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Intersexual segregation in foraging microhabitat use by Magellanic Woodpeckers (*Campephilus magellanicus*): Seasonal and habitat effects at the world's southernmost forests

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Abstract Animals facing seasonal food shortage and habitat degradation may adjust their foraging behaviour to reduce intraspecific competition. In the harsh environment of the world's southernmost forests in the Magellanic sub-Antarctic ecoregion in Chile, we studied intersexual foraging differences in the largest South American woodpecker species, the Magellanic Woodpecker (*Campephilus magellanicus*). We assessed whether niche overlap between males and females decrease when food resources are less abundant or accessible, that is, during winter and in secondary forests, compared to summer and in old-growth forests, respectively. We analysed 421 foraging microhabitat observations from six males and six females during 2011 and 2012. As predicted, the amount of niche overlap between males and females decreased during winter, when provisioning is more difficult. During winter, males and females (i) used trees with different diameter at breast height (DBH); (ii) fed in trunk sections with different diameters; and (iii) fed at different heights on tree trunks or branches. Vertical niche partitioning between sexes was found in both old-growth and secondary forests. Such a niche partitioning during winter may be a seasonal strategy to avoid competition between sexes when prey resources are less abundant or accessible. Our results suggest that the conservation of this forest specialist, dimorphic and charismatic woodpecker species requires considering differences in habitat use between males and females.

Key words: *Campephilus magellanicus*, foraging strategy, intersexual niche overlap, resource partitioning, sub-Antarctic forests.

INTRODUCTION

Intersexual foraging differences leading to intraspecific niche partitioning are widespread among vertebrates (Selander 1966; Catry *et al.* 2006; Ruckstuhl 2007), with these differences arising from distinct abilities of both sexes to compete for food, food preferences and nutritive needs (Catry *et al.* 2006; Ruckstuhl 2007). Resource partitioning between sexes occurs at varying spatial scales, ranging from broad geographical partitioning (e.g. Giant Petrel, *Macronectes* spp., González Solís *et al.* 2000) to microhabitat differences (e.g. New Guinean whistlers *Pachycephala* spp., Freeman 2014). Morphological and behavioural differences between sexes contribute to foraging niche partitioning, thus reducing intraspecific competition under resource limitations (Selander 1966; Slatkin 1984; Osiejuk 1994; Hogstad 2010).

Foraging niche partitioning between sexes has been reported for some woodpecker species from the northern hemisphere, such as the White-backed Woodpecker (*Dendrocopos leucotos*; Aulèn & Lundberg 1991) and the Eurasian three-toed Woodpecker (*Picoides tridactylus alpinus*; Pechacek 2006). In these woodpecker species, male and females exhibit differences in foraging behaviours and in their use of microhabitat substrates, with male woodpeckers tending to be larger and dominant, relegating females to low-quality habitats or microhabitats (e.g., Kilham 1970; Hogstad 1978; Osiejuk 1994; Pasinelli 2000; Pechacek 2006). The beneficial role of sexual niche partitioning for foraging efficiency and reproductive success becomes more evident as the amount of food available within territories decreases (Wilson 1975;

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Austin 1976; Przybylo & Merilä 2000). Indeed, foraging partitioning may improve the rate of food acquisition for diet-specialist species like woodpeckers, for which the amount of available food (e.g., saproxylic invertebrates) is influenced by changing environmental conditions (e.g., seasonal climate, human disturbances, wildfires). Therefore, to investigate the effects of differential environmental conditions on sexual niche partitioning has a potential use on the planning for sustainable forest management.

The Magellanic Woodpecker (*Campephilus magellanicus*) is the largest woodpecker species in South America (~36–38 cm body length, 276–363 g weight, Short 1982) and endemic to the temperate and sub-Antarctic forests of southwestern South America from 35 to 56°S (Short 1970, Rozzi & Jiménez 2014). This species lives in family groups of 2–5 members composed of a breeding pair and offspring from previous years. In old-growth forests, woodpecker territories average between 40 and 60 ha, depending on season, and sometimes shift spatially among years (Ojeda & Chazarreta 2014). The breeding season lasts for ~65 days, between mid- to late-spring and early- to mid-summer (Ojeda 2004). Parents share duties in nest excavation, incubation, and chick rearing. Offspring stay with parents for up to 4 years (Chazarreta *et al.* 2011). Even though the Magellanic Woodpecker is often described as a forest specialist feeding mostly on large wood-boring larvae that are extracted by drilling live or dead tree trunks and branches (Ojeda & Chazarreta 2014), they have been reported to feed on alternative food sources, such as terrestrial coleoptera and hymenoptera, sap flowing from trees, small fruits and flowers, and even vertebrates like lizards and passerine chicks (McBride 2000; Ojeda 2003; Schattler & Vergara 2005).

The Magellanic Woodpecker exhibits sexual dimorphism, with females having a bill 12% shorter and body weight 16% lighter than males (276–312 g, mean = 291.3 g, $n = 6$ *vs.* 312–363 g, mean = 338.4 g, $n = 7$, respectively; Short 1982; Chazarreta *et al.* 2012). Strong sexual dimorphism in plumage colour also occurs: males have a scarlet-red head and a short-straight crest, whereas females have a black head with red feathers at the base of the bill and a long forward-curled crest. Sexual differences in bill length are associated with differences in foraging behaviour and prey characteristics. Chazarreta *et al.* (2012) reported that male woodpeckers tend to forage on larger substrates (i.e., on the main boles of the foraging trees) and at intermediate heights from the ground (5–10 m), whereas females forage higher towards the crown (>15 m) and on smaller substrates, such as branches. These sexual differences in foraging behaviour and microhabitat substrates result in males capturing, eating and provisioning young with larger larvae of wood-boring insects than females (Ojeda 2004; Lizama *et al.* 2013).

Here, we assessed intersexual foraging differences in Magellanic Woodpeckers inhabiting the world's southernmost forests on Navarino Island, in the Cape Horn Biosphere Reserve, Chile (Fig. 1; Rozzi & Jiménez 2014). The climatic conditions of these sub-Antarctic forests, along with a recent history of human disturbance during the 20th century, lead to a marked variability in spatial and seasonal resource availability and habitat quality for bird species (Vergara & Schlatter 2006; Soto *et al.* 2017). The Magellanic Woodpecker is a year round resident, and a charismatic species sensitive to fragmentation and loss of old-growth forest (McBride 2000; Arango *et al.* 2007; Soto *et al.* 2012; IUCN 2016). Habitat heterogeneity resulting from seasonal climatic variability and anthropogenic habitat transformations may affect foraging behaviour and space use of this species, but the strength of these effects may differ between males and females (e.g., see Vergara & Schlatter 2004; Schattler & Vergara 2005; Soto *et al.* 2012). In order to answer the question of how both sexes differ on their foraging niche given seasonal and environmental changes on resource availability, we tested the following two predictions:

First, we predicted that foraging partitioning between males and females of Magellanic Woodpecker will be greater during winter than in summer. During the austral winter, Magellanic Woodpeckers may be exposed to food shortages in sub-Antarctic forests due to the scarcity of prey other than wood-boring larvae, such as adult insects and mature fruits (Ojeda 2003; Ojeda & Chazarreta 2006). Our recent findings indicate that Magellanic Woodpeckers enlarge their territories from 0.89 km^2 in the summer to 1.03 km^2 in the winter (15% increase, $n = 6$ and 11, respectively), likely resulting from lower levels of territorial behaviour and scarcity of resources.

Second, we predicted that foraging partitioning between male and females will be greater in secondary forest than in old-growth forest. Logging and burning of forests by European and Chilean settlers on Navarino Island during the 20th century have reduced the extent of old-growth forest and generated a mosaic of habitat patches of varying foraging quality (Rozzi *et al.* 2006; Soto *et al.* 2017; Fig. 1). In general, trees in secondary forests have a less advanced stage of decay and a lower abundance of large wood-boring insects than in old-growth forest (see Vergara *et al.* 2017).

MATERIALS AND METHODS

Study area

We conducted this study in the Omora Ethnobotanical Park (54°57′S, 67°39′W), located on the northern slope of

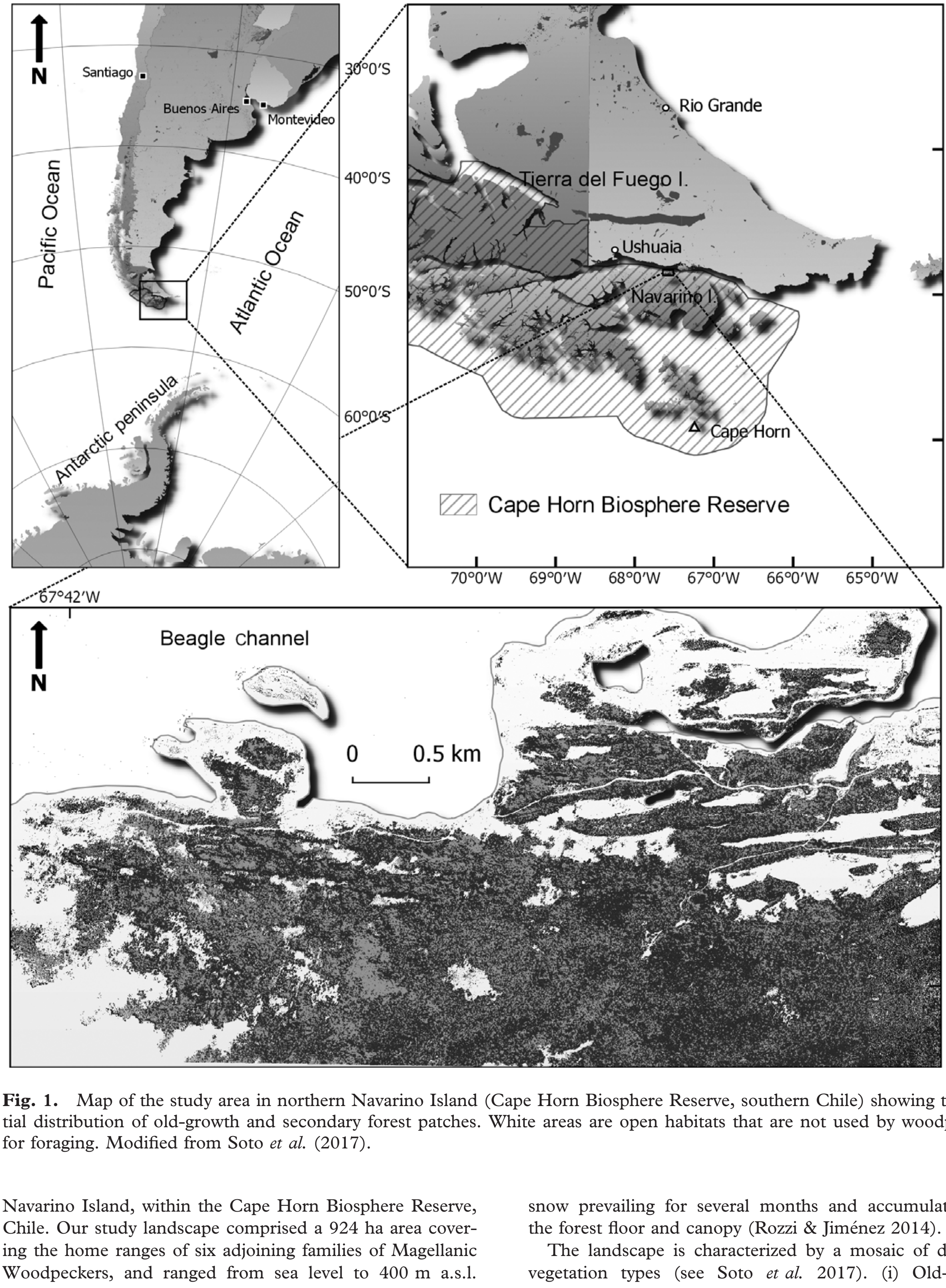

Fig. 1. Map of the study area in northern Navarino Island (Cape Horn Biosphere Reserve, southern Chile) showing the spatial distribution of old-growth and secondary forest patches. White areas are open habitats that are not used by woodpeckers for foraging. Modified from Soto *et al.* (2017).

Navarino Island, within the Cape Horn Biosphere Reserve, Chile. Our study landscape comprised a 924 ha area covering the home ranges of six adjoining families of Magellanic Woodpeckers, and ranged from sea level to 400 m a.s.l. (Fig. 1) The mean annual temperature in the area is 5.6°C and the mean annual precipitation is 467 mm. During the summer, daily high temperatures can reach up to 25°C, where as daily high winter temperatures average 0°C, with snow prevailing for several months and accumulating on the forest floor and canopy (Rozzi & Jiménez 2014).

The landscape is characterized by a mosaic of different vegetation types (see Soto *et al.* 2017). (i) Old-growth (OGF) and secondary forests (SF) are both dominated by the high deciduous beech or "Lenga" (*Nothofagus pumilio*) and the evergreen beech or Magellanic "Coigüe" (*Nothofagus betuloides*), accompanied by Winter's bark or "Canelo"

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Table 1. Tree variables (mean ± SD (n)) in secondary and old-growth forest in the Omora Ethnobotanical Park, Chile

Variable	Secondary forest	Old-growth forest	t	P
Tree measurements n	110	73		
DBH (cm)	34.7 ± 21.2	41.0 ± 18.3	−2.14	0.034
Height (m)	13.7 ± 5.1	15.2 ± 4.5	−2.14	0.034
Decay index	1.8 ± 1.1	1.9 ± 1.1	−0.42	0.676
Tree species composition (%)				
Nothofagus pumilio	34.0	55.1		
Nothofagus betuloides	48.1	37.7		
Nothofagus antarctica	10.4	7.2		
Drimys winteri	7.5	0.0		

Measured trees were randomly selected within 50 m of woodpecker feeding observations.

(*Drimys winteri*); where as in wet areas by the low deciduous beech or “Ñirre” (*Nothofagus antarctica*). SF patches are mostly homogeneous and even-aged but still include some dead standing old-growth trees (>100 years). SF can be recognized by the smaller Diameter at Breast Height (DBH) and lower height of trees compared to OGF. (ii) Scrublands, dominate in naturally or anthropogenically disturbed areas; and (iii) wetland habitats are composed of peatlands, moorlands, bogs and fields of rushes (*Marsippospermum grandiflorum*; Rozzi *et al.* 2006). Of these vegetation types, woodpeckers use only OGF and SF as foraging and nesting habitat (Fig. 1; Soto *et al.* 2017).

We identified the used tree species and measured the characteristics of four randomly selected trees in OGF and SF while undertaking foraging observations (see below). These random locations were generated within circular 50 m-radius plots centred on the location of every tree used for foraging, using a uniform random sample of angles (1–360°) and distances (5–50 m) in order to avoid spatial bias from additive GPS error. The stands differ markedly in structure and tree species composition (Table 1). OGF includes trees with greater height (mean ± SD = 15.2 ± 4.5 m; $n = 73$) than SF (mean ± SD = 13.7 ± 5.1 m; $n = 110$, $t = -2.1$, $P = 0.03$), and with a larger DBH (mean ± SD = 41.0 ± 18.3 cm; $n = 73$) than SF (mean ± SD = 34.7 ± 21.2 cm, $n = 110$, $t = -2.1$, $P = 0.03$). The most represented tree species in OGF was *N. pumilio* (55.1%) whereas in SF it was *N. betuloides* (48.1%). However, for both forest age classes and species, decay stages and wood-boring infestation signs are positively correlated (Soto *et al.* 2017).

Foraging observations

We recorded foraging microhabitat use by woodpecker pairs during two contrasting seasons: (i) the warm season or austral summer (January–March of 2012 and 2013; i.e., immediately after fledging), and (ii) the cold season, or austral winter (June–August of 2012; i.e., just before breeding season). We radio-tracked six adult male woodpeckers, each belonging to a different family group. Tracked woodpeckers were targeted for mist nest captures with playback and wooden decoy. Males were colour-banded, fitted with VHF radio-backpacks (ATS, model A1250, Buehler *et al.* 1995) and released at the site of capture. We located individuals by using the homing technique, which consisted of locating the source of the VHF signal emitted by a transmitter attached to the dominant male woodpecker of a given family group (Soto *et al.* 2017). Once located, we identified family members (i.e., the adult female and juveniles) based on specific colour differences and colour bands. We recorded foraging behaviours as soon as woodpeckers were contacted until the adult male and female flew out of the sight of observers, usually for more than 10 min. Given that Magellanic Woodpeckers on Navarino Island often quickly tolerate human presence (Román *et al.* 2013), individual behaviour was recorded by two researchers from distances of ca. 20 m, shortly after woodpeckers were contacted. Each observation was classified into non-foraging behaviours such as resting, preening, drumming, vocalizing and observing, and foraging behaviours including probing, pecking, debarking and excavating (Chazarreta *et al.* 2012).

To ensure data independence in time, we conducted only one daily observation bout per family group. Each day, we changed the time when we monitored birds in order to collect data at different hours for each sampled family group. We recorded behaviour by using 10 × 42 binoculars. For each adult male and female woodpecker, we recorded the following structural attributes of trees used for foraging, each being considered as a distinct habitat component of their niche: (i) tree diameter (DBH), measured with a diameter-tape, and the absolute height of the tree measured with a clinometer and a laser rangefinder; (ii) foraging diameter and foraging height (i.e. the diameter and the height of the tree where a woodpecker was feeding), with diameter estimated relative to the bird’s size and height measured with a clinometer and a laser rangefinder, respectively; (iii) tree species; and (iv) decay stage (see Soto *et al.* 2017). We classified decay stage into six categories (1 to 6), from healthy trees (1) to snags or dead trees (6) (i.e., rotten dead trees with no bark; Vergara & Schlatter 2004). For each observation where woodpeckers were recorded feeding, we determined the forest type as OGF or SF. In order to compare the trees used for foraging with those available in the stand, we measured the same characteristics of four nearby randomly selected trees (see above).

Data analysis

We compared characteristics (diameter, height, decay, species) between the trees used for foraging and those available (the randomly selected trees) by using chi-square analysis. To assess foraging differences between adult males and females we undertook three steps. First, we determined the overall difference between sexes with regard to tree species and the structural attributes of the trees that female and male woodpeckers used for foraging. Second, we determined whether sexual differences in the attributes of the trees used for foraging changed between seasons and between habitat types. Third, we estimated niche overlap between males and females in tree attributes and behavioural variables by using Schoener's niche overlap index (SNOI; Schoener 1968). Schoener's overlap index ranges between 0 (no overlap) and 1 (complete overlap), with values >0.6 being evidence of a significant overlap in resource use (Wallace 1981). To compute SNOIs, tree diameter and height were each classified into seven categories, tree-decay stages into six categories, and four different tree species were used (*Nothofagus pumilio*, *N. betuloides*, *N. antarctica* and *D. winteri*). We used these categories to ensure enough replication across the forest habitats and because these represent the spectrum of available resources in each habitat type. The SNOIs were calculated for each woodpecker pair, season, and forest type.

To test for differences between sexes with regard to the used tree attributes, behavioural variables, and niche overlap indices, we used Linear Mixed-effect Models (LMM) using the nlme, multcomp, and AICcmodavg packages implemented in R version 2.15.3 (R Core Team 2014). LMM included the woodpecker pair and individual as nested random effects to account for these dependencies. In a first analysis, we specified the log-transformed tree attributes as dependent variables, whereas the sex (male *vs.* female), season (summer *vs.* winter), forest type (OGF *vs.* SF), and their interactions, were included as fixed effects. These models were fitted using Maximum Likelihood in order to get unbiased estimates of the fixed effects. In a second analysis, we tested for the effects of season and forest type on SNOI values (niche overlap) between males and females. SNOI values were normalized by using arcsine transformation (Crawley 2007) and LMMs explaining them were fitted using Restricted Maximum Likelihood in order to provide unbiased estimates for the random effects. The best-supported models were identified by using Akaike's information criterion corrected for small sample sizes and the Akaike weights (AICc, w_i, Burnham & Anderson 2002).

Table 2. Number of foraging observations per Magellanic Woodpecker family, sex, and season (n = 421) during winter and summer in 2012 and 2013 in the Omora Ethnobotanical Park, Chile

	Males		Females		
Family	Winter	Summer	Winter	Summer	Total
W1	13	29	13	19	74
W2	8	25	7	17	57
W3	23	26	16	18	83
W4	2	22	1	20	45
W5	15	21	16	13	65
W6	21	32	16	28	97

RESULTS

A total of 421 foraging behavioural observations were analysed (Table 2). Birds foraged mainly on *N. pumilio* (49%), *N. betuloides* (39%), *N. antarctica* (10.8%) and marginally on *D. winteri* (1.1%). Those proportions did not follow the pattern of availability of each tree species of the randomly selected trees (X^2 = 8.2, df = 3, P = 0.04), with woodpeckers foraging preferentially on *N. pumilio*. No differences, however, were found in the tree species used by males and females (X^2 = 2.41, df = 3, P = 0.49).

For the seasons and habitats considered, sexes differed significantly in the DBH of trees used for foraging (P = 0.01), foraging diameter (P < 0.001) and foraging height (P = 0.01), as shown in Tables 3 and 4. Sexes neither differ in the height nor in the decay

Table 3. Seasonal foraging behaviour of Magellanic Woodpeckers at the Omora Ethnobotanical Park, Chile during 2012 and 2013

	Males		Females	
Variable	Winter	Summer	Winter	Summer
Tree DBH (cm)	56.4 ± 26.9 (80)	54.8 ± 25.7 (143)	47.8 ± 24.4 (68)	46.8 ± 25.1 (103)
Tree height (m)	14.2 ± 7.2 (82)	14.0 ± 6.6 (123)	15.2 ± 6.5 (69)	13.8 ± 7.0 (86)
Foraging diameter (cm)	35.7 ± 17.5 (80)	36.1 ± 18.8 (112)	14.2 ± 9.9 (69)	24.2 ± 17.3 (77)
Foraging height (m)	5.8 ± 5.2 (82)	5.5 ± 4.4 (122)	9.4 ± 5.6 (69)	6.0 ± 4.5 (86)
Decay index	2.7 ± 1.3 (81)	3.0 ± 1.4 (126)	2.3 ± 1.2 (63)	3.1 ± 1.6 (89)

Characteristics of trees in which males and females were observed foraging are shown (mean ± SD (n)).

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Table 4. Forest types and tree characteristics where male and female Magellanic Woodpeckers were observed foraging at the Omora Ethnobotanical Park, Chile during 2012 and 2013 (mean ± SD (*n*))

	Males		Females	
Variable	Old-growth	Secondary	Old-growth	Secondary
Tree DBH (cm)	57.4 ± 20.2 (83)	54.2 ± 29.0 (140)	51.9 ± 26.5 (63)	44.5 ± 23.4 (108)
Tree height (m)	15.9 ± 6.3 (78)	13.0 ± 6.9 (127)	16.7 ± 6.7 (58)	13.1 ± 6.5 (97)
Foraging diameter (cm)	36.7 ± 16.3 (71)	35.5 ± 19.3 (121)	20.4 ± 18.1 (54)	18.9 ± 13.1 (92)
Foraging height (m)	7.0 ± 5.1 (77)	4.7 ± 4.3 (127)	8.7 ± 5.6 (58)	6.9 ± 5.0 (97)
Decay index	2.5 ± 1.3 (78)	3.2 ± 1.4 (129)	2.3 ± 1.4 (54)	3.0 ± 1.5 (98)

Table 5. Candidate mixed linear models explaining variation in tree DBH, tree height, foraging diameter, foraging height and decay index for foraging observations in relation to sex, season and forest type used by Magellanic Woodpeckers

Dependent variable	Candidate models	AICc	ΔAICc	w_i
Tree DBH	Sex + Forest type	586.0	**0.0**	0.39
	Season + Sex + Forest type	587.2	**1.2**	0.22
	Sex	588.0	**1.9**	0.15
	Forest type × Sex	588.0	2.0	0.14
	Season + Sex	588.7	2.6	0.10
Tree height	Forest type	717.5	**0.0**	0.32
	Season + Forest type	717.7	**0.1**	0.31
	Sex + Forest type	719.3	**1.8**	0.13
	Season + Sex + Forest type	719.5	2.0	0.12
	Season × Sex + Forest type	719.6	2.1	0.11
Foraging diameter	Season × Sex	583.6	**0.0**	0.66
	Season × Sex + Forest type	585.7	2.1	0.23
	Season × Sex + Forest type × Sex	587.3	3.6	0.11
	Season + Sex	596.8	13.2	0.00
	Season + Sex + Forest type	598.8	15.2	0.00
Foraging height	Season × Sex + Forest type	728.5	**0.0**	0.69
	Season × Sex + Forest type × Sex	730.3	**1.8**	0.28
	Season + Sex + Forest type	735.6	7.2	0.02
	Season + Sex × Forest type	737.5	9.1	0.01
	Season × Sex	738.4	10.0	0.01
Decay index	Season × Sex + Forest type	302.4	**0.0**	0.34
	Season + Forest type	302.8	**0.4**	0.28
	Season + Sex + Forest type	303.5	**1.1**	0.19
	Season × Sex + Forest type × Sex	304.4	2.0	0.12
	Season + Forest type × Sex	305.5	3.1	0.07

Best-supported models ($\Delta AIC_c < 2$) are bolded.

stage of the trees used. The best-supported LMMs (ΔAICc < 2) considering tree DBH, tree height, foraging diameter, foraging height and decay index as response variables included the additive effects of sex, season and forest type as well as the interactive effect of season and sex (Table 5).

Tree DBH was accounted for woodpecker's sex and forest type, as indicated by the best supported models (Table 6). Males fed on trees with larger DBH than females (55.4 ± 26.1 cm, $n = 239$ and 47.2 ± 24.7 cm, $n = 184$, respectively) and trees used by woodpeckers had larger DBH in OGF than in SF (Table 6). Tree height depended only on forest type, with woodpeckers foraging on taller trees in OGF than in SF. Foraging diameter was influenced by the sex × season interaction, with males foraging on larger diameters than females on both seasons (35.9 ± 18.2 cm, $n = 192$ and 19.5 ± 15.1 cm, $n = 146$, respectively), while sexual differences were more pronounced during winter (Tables 5 and 6).

In summer, woodpeckers of both sexes foraged lower on the trees than when compared with winter (Table 6). For both seasons, foraging height was lower for males than for females (5.6 ± 4.7 m, $n = 204$ and 7.5 ± 5.3 m, $n = 155$, respectively; $P = 0.005$; Table 6), but differences in the height of foraging sites between males and females were stronger in winter than in summer, as shown by a significant sex × season interaction ($P = 0.002$; Table 6). Although our foraging observations showed

Table 6. Averaged coefficients of the best-supported mixed linear models listed in Table 5 ($\Delta AIC_c < 2$) explaining foraging attributes of Magellanic Woodpeckers at the Omora Ethnobotanical Park, Chile

Dependent variable	Explicative variable	Coefficient ± SD	*P*
Tree DBH	Sex	0.20 ± 0.05	0.003
	Forest type	−0.11 ± 0.06	0.052
	Season	−0.05 ± 0.05	0.349
Tree height	Forest type	−0.25 ± 0.08	0.001
	Season	−0.10 ± 0.07	0.165
	Sex	−0.04 ± 0.07	0.697
Foraging diameter	Season	0.49 ± 0.10	<0.001
	Sex	0.97 ± 0.10	<0.001
	Season × Sex	−0.50 ± 0.13	<0.001
	Forest type	0.01 ± 0.08	0.303
	Sex × Forest type	−0.10 ± 0.13	0.449
Foraging height	Season	−0.49 ± 0.12	<0.001
	Forest type	−0.24 ± 0.10	0.001
	Season × Sex	0.48 ± 0.15	0.002
	Sex	−0.54 ± 0.14	0.005
	Sex × Forest type	−0.13 ± 0.16	0.400
Decay index	Forest type	0.19 ± 0.05	<0.001
	Season	0.17 ± 0.07	0.016
	Season × Sex	−0.15 ± 0.09	0.075
	Sex	0.11 ± 0.08	0.222
	Sex × Forest type	−0.03 ± 0.09	0.729

For each model covariate, the coefficient value (SD) and *P*-values are shown. Foraging attributes include tree DBH, tree height, foraging diameter, foraging height and decay index.

woodpeckers foraging at lower heights in SF than in OGF, females and males used trees of similar heights at both forest types (14.4 ± 6.8 m, $n = 155$ and 14.1 ± 6.8 m, $n = 205$, respectively). Foraging trees used by woodpeckers were more decayed in SF than in OGF and woodpeckers foraged on more decayed trees in summer (Table 6). However, females and males used trees with similar decay stages on both forest types (2.78 ± 1.5, $n = 152$ and 2.91 ± 1.4, $n = 207$, respectively; Table 6).

The most parsimonious models showed that the amount of overlap between males and females in terms of tree DBH, tree height, foraging diameter and foraging height depended on season, but not on forest type (Table 7). Males and females exhibited smaller overlap values during winter than during summer (Table 8, Fig. 2). However, we found support only for the null model (without predictors) when including the tree height overlap as a response variable (Table 7).

Table 7. Candidate models explaining niche overlap between male and female Magellanic Woodpeckers in relation to tree DBH, tree height, foraging diameter, foraging height, decay index and tree species

Dependent variable	Candidate models	AIC_c	ΔAIC_c	w_i
Tree DBH overlap	Nul model	10.1	0.0	0.628
	Season	11.5	1.4	0.308
	Forest	15.3	5.2	0.046
	Season + forest	17.4	7.3	0.016
	Season × forest type	22.7	12.6	0.001
Tree height overlap	Nul model	0.6	0.00	0.802
	Forest type	5.5	4.9	0.073
	Season	5.9	5.3	0.061
	Season + forest type	11.3	10.8	0.004
	Season × forest type	16.7	16.1	0.000
Foraging diameter overlap	Nul model	18.4	0.00	0.604
	Season	19.9	1.5	0.286
	Forest type	22.5	4.1	0.079
	Season + forest type	24.6	6.2	0.028
	Season × forest type	29.5	11.1	0.002
Foraging height overlap	Season	26.9	0.0	0.715
	Nul model	29.3	2.5	0.208
	Season + forest type	32.2	5.4	0.049
	Forest type	33.9	7.1	0.021
	Season × forest type	35.9	9.0	0.008

No model for decay index and tree species were selected. Best-supported models ($\Delta AIC_c < 2$) are bolded.

Table 8. Coefficients of the best-supported models listed in Table 7 ($\Delta AIC_c < 2$) explaining niche overlap of Magellanic Woodpeckers at the Omora Ethnobotanical Park, Chile

Dependent variable	Explicative variable	Coefficient ± SD	*P*
Tree DBH overlap	Season (summer)	0.21 ± 0.09	0.043
Foraging diameter overlap	Season (summer)	0.25 ± 0.12	0.060
Foraging height overlap	Season (summer)	0.58 ± 0.21	0.019

For each model covariate, the coefficient value (SD) and *P*-values are shown.

DISCUSSION

The results of our study support intersexual niche partitioning in the Magellanic Woodpecker, as reported in forest ecosystems at lower latitudes (Chazarreta *et al.* 2012). Sexual differences in foraging microhabitat use in woodpecker species has long been recognized (e.g., Selander 1966) and it seems to be a widespread phenomenon in woodpecker species worldwide (Ligon 1968; Kilham 1970; Austin 1976; Hogstad 1977, 2010; Aulèn & Lundberg 1991; Pasinelli 2000; Pechacek 2006; Franzeb 2010). However, this is the first study to explore how niche

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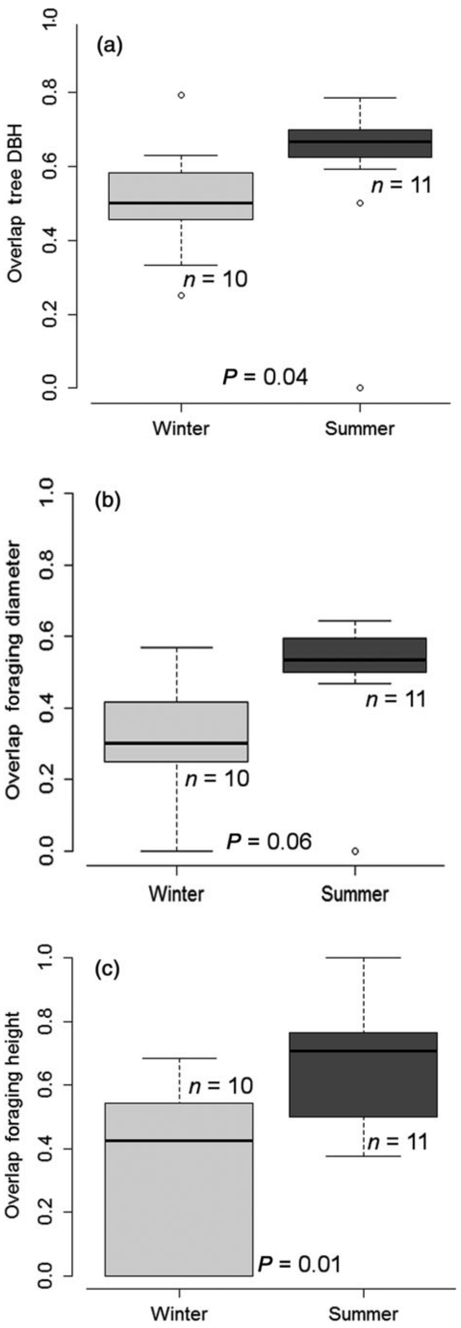

Fig. 2. Seasonal variation in the Schoener's niche overlap index between sexes of Magellanic Woodpeckers in sub-Antarctic forests, including the overlap in (a) tree DBH, (b) foraging trunk diameter, and (c) foraging height. (*n*) correspond to the samples sizes to calculate overlaps by woodpecker breeding pair, season, and forest type.

partitioning varies between habitat of different qualities and between seasons.

Magellanic Woodpeckers live and forage in family groups (Ojeda 2004; Chazarreta *et al.* 2012), in contrast to other woodpecker species in which the mates forage in different locations throughout their home-ranges (Hogstad 2009, 2010; Czeszczewik 2010). In spite of their strong pair and family bond throughout the year, our results show that male and female Magellanic Woodpeckers differ in their foraging behaviour (see also Chazarreta *et al.* 2012). They exhibited niche partitioning in relation to tree size and foraging height, with males foraging in larger-diameter trees, on large bole sections, and lower in the tree than females, which were more often observed on small branches of the tree crowns. These results are consistent with those of Chazarreta *et al.* (2012) showing that foraging activity of female woodpeckers is more intensive in the smaller-diameter trees and branches.

Sexual differences in foraging behaviour were dependent on season, but not on forest type, as shown by the differences in foraging niche overlap between male and female woodpeckers. The emergence of this pattern may be due to the increased availability of resources during the summer, reflected on observations of woodpeckers foraging on alternative prey to wood-boring larvae, such as adult insects, earthworms, fleshy fruits, as well as eggs and nestlings of small passerines, all absent during winter (Schattler & Vergara 2005; Lizama *et al.* 2013; see also Ojeda & Chazarreta 2006). The results presented in this study partially support the hypothesis that niche segregation may decrease when more resources are available due to the relaxation of intraspecific competition (e.g., Hogstad 1977; Smith 1990; Pechacek 2006). As we predicted, foraging niche overlap was greater in summer than in winter, when female woodpeckers foraged on tree diameters at heights more similar to those of males. These results are consistent with other studies on social woodpecker species living in cold regions, which also exhibit a larger foraging niche overlap between males and females during summer (Pasinelli 2000; Czeszczewik 2010; Hogstad 2010).

Seasonal variation in niche overlap may result from seasonal changes in foraging techniques, such that males and females are more specialized in particular niche dimensions during winter, and hence avoid competition between mates (Pechacek 2006). In summer, male woodpeckers may share foraging substrates with females, as evidenced by greater similarity in the foraging diameters and foraging heights observed for males and females.

Contrary to our second prediction, Magellanic Woodpeckers did not exhibit greater partitioning between sexes when foraging in SF than OGF. However, sub-Antarctic SF may provide low quality habitats for woodpeckers, offering lower levels of foraging resources (e.g., Vergara & Schlatter 2004, 2006). Although we do not have detailed information on the relative quality of the forest types, based on recent work on the abundance of insects in the field and on the number of exit holes on the trees, as a proxy of quality of the food base, we assumed that OGF was a better feeding habitat than SF (see Soto *et al.* 2017). Further work is needed to test this hypothesis.

The absence of a difference in foraging partitioning between forest types may also be explained by the habitat selection pattern of woodpeckers at the landscape-scale. Within their home ranges, SF stands are used less frequently by woodpeckers than OGF (Vergara & Schlatter 2006). Woodpeckers with large home ranges show a higher percentage of SF within their range, compared with woodpeckers with smaller home ranges located in landscapes dominated by OGF (Soto *et al.* unpublished data). Thus, even if suspected to be of lower quality for foraging, SF may still be used – at least temporarily – when there is not enough OGF within the home range and during critical periods. However, for a family to breed, OGF with large trees suitable for woodpeckers to build their nests is needed, as tree sizes in SF are too small for a breeding cavity. Such cavities are also required as roost site for spending the night (Ojeda 2004).

We conclude that male and female Magellanic Woodpeckers show seasonal differences in foraging niche, but that other factors accounting for spatio-temporal changes in food availability (e.g., annual climate, predation risk) might also promote niche partitioning. Such sexual differences in habitat use should be considered when forest landscape planning is developed in sub-Antarctic forests (e.g., Van Toor *et al.* 2011). First, we suggest that not only the larger and more decayed trees, which are preferably used by males, should be retained when harvesting, but also some smaller trees that are used by females. Second, landscape-scale forest planning and management should recognize sexual foraging differences in Magellanic Woodpeckers by retaining OGF stands in order to increase the viability of local populations.

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REFERENCES

Arango X., Rozzi R., Massardo F., Anderson C. & Ibarra T. (2007) Descubrimiento e implementación del pájaro carpintero gigante (*Campephilus magellanicus*) como especie carismática: una aproximación biocultural para la conservación en la Reserva de Biosfera Cabo de Hornos. *Magallania (Chile)* **35,** 71–88.

Aulèn G. & Lundberg A. (1991) Sexual dimorphism and patterns of territory use by the White-backed Woodpecker *Dendrocopus leucotos*. *Ornis Scand.* **22,** 60–4.

Austin G. T. (1976) Sexual and seasonal differences in foraging of Ladder-backed Woodpeckers. *Condor* **78,** 317–23.

Buehler D. A., Fraser J. D., McAllister L. S., Fuller M. R. & Seegar J. K. D. (1995) Captive and field tested radio attachment techniques for Bald Eagles. *J. Field Ornithol.* **66,** 173–80.

Burnham K. P. & Anderson D. R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer, New York.

Catry P., Phillips R. A. & Croxall J. P. (2006) Sexual segregation in birds: patterns, processes and implications for conservation. In: *Sexual Segregation in Vertebrates: Ecology of the Two Sexes* (eds K. Ruckstuhl & P. Neuhaus) pp. 351–78. Cambridge University Press, Cambridge.

Chazarreta L., Ojeda V. S. & Trejo A. (2011) Division of labour in parental care in the Magellanic Woodpecker *Campephilus magellanicus*. *J. Ornithol.* **152,** 231–42.

Chazarreta L., Ojeda V. S. & Lammertink M. (2012) Morphological and foraging behavioural differences between sexes of the Magellanic Woodpecker (*Campephilus magellanicus*). *Ornitol. Neotrop.* **23,** 529–44.

Crawley M. J. (2007) *The R-Book*. John Wiley and Sons Ltd., Chichester.

Czeszczewik D. (2010) Wide intersexual niche overlap of the specialized White-backed Woodpecker *Dendrocopos leucotos* under the rich primeval stands in the Bialowieza forest, Poland. *Ornis Polonica* **51,** 241–51.

Franzeb K. E. (2010) Red-cockaded Woodpecker male/female foraging differences in young forest stands. *Wilson J. Ornithol.* **122,** 244–58.

Freeman B. (2014) Sexual niche partitioning in two species of New Guinean *Pachycephala* whistlers. *J. Field Ornithol.* **85,** 23–30.

González Solís J., Croxall J. P. & Wood A. G. (2000) Sexual dimorphism and sexual segregation in foraging strategies of northern giant petrels, *Macronectes halli*, during incubation. *Oikos* **90,** 390–8.

Hogstad O. (1977) Seasonal change in intersexual niche differentiation of the Three-toed Woodpecker *Picoides tridactylus*. *Ornis Scand.* **8,** 101–11.

Hogstad O. (1978) Sexual dimorphism in relation to winter foraging and territorial behaviour of the Three-toed Woodpecker *Picoides tridactylus* and three *Dendrocopos* species. *Ibis* **120,** 198–203.

Hogstad O. (2009) Sexual differences of labour during breeding activities and territory use in the Lesser spotted Woodpecker *Dendrocopos minor*. *Ornis Norvegica* **32,** 42–8.

Hogstad O. (2010) Sexual differences in foraging behaviour in the Lesser spotted Woodpecker *Dendrocopos minor*. *Ornis Norvegica* **33,** 135–46.

IUCN. (2016). IUCN Red List of Threatened Species. Version 2016.2. Available from URL: http://www.iucnredlist.org/details/22681414/0

Kilham L. (1970) Feeding behaviour of Downy woodpeckers. I. Preference for paper birches and sexual differences. *Auk* **87,** 544–56.

Ligon J. D. (1968) Sexual differences in foraging behaviour in two species of *Dendrocopos* woodpeckers. *Auk* **85,** 203–15.

Lizama M. E., Soto G. E., Vergara P. M., Rozzi R. & Jiménez J. E. (2013) Sexual differences in nest attendance by Magellanic woodpeckers (*Campephilus magellanicus*) in the southernmost forest of the world. *98th Ecological Society of America Annual Meeting PS 58–65.*

McBride P. (2000) *Magellanic Woodpecker (*Campephilus magellanicus*) habitat selection in deciduous* Nothofagus *forests of Tierra del Fuego*. MS Thesis, Western Washington University, Bellingham, WA, USA.

Ojeda V. S. (2003) Magellanic Woodpecker frugivory and predation on a lizard. *Wilson Bull.* **115,** 208–10.

Ojeda V. S. (2004) Breeding biology and social beaviour of Magellanic woodpeckers (*Campephilus magellanicus*) in Argentine Patagonia. *Eur. J. Wildl. Res.* **50,** 18–24.

Ojeda V. S. & Chazarreta L. (2006) Provisioning of Magellanic Woodpecker (*Campephilus magellanicus*) nestlings with vertebrate prey. *Wilson J. Ornithol.* **118,** 251–4.

Ojeda V. & Chazarreta L. (2014) Home range and habitat use by Magellanic Woodpeckers in an old-growth forest of Patagonia. *Can. J. For. Res.* **44,** 1265–73.

Osiejuk T. S. (1994) Sexual dimorphism in foraging behaviour of the Great spotted Woodpecker *Dendrocopos major* during winters with rich crops of Scotch pine cones. *Ornis Fennica* **71,** 144–50.

Pasinelli G. (2000) Sexual dimorphism and foraging niche partitioning in the Middle spotted Woodpecker *Dendrocopos medius*. *Ibis* **142,** 635–44.

Pechacek P. (2006) Foraging behaviour of Eurasian three-toed woodpeckers (*Picoides tridactylus alpinus*) in relation to sex and season in Germany. *Auk* **123,** 235–46.

Przybylo R. & Merilä J. (2000) Intersexual niche differentiation in the Blue tit (*Parus caeruleus*). *Biol. J. Lin. Soc.* **69,** 233–44.

R Development Core Team (2014) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna. ISBN 3-900051-07-0, http://www.R-project.org

Román I., Jiménez J. E., Vergara P. & Rozzi R. (2013) Magellanic Woodpecker (*Campephilus magellanicus)* responses when approached by humans in the context of ecotourism. *98th Ecological Society of America Annual Meeting PS 58-59.*

Rozzi R. & Jiménez J. E., eds (2014) *Magellanic sub-Antarctic Ornithology. First Decade of Long-term Bird Studies at the Omora Ethnobotanical Park, Cape Horn Biosphere Reserve, Chile*. University of North Texas Press, USA-Universidad de Magallanes, Punta Arenas.

Rozzi R., Massardo F., Anderson C., Heidinger K. & Silander J. Jr (2006) Ten principles for biocultural conservation at the southern tip of the Americas: the approach of the Omora Ethnobotanical Park. *Ecol. Soc.* **11**(1), 43. [online] URL: http://www.ecologyandsociety.org/vol11/iss1/art43/

Ruckstuhl K. E. (2007) Sexual segregation in vertebrates: proximate and ultimate causes. *Integr. Comp. Biol.* **47,** 245–57.

Schattler R. P. & Vergara P. (2005) Magellanic Woodpecker (*Campephilus magellanicus*) sap feeding and its role in the Tierra del Fuego forest bird assemblage. *J. Ornithol.* **146,** 188–90.

Schoener T. (1968) The Anolis lizards of Bimini: resource partitioning in a complex fauna. *Ecology* **49,** 704–26.

Selander R. K. (1966) Sexual dimorphism and differential niche utilization in birds. *Condor* **68,** 113–51.

Short L. L. (1970) The habits and relationships of the Magellanic Woodpecker. *Wilson Bull.* **82,** 115–29.

Short L. L. (1982) *Woodpeckers of the World*. Delaware Museum of Natural History, Foris Publications, Cinnaminson, NJ.

Slatkin M. (1984) Ecological causes of sexual dimorphism. *Evolution* **38,** 622–30.

Smith T. B. (1990) Resource use by bill morphs of an African finch: evidence for intraspecific competition. *Ecology* **71,** 1246–57.

Soto G. E., Vergara P. M., Lizama M. E. *et al.* (2012) Do beavers improve the habitat quality for Magellanic Woodpeckers? *Bosque (Chile)* **33,** 271–4.

Soto G. E., Pérez-Hernández C. G., Hahn I. J., Rodewald A. D. & Vergara P. M. (2017) Tree senescence as a direct measure of habitat quality: linking red-edge vegetation indices to space use by Magellanic Woodpeckers. *Remote Sens. Environ.* **193,** 1–10.

Van Toor M. L., Jaberg C. & Safi K. (2011) Integrating sex-specific habitat use for conservation using habitat suitability models. *Anim. Conserv.* **14,** 512–20.

Vergara P. & Schlatter R. P. (2004) Magellanic Woodpecker (*Campephilus magellanicus*) abundance and foraging in Tierra del Fuego, Chile. *J. Ornithol.* **145,** 343–51.

Vergara P. & Schlatter R. P. (2006) Aggregate retention in two Tierra del Fuego *Nothofagus* forests, short-term effects on bird abundance. *For. Ecol. Manage.* **225,** 213–24.

Vergara P. M., Meneses L. O., Grez A. A. *et al.* (2017) Occupancy pattern of a long-horned beetle in a variegated forest landscape: linkages between tree quality and forest cover across spatial scales. *Landscape Ecol.* **32,** 279–93.

Wallace R. K. Jr (1981) An assessment of diet-overlap indexes. *Trans. Am. Fish. Soc.* **110,** 72–6.

Wilson D. S. (1975) The adequacy of body size as a niche difference. *Am. Nat.* **109,** 769–84.

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