006), which also selected for particular nest orientations.

Cavity characteristics have been associated with reuse for many species of cavity nesters (Aitken *et al.* 2002; Aitken & Martin 2004). However, reuse of cavities by Austral parakeets was only weakly explained by the data, although models suggested that isolated *N. pumilio* nest-trees with greater decay, and particular cavity features were more frequently reused. Despite the low reuse of cavities (26%), those which were reused were consistently the same nests. Low rates of cavity reuse may be due to behavioural avoidance of ectoparasites from the cavity acquired through previous use, or a high probability of predation (Renton & Salinas-Melgoza 1999; Berkunsky & Reboreda 2009). High rates of cavity reuse have been considered an indirect signal of low cavity availability (Aitken & Martin 2004) evidenced by competition for cavities (Snyder *et al.* 1987; Prestes *et al.* 1997; Heinsohn *et al.* 2003). Similarly, a few studies found that high rates of nest-site fidelity were associated with high rates of cavity reoccupation (Snyder *et al.* 1987; Waltman & Beissinger 1992). This may explain the consistency of nest reuse over the years by the Austral parakeet, with a reasonable probability of it being the same pair.

Reproductive parameters varied between nest-tree species, with *N. pumilio* nests recording higher reproductive values than nests in *A. araucana*. This should be interpreted cautiously, however, due to the low sample size of nests in *A. araucana*. Also, nests in natural and excavated cavities had different reproductive values with higher values for nests in natural cavities, despite the greater use of excavated cavities in relation to their availability. This suggests that cavity site features selected by excavators are not optimal for the Austral parakeet. Finally, higher reproductive values in 2009 and lower values in 2010 may be explained by factors other than cavity or nest-site characteristics, since they did not exhibit variation between years, indicating a constant temporal selection of nesting sites by the Austral parakeet. Possible explanations may be differential food availability between years that cause strong differences in reproduction, although further studies are needed to assess this observation.

Conservation

The south temperate forest, distributed between 35°S and 56°S, has been modified and reduced in size by different causes over time, such as natural and anthropogenic fire (used for hunting and forest clearing for agro-industry), logging and exotic species introduction (Armesto *et al.* 1994; Veblen *et al.* 1999). Logging and fire diminishes the extent of old growth forests, replacing them with mid-successional forest. Mid-successional forests have the lowest proportion of use by south temperate bird species despite their proximity to old-growth forests (Díaz *et al.* 2005), due to the absence of old growth structural elements that are important habitat features for these birds (Armesto *et al.* 1996; Willson & Armesto 1996; Aravena *et al.* 2002). Current trends of mid-successional replacement of old growth forest diminish the expectations for regional persistence of birds that depend on old growth features (e.g. Goodall *et al.* 1946; Willson *et al.* 1994; McPherson 1999; Sieving *et al.* 2000; Reid *et al.* 2004).

Our results suggest that *N. pumilio* provides important nesting habitat for the Austral parakeets of northern Patagonia by offering high availability of trees with cavities, especially as scattered patches within forests

dominated by *A. araucana*. Other timber and fire-susceptible *Nothofagus* species distributed across western Patagonia have also been shown to have a high proportion of cavities (Díaz *et al.* 2005; Cornelius 2008). *Nothofagus pumilio* has also been shown to be an important source of food for the Austral parakeet (Díaz & Kitzberger 2006). While *A. araucana* is currently protected under several laws (Gonzalez *et al.* 2006), thus protecting also the fauna associated with it, *N. pumilio* and other *Nothofagus* are regularly logged for timber, handcraft and lumber, with weak regulations and control. This study shows the importance of *N. pumilio* patches in *A. araucana* forests, which should clearly be considered in forest management decisions. Endemic south temperate forest cavity nesters (Armesto *et al.* 1996) may be under serious conservation risk if even-aged stands continue to replace old growth forests. These findings provide a meaningful framework for the formulation of forestry regulations that may affect Patagonian cavity nesters.

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