

MORPHOLOGICAL AND FORAGING BEHAVIORAL DIFFERENCES BETWEEN SEXES OF THE MAGELLANIC WOODPECKER (*CAMPEPHILUS MAGELLANICUS*)

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Resumen. – **Diferencias morfológicas y de comportamiento alimentario entre sexos del Carpintero Gigante (*Campephilus magellanicus*).** – La divergencia ecológica producto de diferencias morfológicas y comportamentales junto con la dominancia social, promueve la separación de nichos entre sexos en aves. La ausencia de competidores favorecería estas diferencias intersexuales. El Carpintero Gigante (*Campephilus magellanicus*) es el único pícido de gran tamaño en los bosques de *Nothofagus* de la Patagonia, sin competidores. Una investigación preliminar documentó diferencias morfológicas entre sexos y postuló la existencia de diferencias en el comportamiento alimentario, correlacionadas con ese dimorfismo. Nuestros objetivos fueron analizar las diferencias morfológicas e investigar si existen diferencias intersexuales en el comportamiento alimentario. Obtuvimos datos morfológicos de colecciones de museos y registros comportamentales de poblaciones de Patagonia Argentina. Estimamos amplitud y solapamiento de nichos en variables de alimentación. Los machos fueron más grandes y tuvieron picos 12,4% más largos que las hembras. Ambos sexos se alimentaron principalmente sobre árboles vivos, pero los machos usaron sustratos más grandes (troncos) que las hembras y alturas intermedias (5–10 m), mientras que las hembras usaron sustratos más pequeños (ramas) dentro de la copa, a mayor altura (> 15 m). La tasa de captura de presas fue similar entre sexos (0,28 presas/min), pero los machos capturaron presas más grandes (larvas xilófagas) que las hembras (presas superficiales). Registramos dominancia social de los machos. Según el análisis de amplitud de nicho, las hembras fueron más generalistas que los machos en el uso de microhábitats y en la posición del cuerpo mientras se alimentaban. El dimorfismo sexual en tamaño corporal y largo del pico fue acorde a la especialización por sustratos en los sexos, lo cual fue probablemente reforzado por la dominancia de los machos. La falta de competencia interespecífica en este bioma contribuiría a la diferenciación observada entre los sexos.

Abstract. – Ecological differentiation arising from morphological and behavioral differences, together with social dominance, is known to promote niche differentiation between sexes in birds. The absence of competing species would favor intersexual differences. The Magellanic Woodpecker (*Campephilus magellanicus*) is the only large woodpecker in the southern beech *Nothofagus* forests of Patagonia, with no competitors. Sexual divergence in morphology had been documented by preliminary research, and differences in foraging behavior were proposed as a correlate. Our aims are to analyze intersexual divergence in morphology and to investigate whether the behavioral differences exist. We obtained morphological data from ornithological collections and foraging records from populations from Argentine Patagonia. We estimated foraging niche breadth and the overlap of foraging variables. Adult males were larger and had bills 12.4% longer than those of females. Both sexes foraged mostly on living trees, but males foraged on larger substrates (trunks) at intermediate heights (5–10 m), while females foraged

higher within the crown (> 15 m) on smaller substrates (branches). The rate of captured prey was similar between sexes (0.28 prey/min), but males consumed larger prey (wood-boring larvae) than females (near-surface prey). Social dominance by males was recorded. Based on analysis of niche breadth, females were more generalist than males in microhabitat use and body posture when foraging. Sexual dimorphism in body and bill size seems to be in line with specialization in the use of different substrates between the sexes, which is probably reinforced by male dominance. Lack of interspecific competition in this biome probably contributed to the differentiation observed between sexes. *Accepted 23 December 2012.*

Key words: Magellanic Woodpecker, *Campephilus magellanicus*, Austral Temperate Forest, insular biome, niche breadth, sexual dimorphism.

INTRODUCTION

Sexual dimorphism in size and morphology is widespread among animals (Hedrick & Temeles 1989) and has traditionally been related to sexual selection, especially in bird species with a polygamous mating system (Amadon 1959, Selander 1972). Nevertheless, the evolutionary origin of sexual dimorphism has multiple pathways (Hedrick & Temeles 1989), and there are many cases where different size and morphology between males and females can be related to ecological causes (Slatkin 1984, Shine 1989), as in Green Woodhoopoes (*Phoeniculus purpureus*, Radford & Plessis 2003), Darwin's finches (Grant 1986), and Varied Sittella (*Daphoenositta chrysoptera*) and treecreepers (Climacteridae) (Noske 1986).

Segregation between sexes in morphological traits is thought to alleviate intersexual competition (Selander 1966, Ruckstuhl & Clutton-Brock 2005). The absence of competing species would favor a larger niche width of a species, leading to greater structural dimorphism and the subdivision between sexes of the foraging niche (Selander 1966, Shine 1989). Social dominance, where the dominant sex (usually male) excludes the subordinate from favored patches or substrates, explains sexual niche segregation in several cases (Hogstad 1978, Morse 1980, Peters & Grubb 1983, Matthysen *et al.* 1991, Osiejuk 1994, Ruckstuhl 2007).

Woodpeckers (Picidae) are often sexually dimorphic in plumage and morphology, and thus, are an interesting group for studying differences in foraging behaviors between male and female (Catry *et al.* 2005). In particular, sexual differences in bill size have been related to differences in feeding behavior, explored habitats, and consumed items (Selander 1966, Aulén & Lundberg 1991). The southern beech (*Nothofagus*) temperate forests covering southern Chile and Argentina (35°S–56°S), comprise a narrow strip ca. 2000 km long and up to 120 km wide that evolved in isolation from other South American forests, constituting a habitat island with high levels of endemism (Vuilleumier 1985, Armesto *et al.* 1996). In the interior of *Nothofagus* forests, only two woodpecker species occur, the small Striped Woodpecker (*Veniliornis lignarius*, ~ 16 cm, 35–38 g) and the very large Magellanic Woodpecker (*Campephilus magellanicus*, ~ 40 cm, 276–363 g) (Short 1982). In this particular setting, the Magellanic Woodpecker has no potential ecological competitor and therefore would show a broad woodpecker niche (Short 1970a). Pioneering research conducted by Short (1970a) revealed a noticeable sexual dimorphism in bill size (males larger than females), which he proposed would correlate to differences in feeding behavior and explored habitat, but this remained untested. Our aims are to analyze sexual dimorphism in morphology of Magellanic Woodpeckers and to explore sex-specific

foraging behavior and feeding habitats of this species.

METHODS

Study area. Study sites ($n = 8$) were located within the Lanín ($39^{\circ}35'–41^{\circ}19'S$) and Nahuel Huapi National Parks ($71^{\circ}17'–71^{\circ}36'W$), north and south of Bariloche city, in northern Argentine Patagonia. The climate in the region is characterized by a relatively long winter with rain and snow and by dry summers, with mean monthly winter (June–August) temperatures of $2^{\circ}–3^{\circ}C$, and summer (December–March) temperatures of $12^{\circ}–14^{\circ}C$ (data from Bariloche Airport, $41^{\circ}09'S$, $71^{\circ}10'W$).

Subalpine forests between 1100–1700 m a.s.l. are composed of pure stands of the deciduous lenga *Nothofagus pumilio*. Our field sites were old-growth lenga stands over 1000 ha each, which were contiguous with other *Nothofagus* stands. Lenga forest was selected because of the great extent of this forest type in the study area and its mostly open understory that allows following woodpeckers for monitoring their behavior.

Species. Magellanic Woodpeckers show a noticeable sexual plumage dimorphism, which facilitates field studies involving sex recognition. They reproduce in monogamous pairs and live in stable family groups consisting of 2–5 individuals, with offspring delaying dispersal for up to four years (Chazarreta *et al.* 2011). Family groups move in relatively limited areas of forest (ca. 100 ha) all year round, and members of a group keep in close proximity (Ojeda 2004).

Morphology. We measured morphology from specimens held in 19 ornithological collections (see Acknowledgments) in order to explore differences between sexes. Fifty-nine males and 64 females were measured follow-

ing Baldwin *et al.* (1931) guidelines. We only used adult specimens as determined from plumage patterns (Ojeda 2004), museum labels, and size (Short 1970a). We collected the following variables from each skin: wing and tail length, culmen cord (bill length), and tarsus, toe (third), and claw (third) length. Some skins were damaged so we were unable to collect all measurements from those specimens ($n = 7$). We took most measurements to the nearest 0.01 mm when using calipers, and to the nearest 1 mm using a ruler for wings and tail.

Nearly all specimen measurements (98%) were taken by one of us (LC) and the remainder was taken by museum curators instructed by LC. Although skin dimensions vary with specimen age, preparation technique, and storage conditions (Bortolotti 1984), we considered this variation a random effect in our data set.

Foraging behavior. We conducted fieldwork during three consecutive years from early spring to late summer (September–April, 2008–2010). Most behavioral data (85% of observation hours) were obtained from a population of eight pairs and family groups (Challhuaco site, 15 km southeast of Bariloche) banded during a long-term study of the species (Ojeda 2004, Chazarreta *et al.* 2011). Thus, foraging data were mostly based on color-ringed males and females of known age and reproductive status. Additionally, we collected similar data on adult (according to both plumage and behavior) unringed birds located at other lenga forest sites. At these sites, whenever two or more unringed adult birds of the same sex were encountered, they were studied only if they were separated by more than 3 km, representing different territorial birds.

We studied foraging behavior by following focal individuals under continued sampling of variable periods (Martin & Bateson 2008). We conducted observations during all daytime

hours (approximately from 08:00–20:00 h, = GMT-0300) and only when birds were actively foraging. To minimize the effect of weather, we did not work under conditions of heavy rain, snow or hard wind.

A territory was searched systematically until we encountered a woodpecker family. We then followed in turns, one of its members randomly selected, for as long as it remained in sight, and recorded a continuous account of its movements, foraging techniques, and other behaviors by dictating them into a tape recorder, writing field notes, and using a stopwatch to record time. Distances between members of a pair were taken into account and visually estimated. Behavior during the first 30 s after detection was excluded (Morrison 1984). In the banded population, the same individual was not observed more than once a day to increase sample independence. To obtain detailed observations we used 10 x 40 binoculars. Usually, we could approach woodpeckers closely (~ 10 m) without apparent disturbance. Most observations were of adult individuals that occurred in family groups or pairs, but six observations were of solitary males. We never met solitary females during the study.

For each adult bird we recorded: sex, foraging and searching technique, and microhabitat (portions of the trees) using variables similar to those considered in other studies of foraging behavior of woodpeckers (Selander 1966, Jackson 1970, Kilham 1972, Askins 1983, Pasinelli & Hegelbach 1997, Stenberg & Hogstad 2004, Newell *et al.* 2009). We defined searching/foraging techniques as: 1) excavating: subcambial excavation, digging deep (> 2 cm) holes; 2) debarking: striking the bill against the substrate to remove some of the exterior (bark, wood, lichens), or digging superficially; 3) probing: inserting the bill or tongue into cracks or crevices, or into excavations created by excavating, or picking insects off the bark surface; and 4) scanning: explor-

ing the substrate with lateral head movements in order to find prey. Surface gleaning (picking prey off the surface) was not considered as a tactic itself because it was rarely observed. Most near-surface prey occurred under the first layer of bark. Scanning tends to be a dynamic technique: the birds climb on a stem or branch after and before using another foraging technique, usually upward, and alternate soft pecking, listening and movement hops. During a sequence, we also recorded behaviors beyond specific foraging and searching techniques, which were categorized as: 5) food handling: when the focal bird handled prey for itself or its offspring; 6) movement: when changing location within substrate or among substrates; and 7) other behaviors, which were recorded as detailed as possible (preening, resting, vocalizing, etc.). Body position while foraging was also recorded, distinguishing between semi-horizontal with head up, semi-horizontal with head down, and vertical with head up. Type of captured prey were assigned to broad categories: wood-boring larvae; near-surface prey (mainly arachnids, adult insects or pupae), and indeterminate, when we were unable to recognize a prey (usually because of their small size). We also recorded all agonistic interactions involving focal birds: interferences (a dominant bird flies towards a subordinate and makes it fly to another location), and chases on trunks or in flight.

Foraging substrates. We defined “snag” as a standing dead tree with or without branches, “stump” as a dead tree < 3 m high, and “coarse woody debris” as downed wood. Foraging substrate diameters were estimated relative to the focal bird’s back width (folded wings), which is around 75 mm in Magellanic Woodpeckers. We estimated foraging heights in two ways: 1) relative to the tree height, in three categories (lower, mid, and higher third of the tree), and 2) absolute foraging height

above ground, in four classes (0–5 m, 5.1–10 m, 10.1–15 m, > 15 m). The absolute height was estimated using an electronic clinometer. Additional features recorded at foraging location were: bark/ no bark, branch joint or trunk fork, and woodpecker-excavated pits (foraging holes).

Data analyses. With the morphological variables recorded for skins, we explored differences between sexes using generalized linear models (GLM) with logistic link function and binomial error structure (Crawley 2007). We checked for multi-collinearity, transformed the variables as needed, and ran models with all variables. We fitted several models using different combinations of the variables as predictors, including their interactions. Fitted models were compared and hierarchically ordered using the Akaike Information Criterion (AIC) (Akaike 1973, Richards 2005), choosing the model with the lowest AIC value. Models were simplified by removing non-significant interaction terms first and then, non-significant predictors to generate the minimal adequate model (Crawley 2007).

The proportion of time spent by individuals at each variable state was used in the analyses. We arcsine $\sqrt{\chi}$ -transformed data to meet normality for the analyses. To circumvent a unit-sum constraint, variables with two or more states were reduced by excluding at least one state (the one that had the lowest values in most individuals) (Aebischer *et al.* 1993). For these analyses we only included states strictly referring to foraging techniques (probing, excavating, debarking, and scanning). We assumed no effect of the year and/or month on the foraging behavior and pooled data for analyses. To reduce bias that multiple records may create (Morrison 1984) each individual was treated as a sample unit when determining proportions and sample sizes for statistical tests (Airola & Barrett 1985). Therefore, we

added up the total minutes of the observation sessions (for each individual), and then estimated a single overall proportion of the various foraging variables.

To assess whether one of the sexes was more efficient than the other in capturing prey, we compared the success rates for each individual as the number of captured prey per minute and per number of used substrates, using the unpaired Wilcoxon signed rank test for independent data.

We analyzed differences in foraging behavior between sexes by conducting a Principal Component Analysis (PCA) to collapse a set of variables into a reduced number of new axes. All components with eigenvalues > 1 were retained for subsequent analyses. To better understand the foraging behavior relationships between sexes, we calculated niche overlap and breadth values. Foraging niche breadth was calculated for each individual with a standardized version of Levins' index (Hulbert 1978):

$$B = \frac{(1/\sum p_i^2) - 1}{(n - 1)}$$

For each variable, niche breadth (B) was calculated separately. The proportion of foraging time an individual spends foraging at resource state i is p_i , and n is the total number of resource states for the variable under consideration. Values range from one (for equal use of all resource states) to zero, for specialization on one resource state. To evaluate if one of the sexes was more stereotyped than the other, we performed comparisons between sexes for foraging diversity, using the unpaired Wilcoxon signed rank test for independent data. The degree of niche overlap was determined using Schoener's index (Schoener 1968):

$$C_{mf} = 1 - \frac{1}{2} \sum |p_{mi} - p_{fi}|$$

The index was used as an indicator of the amount of overlap between males and females in the use of resource states for a particular variable. Values range from zero (no overlap in resource use) to one (complete overlap), and \bar{p}_m and \bar{p}_f are the mean proportion of foraging time that males and females, respectively, spent at resource state i (difference between sexes at each state are summed).

We performed all statistical analyses using R statistical software version 2.11.1 (R Development Core Team, R Foundation for Statistical Computing, Vienna, Austria, www.R-project.org). PCA was conducted with the package FactoMineR v1.10 (Lê *et al.* 2008) in R. We tested normality and homocedasticity using residual plots and used parametric tests unless the data distributions violated the assumptions. All tests were two tailed; values of $P < 0.05$ were considered significant. We report median and range, and also means \pm SE.

RESULTS

Morphology. Males were larger than females in wing and tail, indicating that males were larger overall. However, the dimension that best differentiated the sexes was the bill length (culmen cord length in Table 1). The models including bill length showed the highest parsimony ranks according to AIC scores. The selected model included as predictors the culmen cord, wing, tail, and claw length. Parameter estimates for the best model are shown in Table 1.

Foraging behavior. Members of the pair nearly always foraged in close proximity (0–50 m) and therefore it was possible to estimate the distance between the focal bird and its mate. The total time of observations was 25 h for 31 males and 22 h for 21 females, spread in 164 sequences; median time per sequence was

73.3 min (1.5–94.5 min) for males and 92.0 min (1.8–107.5 min) for females. Fifty-eight percent of males were observed for 5–30 min and the rest (42%) for more than 30 min. Fifty seven of the females were observed for 5–30 min and 43% for more than 30 min.

Living trees were used by both sexes much more ($> 90\%$ of foraging time) than any other substrate type; hence, comparisons regarding microhabitat use were made only considering those substrates. As an exception, successful captured prey comparisons included observations from all substrates.

According to the PCA, the first component was linked with dimensions (size and height) of the microhabitat, while the second component was related to foraging techniques and qualitative features at the foraging locations (Table 2). Males were associated with large values of the first and second components ($R^2 = 0.4$ and 0.2 , respectively, both components $P < 0.001$, Fig. 1), while females did the opposite ($t_{50} = 5.2$, $P < 0.001$; $t_{50} = -2.9$, $P = 0.005$, PC1 and PC2, respectively).

Males foraged mostly on trunks and at lower heights than females. Females foraged on smaller substrates, which occurred higher in the trees (Fig. 2, Table 2). These correlated features of the foraging substrates resulted in a vertical separation of the sexes, with females foraging in the higher third (crown) more than in the mid and lower thirds of living trees. The highest (terminal) parts of trees were not used as much as other tree portions by either of the sexes.

Males were more associated with foraging locations characterized by the presence of holes than females. Females foraged in both microhabitats with and without bark, but locations covered by bark were the most common situation (Table 2). Closeness to limb joint or trunk fork had no association with the foraging location of Magellanic Woodpeckers. Because both sexes generally foraged on living trees, the use of dead wood as forag-

TABLE 1. Morphometric measurements (mm) of adult male and female Magellanic Woodpeckers. Estimated coefficients, standard error, and *P* value of the variables of the best model are given. The percentage difference is expressed as the difference in mean values between the sexes in relation to that for females. Means \pm SE, sample size (n), and significant differences (*) are shown.

	Males			Females			Estimated coefficient	% Difference
	Mean \pm SE	n	Range	Mean \pm SE	n	Range		
Tail	176.80 \pm 1.30	59	144.50–196	174.70 \pm 1.09	64	151–190	-0.06 \pm 0.03, <i>P</i> = 0.08	1.2
Wing	205.80 \pm 6.18	59	198.50–229	202.70 \pm 4.79	64	198.0–222.5	0.10 \pm 0.06, <i>P</i> = 0.09	2.2
Culmen Cord	54.81 \pm 0.45	59	48.50–63.94	48.75 \pm 0.39	63	43.40–56.00	0.54 \pm 0.12, <i>P</i> < 0.0001*	12.4
Tarsus	36.33 \pm 0.41	59	29.17–42.84	34.26 \pm 0.37	64	25.53–41.40	-	6.0
Toe (third)	25.47 \pm 2.56	58	21.00–36.15	24.9 \pm 2.68	63	22.73–34.48	-	2.3
Claw (third)	20.25 \pm 0.09	58	19.00–21.93	19.29 \pm 0.10	63	16.88–21.18	1.59 \pm 0.49, <i>P</i> = 0.0001*	5.0

TABLE 2. Components extracted by PCA from 18 foraging variables and constructed for 31 males and 21 females Magellanic Woodpeckers. Variables were significant $P < 0.001$ in their correlations and loadings = $|0.45|$ were used for interpretation (Aspey & Blankenship 1977).

	Component	
	PC 1	PC 2
Specific location		
Trunk	-0.76	0.34
Substrate condition		
Live	-	0.36
Relative height		
Mid	-0.70	-0.37
Higher	0.77	0.39
Foraging height		
5.1–10 m	-0.60	-0.34
10.1–15 m	0.36	-
> 15 m	0.42	0.44
Substrate diameter		
> 30 cm	-0.67	-
10–15 cm	0.69	-
< 10 cm	0.36	-
Feature of foraging location		
Bark	-	-0.52
Hole	-	0.75
Foraging techniques		
Excavating	0.35	0.50
Debarking	-	0.32
Probing	-	0.60
Scanning	-	-0.42
Body position		
Semi-horizontal head-up	0.44	-0.29
Vertical	-0.41	0.36
Eigenvalue	3.9	2.8
Explained variance (%)	23	16
Cumulative %	23	39

ing substrate is explained by females using dead branches, usually with no bark (Fig. 2).

The use of foraging locations with holes by males relates to their foraging techniques. Males regularly foraged at pits previously excavated, and at crevices or natural holes (Table 2) using excavating and probing tactics. The most common foraging technique for

both sexes was debarking (Fig. 3). Females were more mobile than males during foraging sequences and this was also reflected by their more intensive use of the scanning technique (Table 2), alternated with debarking. A higher investment of time in movements between substrates by females could be attributed to their tendency to explore small branches in the crown. Body positions adopted by females were distributed among semi-horizontal (both types: with head down and with head up) and vertical, while males foraged in a vertical position most of the time (Fig. 3).

Foraging success rate, measured as: 1) the number of prey obtained per minute and 2) per number of used substrates, was almost equal for males and females (median: 0.07, range: 0–0.28 prey/min., $Z = 268.0$, $P = 0.28$; median: 0.47 range: 0–5 prey/substrate, $Z = 304.0$, $P = 0.7$, respectively). In contrast, when comparing the type of prey, males captured more larvae than females (unpaired Wilcoxon signed rank test $P = 0.007$, Fig. 4). However, we found no differences between sexes for near-surface or indeterminate prey (unpaired Wilcoxon signed rank test, $P > 0.05$ for both comparisons). For males, 82% percent of the successful prey capture events ($n = 106$) occurred after applying the probing technique, and 14% after debarking. Females captured prey by probing in 73% of recorded events ($n = 108$), and by debarking in 25% of the records. These techniques were usually alternated with excavating (especially by males) or scanning (especially by females).

Niche breadth and overlap. Divergences between sexes in foraging behaviors were related to location within substrate, substrate diameter, and relative height (Table 3), in accordance with the previous results (Fig. 2). Females showed greater flexibility in body position on the foraging substrate ($P = 0.002$), explained by their use of horizontal and vertical postures.

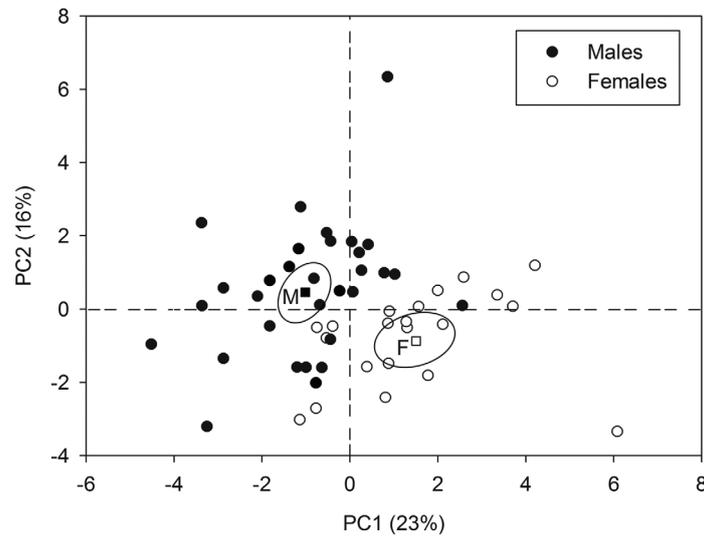


FIG. 1. PCA based on the Magellanic Woodpecker foraging behavior and substrate use variables. PC1 is mainly represented by the specific location within the foraging substrate (trunk vs branch), foraging height (relative and absolute), and substrate diameter (i.e., greater than 30 cm or between 10–15 cm); while PC2 is depicted primarily by the feature of the foraging location (with or without bark). Empty squared symbols represent barycentres (means) of samples' placement within the sex categories, with 95% confidence levels within a category given by ellipses.

Social dominance. Sixteen events of displacement between adults were recorded (44% of the agonistic interactions among family members), all of which corresponded to males displacing their mates from tree trunks. Displacement by females corresponded to adults chasing away their offspring (same or opposite sex, $n = 5$). Two immature floater females were also recorded displacing unrelated immature individuals. Adult males were also seen displacing their offspring; immature birds of the same ($n = 11$) or different ($n = 4$) sex.

DISCUSSION

Adult male and female Magellanic Woodpeckers forage in close proximity and use living lenga trees. Despite this overlap in foraging habitat, our data reveal that sexes partition their shared main substrates (live trees) into

smaller niches: differences in resource use occurred in microhabitat (parts of trees), prey type, and foraging behavior. The differential utilization of microhabitats and behaviors was accompanied by significant morphological differences, with males being larger and having larger bills. Our observations of male dominance support the notion of a possible complementary role of interference as a mechanism to maintain the resource specialization, and the foraging niche partitioning found between the sexes.

According to how the woodpecker species exploit resources, they evolved in different ways. The most common pattern is that males are usually larger than females in several morphological variables (Short 1982), hence allowing sex-specific differences in resource utilization, with females normally foraging on smaller substrates (e.g., *Picooides* spp., *Melanerpes* spp., Short 1970b; Crimson-crested

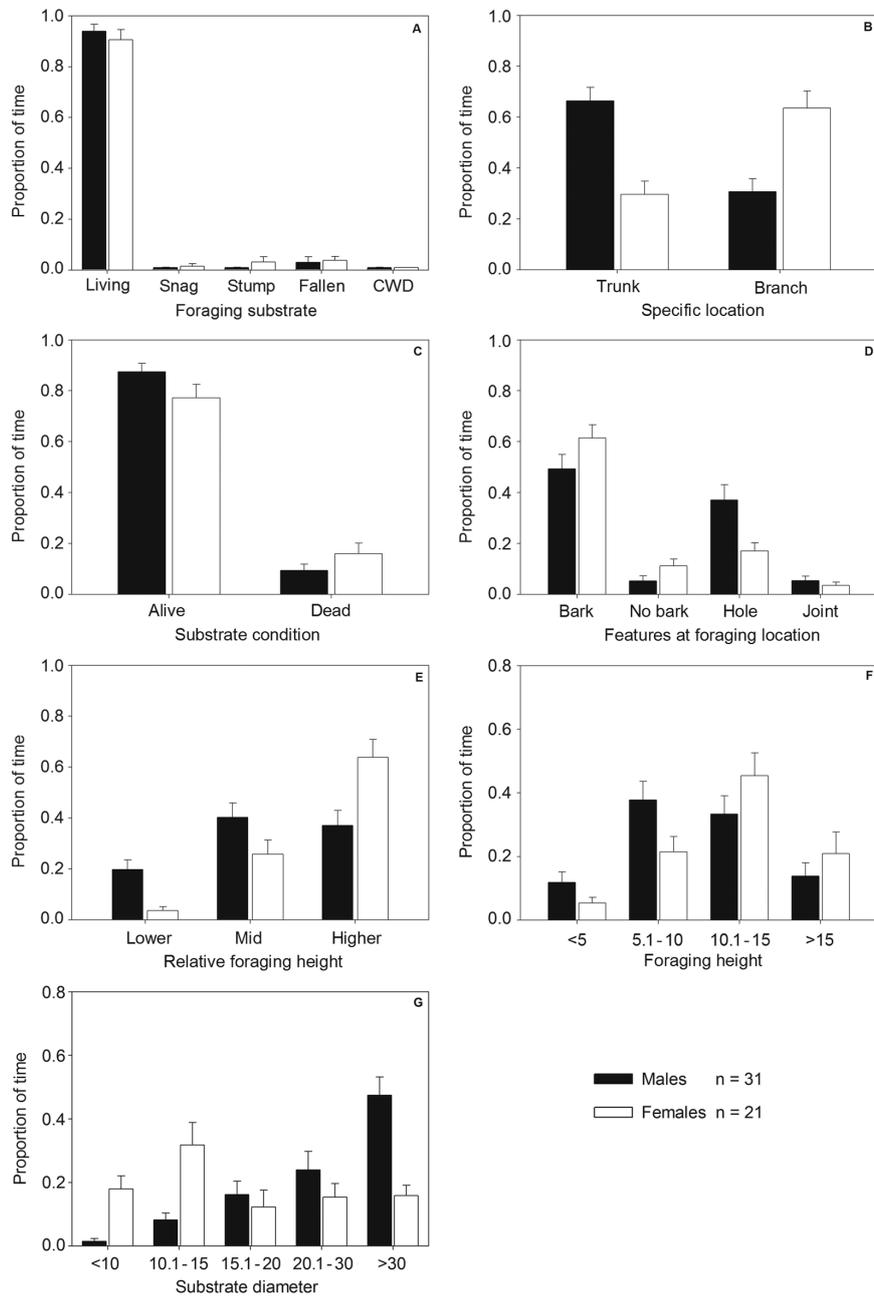


FIG. 2. Proportion of time invested by males and females of the Magellanic Woodpecker at different foraging substrates and characteristics of these foraging substrates: A) type of foraging substrates, B) tree section, C) specific substrate condition, D) characteristic of the foraging location, E) and F) foraging location height, and G) width of the specific substrate. Means and SE are shown.

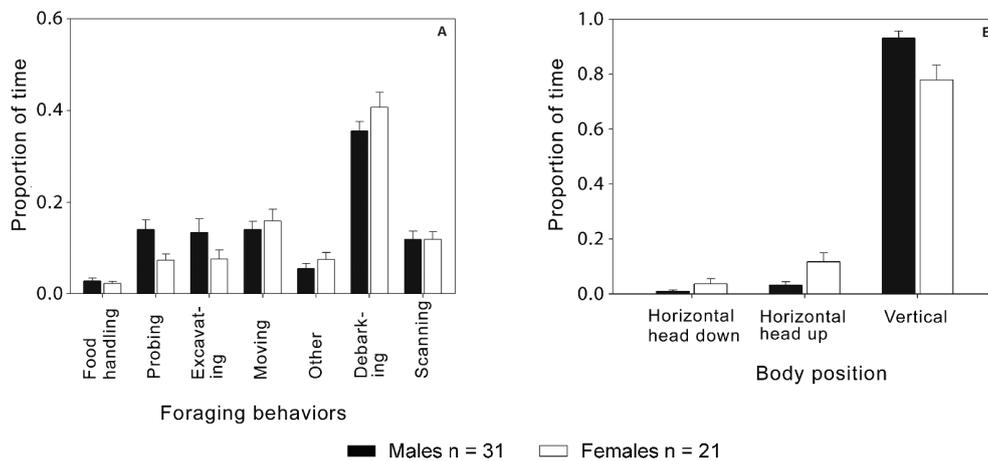


FIG. 3. Proportion of time invested by males and females of the Magellanic Woodpecker in different foraging behaviors (A), and foraging posture within the substrate (B). Means and SE are shown.

Woodpecker, *Campephilus melanoleucos*, Kilham 1972; Great Spotted Woodpecker, *Dendrocopos major*, Osiejuk 1994; White-backed Woodpecker, *D. leucotos*, Stenberg & Hogstad 2004).

Intersexual differences in morphology are more pronounced in insular woodpeckers than in mainland forms of the same or related genera because of a reduced interspecific competitive environment on islands (Selander 1966, Bennett & Owens 2002). In most woodpeckers, sexual dimorphism in bill length does not exceed 10%, but in insular species, the bill of the male is, on average, markedly larger than that of the female (e.g., 27% in the Hispaniola Woodpecker, *Melanerpes striatus*, Selander 1966). Magellanic Woodpeckers that occur in an insular-like environment show a degree of sexual bill dimorphism (12.4%) that is intermediate between truly insular and continental species. This degree of sexual dimorphism resembles populations of Gila (*Melanerpes uropygialis*) and Ladder-backed (*Picoides scalaris*) Woodpeckers occurring at the southern end of the peninsula of Baja California, which apparently are more dimorphic in bill dimensions than are mainland continental

populations of the same species (Selander 1966).

The apparently longstanding existence of the Magellanic Woodpecker without competitors in an isolated biome (Vuilleumier 1985) may explain its degree of sexual dimorphism. In support of this, Short (1970a) noted that the overlap in culmen length between the sexes is smaller in the Magellanic Woodpecker (18%) than in the Ivory-billed Woodpecker (*Campephilus principalis*) (36%) that coexisted with potential competitors. Thus, the dimorphism in bill length between males and females of the Magellanic Woodpecker is in accordance with its possibly broadened “niche” (*sensu* Short 1970a) in the absence of competitors. In parallel, we found that Magellanic Woodpecker males also consumed larger prey from living trunks with thicker bark, compared to small prey obtained on dead or living branches by females. This is in agreement with the specialization hypothesis as a mechanism for resource optimization in this species, found both in other woodpeckers (Kilham 1972, Short 1982, Aulén & Lundberg 1991) and in other bird species (Payne 1984, Winkler & Leisler 1985, Temeles *et al.* 2010).

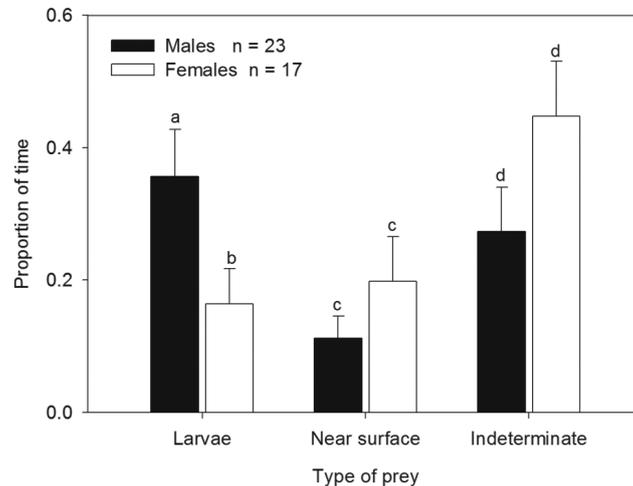


FIG. 4. Proportion of prey type captured by male and female Magellanic Woodpeckers. Means and SE are shown. Male and female sample sizes refer to the amount of individuals observed consuming prey. Prey item sample size: 47 wood-boring larvae, 21 near-surface, and 38 indeterminate for males; 26 wood-boring larvae, 32 near-surface, and 50 indeterminate for females. Different lowercase letters indicate statistical significance ($P < 0.05$) between sexes.

Although males and females overlapped in their niche breadth, the intensity of use of different substrate categories varied between sexes of the Magellanic Woodpecker. Males and females were separated primarily by foraging location and secondarily by foraging behaviors. The most important microhabitat intersexual segregation was the differentiation in trunk (mid and low parts of trees) and crown (highest tree portion). The scarce use of the terminal parts of crowns possibly acts as an anti-predator strategy from known predators, such as *Buteo* spp. or Chilean Hawk (*Accipiter chilensis*) (McBride 2000, Chazarreta et al. 2011).

Concerning the niche breadth in behaviors, males were more stereotyped than females in the body position on substrates, spending much of their time at vertical positions. Flexibility in body posture may represent adaptations to the different subniches used by female Magellanic Woodpeckers. Although both males and females mostly

used the debarking technique, males excavated deep holes more intensively than females. Other studies concerning foraging techniques of woodpeckers often found that males excavate foraging holes significantly more than females. For example, this was observed for *Melanerpes* spp. (Selander 1966, Wallace 1974), Hairy Woodpecker (*Picoides villosus*, Kilham 1965), Arizona Woodpecker (*Picodes arizonae*, Ligon 1968), White-backed Woodpecker (Aulén & Lundberg 1991, Stenberg & Hogstad 2004), and Great Slaty Woodpecker (*Mulleripicus pulverulentus*, Lamertink 2004). Vergara & Schlatter (2004) described the main foraging technique of Magellanic Woodpeckers in pure and mixed lenga forests further south in Patagonia (54°S) as the excavating of holes into hardwood followed by debarking, but differences regarding foraging behavior between sexes were not assessed. Discrepancies with our study (where debarking was most frequent technique) may be due to observations biased

TABLE 3. Foraging niche dimensions for male (n = 31) and female (n = 21) Magellanic Woodpeckers. Z-values are from unpaired Wilcoxon signed rank test. Significant differences are given (* $P < 0.05$).

Foraging category	Niche breadth				Niche overlap	
	Male		Female		Z	
	Median	Range	Median	Range		
Substrate type	0.00	0.0–0.19	0.00	0.0–0.49	376.5	0.95
Specific location	0.27	0.0–0.5	0.28	0.0–0.52	364.5	0.67
Substrate condition	0.01	0.0–1.0	0.40	0.0–1.0	416.5	1.0
Substrate diameter	0.18	0.0–0.74	0.34	0.0–0.91	419.5	0.57
Relative height	0.32	0.0–0.97	0.22	0.0–0.89	246.5	0.72
Height above ground	0.43	0.0–0.91	0.32	0.0–0.95	317.0	0.81
State of foraging location	0.29	0.0–0.71	0.44	0.0–0.92	397.5	0.80
Foraging technique	0.53	0.19–0.87	0.52	0.19–0.76	311.5	0.90
Body posture	0.01	0.0–0.4	0.13	0.0–0.47	489.0*	0.89

over one of the sexes (males) in the former study and/or due to different classification of behaviors.

Agonistic interactions observed for Magellanic Woodpeckers suggest interference competition with dominance by males over females. Social dominance where the male excludes females from favored areas or resources has been proposed as a factor relating to sexual dimorphism and differentiation in several woodpecker species (Ligon 1968, Hogstad 1978, Peters & Grubb 1983, Matthyssen *et al.* 1991, Osiejuk 1994). Although we found no difference between sexes in prey capture rates, we recorded more deep big wood-boring larvae obtained through excavating for males and more near-surface arthropods for females. This suggests males may obtain more energy gain per consumed item, and thus an advantage of social dominance. Interestingly, the same pattern was described for the size/type of prey carried by each sex to active nests during the rearing period (Ojeda & Chazarreta 2006), when the adaptive value of acquiring larger prey becomes a benefit for the offspring survival.

Acting together, morphology and micro-habitat divergence may explain acquisition of

different food resources by each sex of the Magellanic Woodpecker. A causal relationship between these two fields of sexual divergence is among the most difficult hypotheses to test in biology (cause-effect). Now, with both the morphological and behavioral divergence patterns confirmed and quantified, it would be worth designing experimental research addressing the most recognized theories of intraspecific niche differentiation, like past or present intraspecific competition, and isolated evolution (or innate behavioral preference) (Slatkin 1984, Shine 1989).

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REFERENCES

- Aebischer, N. J., P. A. Robertson, & R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74: 1313–1325.
- Airola, D. A., & R. H. Barrett. 1985. Foraging and habitat relationships of insect-gleaning birds in a Sierra Nevada mixed-conifer forest. *Condor* 87: 205–216.
- Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pp. 267–281 in Petrov, B. N., & F. Csaki (eds). 2nd International Symposium on Information Theory. Akademiai Kiado, Budapest, Hungary.
- Amadon, D. 1959. The significance of sexual differences in size among birds. *Proc. Am. Phil. Soc.* 103: 531–536.
- Armesto, J. J., P. León-Lobos, M. T. K. Arroyo. 1996. Los bosques templados del sur de Chile y Argentina: una isla biogeográfica. Pp. 23–28 in Armesto, J. J., C. Villagrán, & M. T. K. Arroyo (eds). *Ecología de los bosques nativos de Chile*. Editorial Universitaria, Santiago, Chile.
- Askins, R. A. 1983. Foraging ecology of temperate-zone and tropical woodpeckers. *Ecology* 64: 945–956.
- Aspey, W. P., & J. E. Blankenship. 1977. Spiders and snails statistical tales: application of multivariate analysis to diverse ethological data. Pp. 75–120 in Hazlett, B. A. (ed.). *Quantitative methods in the study of animal behavior*. Academic Press, New York, New York, USA.
- Aulén, G., & A. Lundberg. 1991. Sexual dimorphism and patterns of territory use by the White-backed Woodpecker *Dendrocopos leucotos*. *Ornis Scand.* 22: 60–64.
- Baldwin, S. P., H. C. Oberholser, & L. G. Worley. 1931. Measurements of birds. *Sci. Publ. Cleveland Mus. Nat. Hist.* 2: 1–165.
- Bennett, P. M., & I. P. F. Owens. 2002. *Evolutionary ecology of birds*. Oxford Univ. Press, Oxford, UK.
- Bortolotti, G. R. 1984. Sexual size dimorphism and age-related size variation in Bald Eagles. *J. Wildl. Managem.* 48: 72–81.
- Catry, P., R. A. Phillips, J. P. Croxall, K. E. Ruckstuhl, & P. Neuhaus. 2005. Sexual segregation in birds: patterns, processes and implications for conservation. Pp. 351–378 in Ruckstuhl, K. E., & P. Neuhaus (eds). *Sexual segregation in vertebrates: ecology of the two sexes*. Cambridge Univ. Press, Cambridge, UK.
- Chazarreta, L., V. S. Ojeda, & A. Trejo. 2011. Division of labour in parental care in the Magellanic Woodpecker *Campephilus magellanicus*. *J. Ornithol.* 152: 231–242.
- Crawley, M. J. 2007. *The R Book*. John Wiley and Sons, Chichester, UK.
- Grant, P. R. 1986. *Ecology and evolution of Darwin's Finches*. Princeton Univ. Press, Princeton, New Jersey, USA.
- Hedrick, A. V., & E. J. Temeles. 1989. The evolution of sexual dimorphism in animals: hypothesis

- ses and tests. *Trends Ecol. Evol.* 4: 136–138.
- Hogstad, O. 1978. Sexual dimorphism in relation to winter foraging behavior and territorial behaviour of the Three-toed Woodpecker *Picooides tridactylus* and three *Dendrocopos* species. *Ibis* 120: 198–203.
- Hurlbert, S. H. 1978. The measurement of niche overlap and some relatives. *Ecology* 59: 67–77.
- Jackson, J. A. 1970. A quantitative study of the foraging ecology of Downy Woodpeckers. *Ecology* 51: 318–323.
- Kilham, L. 1965. Differences in feeding behavior of male and female Hairy Woodpeckers. *Wilson Bull.* 77: 134–145.
- Kilham, L. 1972. Habits of the Crimson-crested Woodpecker in Panama. *Wilson Bull.* 84: 28–47.
- Lammertink, M. 2004. Grouping and cooperative breeding in the Great Slaty Woodpecker. *Condor* 106: 309–319.
- Lê, S., J. Josse, & F. Husson. 2008. FactoMineR: An R package for multivariate analysis. *J. Stat. Softw.* 25: 1–18.
- Ligon, J. D. 1968. Sexual differences in foraging behavior in two species of *Dendrocopos* woodpeckers. *Auk* 85: 203–215.
- Martin, P., & P. Bateson. 2008. *Measuring behavior: an introductory guide.* Cambridge Univ. Press, Cambridge, UK.
- Matthysen, E., T. C. Grubb, & D. Cimprich. 1991. Social control of sex-specific foraging behavior in Downy Woodpeckers, *Picooides pubescens*. *Anim. Behav.* 42: 515–517.
- McBride, P. 2000. Magellanic Woodpecker (*Campephilus magellanicus*) habitat selection in deciduous Nothofagus forests of Tierra del Fuego. M.Sc. thesis, Western Washington Univ., Bellingham, Washington, USA.
- Morrison, M. L. 1984. Influence of sample size and sampling design on analysis of avian foraging behavior. *Condor* 86: 146–150.
- Morse, D. H. 1980. *Behavioral mechanisms in ecology.* Harvard Univ. Press, Cambridge, Massachusetts, USA.
- Newell, P., S. King, & M. Kaller. 2009. Foraging behavior of Pileated Woodpeckers in partial cut and uncut bottomland hardwood forest. *For. Ecol. Managem.* 258: 1456–1464.
- Noske, R. A. 1986. Intersexual niche segregation among three bark-foraging birds of eucalypt forests. *Aust. J. Ecol.* 11: 255–267.
- Ojeda, V. S. 2004. Breeding biology and social behavior of Magellanic Woodpeckers (*Campephilus magellanicus*) in Argentine Patagonia. *Eur. J. Wildl. Res.* 50: 18–24.
- Ojeda, V. S., & L. Chazarreta. 2006. Provisioning of Magellanic Woodpecker (*Campephilus magellanicus*) nestlings with vertebrate prey. *Wilson. J. Ornithol.* 118: 251–254.
- Osiejuk, T. S. 1994. Sexual dimorphism in foraging behavior of the Great Spotted Woodpecker *Dendrocopos major* during winters with rich crops of Scotch pine cones. *Ornis Fenn.* 71: 144–150.
- Pasinelli, G., & J. Hegelbach. 1997. Characteristics of trees preferred by foraging Middle Spotted Woodpecker *Dendrocopos medius* in northern Switzerland. *Ardea* 85: 203–209.
- Payne, R. B. 1984. Sexual selection, lek and arena behavior, and sexual size dimorphism in birds. *Ornithol. Monogr.* 33: 1–53.
- Peters, W. D., & T. C. Grubb. 1983. An experimental analysis of sex-specific foraging in the Downy Woodpecker, *Picooides pubescens*. *Ecology* 64: 1437–1443.
- Radford, A. N., & M. A. du Plessis. 2003. Bill dimorphism and foraging niche partitioning in the Green Woodhoopoe. *J. Anim. Ecol.* 72: 258–269.
- Richards, S.A. 2005. Testing ecological theory using the information-theoretic approach: examples and cautionary results. *Ecology* 86: 2805–2814.
- Ruckstuhl, K. E., & T. H. Clutton-Brock (eds). 2005. *Sexual segregation and the ecology of the two sexes.* Cambridge Univ. Press, Cambridge, UK.
- Ruckstuhl, K. E. 2007. Sexual segregation in vertebrates: proximate and ultimate causes. *Integr. Comp. Biol.* 47: 245–257.
- Schoener, T. W. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* 49: 704–726.
- Selander, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. *Condor* 68: 113–151.
- Selander, R. K. 1972. Sexual selection and dimorphism in birds. Pp. 180–230 in Campbell, B. (ed.). *Sexual selection and the descent of man:*

- 1871–1971. Aldine Publ. Co., Chicago, Illinois, USA.
- Shine, R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Q. Rev. Biol.* 64: 419–461.
- Short, L. L. 1970a. The habits and relationships of the Magellanic Woodpecker. *Wilson Bull.* 82: 115–129.
- Short, L. L. 1970b. Reversed sexual dimorphism in tail length and foraging differences in woodpeckers. *Bird-Banding* 41: 85–92.
- Short, L. L. 1982. Woodpeckers of the world. Delaware Museum of Natural History. Foris Publications, Cinnaminson, New Jersey, USA & Dordrecht, The Netherlands.
- Slatkin, M. 1984. Ecological causes of sexual dimorphism. *Evolution* 38: 622–630.
- Stenberg, I., & O. Hogstad. 2004. Sexual dimorphism in relation to winter foraging in the White-backed Woodpecker (*Dendrocopos leucotos*). *J. Ornithol.* 145: 321–326.
- Témeles, E. J., J. S. Miller, & J. L. Rifkin. 2010. Evolution of sexual dimorphism in bill size and shape of hermit hummingbirds (Phaethornithinae): a role for ecological causation. *Phil. Trans. R. Soc. London B Biol. Sci.* 365: 1053–1063.
- Vergara, P., & R. P. Schlatter. 2004. Magellanic Woodpecker (*Campephilus magellanicus*) abundance and foraging in Tierra del Fuego, Chile. *J. Ornithol.* 145: 343–351.
- Vuilleumier, F. 1985. Forest birds of Patagonia: ecological geography, speciation, endemism, and faunal history. Pp. 255–304 in Buckley, P. A., M. S. Foster, E. S. Morton, R. S. Ridgely, & F. G. Buckley (eds). *Neotropical Ornithology*. Ornithol. Monogr. 36. The American Ornithologists' Union, Washington, D.C., USA.
- Wallace, R. A. 1974. Ecological and social implications of sexual dimorphism in five melanerpine woodpeckers. *Condor* 76: 238–248.
- Winkler, H., & B. Leisler. 1985. Morphological aspects of habitat selection in birds. Pp. 415–434 in Cody, M. L. (ed.). *Habitat selection in birds*. Academic Press, San Diego, California, USA.