

# Configuration and geometry of sap-holes drilled by the White-fronted Woodpecker (*Melanerpes cactorum*): effects of tree-structure, sap-traits and plant health

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**Abstract.** Several species of woodpecker drill holes in living trees to feed on flows of sap. We describe sap-holes drilled by the White-fronted Woodpecker (*Melanerpes cactorum*) on plant species in semi-arid woodlands of northern Argentina, and examine, for the first time, attributes of the plants that may help to explain the configuration and geometry of sap-holes made by a species of woodpecker. Sap-holes vary among plant species, mostly in size and shape, and in their arrangement and location on tree branches. Moreover, patterning of sap-hole are closely similar in structurally similar species, showing foraging decisions of White-fronted Woodpeckers associated with plant structure-types at a supra-specific level. In large trees, sap-holes were small, round and arranged in rows on branches or trunks of large diameter, whereas in smaller *Prosopis* trees, sap-holes were rectangular and located on branches of small diameter. In other species of tree and shrub sap-holes were large and irregular, and on branches of intermediate diameter. The size of holes was positively correlated with substrate diameter for small and intermediate branches of a given group of species, but was independent of diameter in tree species with holes on the trunk. The switch between sap-consumption strategies related to attributes of trees opens the possibility that White-fronted Woodpeckers drill sap-holes trying to maximise sap-harvesting.

**Additional keywords:** drilling behaviour, sap-feeding, sap-tree, semi-arid Chaco forests.

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## Introduction

The foraging strategies of woodpeckers (Picidae) can range from superficial flaking of bark to procure larvae, pupae and emerging adult insects, to deep excavations that can penetrate to pupa and larval galleries (Bull *et al.* 1986; Murphy and Lehnhausen 1998). Other foraging strategies include drilling holes in the bark of trees to store nuts, such as acorns, and seeds (MacRoberts 1970; MacRoberts and MacRoberts 1976; Koenig and Mumme 1987) and making holes that are used as a type of anvil, in which large or hard food items are broken into smaller pieces for consumption (Winkler and Christie 2002; Bondo *et al.* 2008). Because of their drilling ability, woodpeckers can also exploit the sap from the phloem tissue of plants. Species of the genera *Melanerpes*, *Sphyrapicus*, *Picoides* and *Campyphilus* drill holes in branches and trunks of living trees for access to the sap-carrying vessels, and feed on consequent sugar- and energy-rich sap-flows (Blendinger 1999; Eberhardt 2000; Schlatter and Vergara 2005; Kozma 2010).

The holes drilled by woodpeckers for sap-consumption vary in shape and location with the plant species being drilled (Tate 1973; Gyug *et al.* 2009) and the species of woodpecker. Sap-holes can be circular, small and clustered in rows, such as those made by the Acorn Woodpecker (*Melanerpes formicivorus*) (MacRoberts

and MacRoberts 1976); variable in size and either concentrated in canopy branches, as those drilled by the Yellow-bellied Sapsucker (*Sphyrapicus varius*) (Foster and Tate 1966; Tate 1973; Eberhardt 2000; Long 2011), or drilled over the entire tree, as those made by the White-headed Woodpecker (*Picoides albolarvatus*) (Kozma 2010) and the American Three-toed Woodpecker (*Picoides dorsalis*) (Imbeau and Desrochers 2002). Other sap-holes can be rectangular, either in branches of shrubs, as in the Red-naped Sapsucker (*Sphyrapicus nuchalis*) (Ehrlich and Daily 1988) or in trunks, as in the Williamson's Sapsucker (*Sphyrapicus thyroideus*) (Gyug *et al.* 2009). However, previous studies describing sap-consumption by woodpeckers (e.g. Eberhardt 1994, 2000; McLendon 1997; Wilkins 2001; Kozma 2010) did not explore why these species drill sap-holes in certain tree and tree-structures and which factors may influence patterns of sap-holes.

The structure of the bark and vascular tissues, as well the pressure of sap, vary across the branching of individual trees and between individuals of different species (Orians and Jones 2001; Lev-Yadun 2011). These, and other, structural and physiological differences in plants may be associated with the ability of woodpeckers to drill holes and make the sap flow. The aim of this study was to identify patterns in sap-hole drilling by

woodpeckers and explore factors that can explain them. We investigated hole drilling by the White-fronted Woodpecker (*Melanerpes cactorum*) in semi-arid woodlands of northern Argentina. This species drills holes in living branches and trunks of several species of trees and shrubs to feed on sap-flows, and sap is an important item in their diet, mainly during the dry winter season when the availability of food resources declines (Genise *et al.* 1993; Blendinger 1999; Núñez Montellano *et al.* 2013). Specifically, we explore: (1) the configuration of sap-holes in the plant species used, defined as the relative position of a hole with respect to the other holes (arrangement) and relative to the plant structure (location in branches and trunks); and to the diameter of drilled branches or trunks; (2) the geometry (shape and size) of sap-holes in the various species of plants. We then determine the importance of structural and bark variables of plants, the health of plants, and sugar concentration of sap and sap-flow of plants on the configuration and geometry of the sap-holes. Whether White-fronted Woodpeckers switch between foraging strategies when feeding on sap on different species of plant, this would suggest the ability of Woodpeckers to process information of plant attributes in order to maximise harvesting of sap.

## Materials and methods

### Study area

The study was conducted in Rivadavia Banda Sur (24°11'S, 62°53'W), province of Salta, Argentina. The area is located in the semi-arid Chaco subregion of the Chaco phytogeographical province (Cabrera 1976). The climate is subtropical, with dry winters (June–September) and warm rainy summers (December–March), and an average annual rainfall of 650 mm, concentrated between November and March (Minetti 1999). The system has a homogeneous landscape and the vegetation is characterised by sparse secondary woodlands (i.e., woodlands subjected to anthropogenic disturbances such as fire, logging and overgrazing) and shrublands.

White-fronted Woodpeckers are more abundant near ponds than away from watersources (Macchi *et al.* 2011) and the study was conducted in three sites adjacent to permanent ponds. Each of the study sites was a 100-m wide strip of vegetation surrounding a pond in a woodland sector characterised by a higher density of tall trees and an understory with lower light levels and higher humidity than in the remaining vegetation matrix (Macchi *et al.* 2011). The three ponds had a surface area of 5.8 ha, 1.3 ha and 0.6 ha respectively. The water level of the ponds varied significantly through the year; the surface area at the end of the dry season (October) was 25% of the maximum levels in summer (December–February). The upper tree stratum (8–11 m tall) is dominated by *Prosopis nigra* and *Aspidosperma quebracho-blanco* and the columnar cactus *Stetsonia coryne*. The intermediate stratum (4–8 m tall) is dominated by *Bulnesia sarmientoi*, *Geoffroea decorticans*, *Prosopis ruscifolia*, *Ziziphus mistol*, *Ruprechtia triflora* and *Tabebuia nodosa*, and the shrub stratum dominated by *Maytenus vitis-idaea*, *Capparis salicifolia* and *Capparis speciosa*. Surveys were conducted in autumn–winter in 2008 and 2009 (July–August 2008, May–June 2009 and September 2009), because sap is the main food resource for White-fronted Woodpeckers in this period (Núñez Montellano *et al.* 2013).

### Plant species and sap-consumption

The White-fronted Woodpecker is the only species of animal in the semi-arid Chaco that drills holes in living branches and trunks of shrubs and trees to feed on sap-flows (Núñez Montellano 2013). The plant species used for sap-feeding varied between survey periods, but eight species were frequently used and in all survey periods (Núñez Montellano *et al.* 2013): two shrubs – *Capparis salicifolia* and *Capparis speciosa* (Capparaceae) – and six trees – *Bulnesia sarmientoi* (Zygophyllaceae), *Chloroleucon foliolosum*, *Prosopis ruscifolia*, *Prosopis* spp. (includes *P. alba* and *P. nigra*) (Fabaceae), *Ziziphus mistol* (Rhamnaceae), and *Aspidosperma quebracho-blanco* (Apocynaceae). We analysed the patterns of sap-holes on those eight species.

White-fronted Woodpeckers live in cooperative groups and maintain permanent group territories in which all individuals forage and cooperate in territorial defence and care of nestlings (Macchi *et al.* 2011). We followed 10 groups of White-fronted Woodpeckers and delimited their territories to facilitate observations on sap-consumption; all territories were maintained throughout the entire study period (July 2008 – September 2009). Birds were mist-netted and colour-banded to ensure that the same territories were maintained by the same groups. Each group consisted of 3.0–4.4 birds. In autumn, the territories covered 0.8–2.1 ha (Núñez Montellano 2013). During each of the survey periods, we conducted focal observations on individual and groups of Woodpeckers in each territory for 2–3 days (~7 hours each day, in the early morning and late afternoon), and recorded each plant visited for sap-feeding and the time spent feeding on sap (in minutes). This ensured that holes that were drilled in plants were for sap-consumption and were made by this species of woodpecker. Of the plants used for sap-feeding, we chose one plant of each species in each territory for further characterisation of sap-holes, making a total of 6–10 plants per species (some plant species were not present in one or more territories). Chosen plants were those individuals most actively used for consumption of sap (defined as accumulated time spent by individual woodpeckers on the plant).

### Shape, size and configuration of sap-holes

The sap-holes drilled by White-fronted Woodpeckers do not change significantly once completed, as we observed over 5 years of intensive fieldwork in the study area (Núñez Montellano 2013). According to our observations, woodpeckers spend between hours and days (depending on the size of the holes) excavating a sap-hole prior to completion. The criterion for inclusion of plants in the analysis was the presence of active sap-holes, i.e. holes with definitive shape and size (excluding 'exploratory holes'; see Discussion) used for consumption during the sampling period, and excluding old sap-holes (holes from which sap was not flowing). The configuration (location and arrangement) and shape of sap-holes were described qualitatively. We classified plants into categories according to the location, arrangement and shape of most (>50%) of their sap-holes. (1) Location of sap-holes was classified as: *trunk*, where sap-holes were on the main trunk of the tree or shrub; *primary branches*, where holes were on branches arising from the main trunk in the centre of the crown or branches arising from the main forks of the trunk; *trunk and primary branches*, where sap-holes were on the main trunk of

the tree or shrub but also in primary branches; and *secondary branches*, which were the terminal branches arising from primary branches. (2) Arrangement of sap-holes was classified as: *scattered*, where most of the sap-holes were distributed at random on trunks and branches; or in *rows*, where three or more sap-holes were aligned horizontally or vertically and close together ( $\leq 50$  mm) on the trunks and branches. (3) For shape, holes were classified as: *round*, *rectangular* or *irregular* (when holes were neither round nor rectangular).

We measured the diameter of branches with active sap-holes using either a metric tape (diameters  $>15$  cm) or calipers (diameters  $<15$  cm) (Digimess, Buenos Aires, Argentina). To measure the size of sap-holes, we photographed each sap-hole with a millimetre-scaled ruler, used as a metric reference, placed on the same plane as the contour of the hole (Fig. 1). Photographs were taken with a Sony DSC-H2 6 megapixel digital camera (Sony Corp, Tokyo, Japan), from a distance of up to 10 cm, according to the size of the sap-hole, and at an angle of  $90^\circ$ , using the macro function. Images were digitally analysed with the program Image Tools (Wilcox *et al.* 2002). For each photograph ( $2816 \times 2112$  pixels) we calculated the area of each sap-hole in  $\text{mm}^2$ .

#### *Correlates of configuration and geometry (shape and size) of sap-holes*

In examining the relationship between the configuration and geometry of sap-holes with tree structure, we considered the following variables. (1) *Crown-area* and *diameter at breast height* (DBH) were used as measures of the size of plants, because the range of trunk and branch diameters available for White-fronted Woodpeckers increases with increasing plant size. For

crown-area, we calculated the area of the ellipse formed by the maximum diameter of the crown and its perpendicular. DBH was measured 1.30 m above the ground for trees and at 0.80 m for shrubs (*Capparis salicifolia*, *Capparis speciosa*). (2) *Health of plants*, measured as the proportion of dead primary branches and trunks in the plant, assuming that the greater the number of dead branches the higher the use of main trunks for drilling sap-holes. The following classes were identified: dead (no living tissues), mostly dead or dry ( $>50\%$  of crown dead), partly dead ( $\leq 50\%$  of crown dead), and wholly alive (no dead tissue). (3) *Bark-thickness*, which may affect access to phloem, influencing the size and configuration of sap-holes, was measured by extracting 1–4 samples of bark from the main trunk of the plants, at 1.30 m above ground for trees and at 0.80 m above ground for small trees and shrubs. A punch was used to extract the bark. The punch had approximately the same diameter as the birds' bills and was the same as was used to collect sap from plants. To measure the bark, we introduced the punch into the bark using a hammer before removing the punch to obtain some bark. The thickness of the bark of each plant was measured with calipers from the outer part of the bark to the phloem. (4) *Sap-flow*, which may influence the size of sap-holes drilled by Woodpeckers. We measured sap flow in autumn (May–June) 2009 by making a hole at breast height on each plant using a punch and collecting all the sap that flowed with three 2.5-cm square filter papers placed on the exposed plant tissue for 5 min. Before the collection of sap samples, we dried the filter papers in an oven at  $40^\circ\text{C}$ , weighed them with a Mettler H54AR balance (Mettler Instrument Corp., NJ, USA) and placed them in Eppendorf tubes. After collecting the sap sample, filter papers were replaced in Eppendorf tubes and kept first in a portable refrigerator and then in a freezer at  $-18^\circ\text{C}$ . In the laboratory, filter papers were weighed



**Fig. 1.** Holes drilled by the White-fronted Woodpecker for sap-consumption in: (a) *Prosopis ruscifolia*; and (b) *Chloroleucon foliolosum*. Millimetre ruler is aligned on the same plane as the contour of the sap-holes.

to record fresh weight of the sap sample, with the amount of sap in the sample the difference between dry pre-sampling weight and the post-sampling weight. Time of day, cloud cover, and precipitation are all known to affect photosynthesis and sap-flow (Lambers *et al.* 1998). However, it was not logistically possible to sample all plants at the same time of day. To minimise the effect, we sampled trees only between 1200 and 1700 h under similar environmental conditions (we never sampled during rainfall and windy days) (Pejchar and Jeffrey 2004). (5) *Sugar concentration* in sap is an indirect measure of available energy (Crawley 1983), which may influence the size of sap-holes drilled by Woodpeckers. For each sap sample (taken for sap-flow, above), filter papers were placed in an assay tube with 3 mL of 100% methanol ACS (Sintorgan, Buenos Aires, Argentina), undiluted. These samples were then stored at 4°C for later analysis. Sugar concentration was determined by spectrophotometric using the phenol-sulfuric acid method with sucrose as a standard at wavelength set at 490 nm (DuBois *et al.* 1956). We duplicated and averaged the analysis of sugar concentration for each sample. We determined total sugar concentration of the sap sample as sucrose equivalents ( $\mu\text{g}$  total sugar per  $\mu\text{g}$  of sap-sample ( $\mu\text{g } \mu\text{g}^{-1}$ ).

#### Data analyses

For all analyses, we averaged data in order to have a single value per tree of a given type of sap-hole and of a branch or trunk diameter with sap-holes. We explored the relationship between species of plants used for sap-consumption and variables of location, arrangement and shape of sap-holes in the plants with correspondence analysis (CA) and we used general linear models (GLM) to compare the size of sap-holes among plant species. We incorporated heterogeneous residual variances of species into the model to achieve homocedasticity, which was checked with residual plots. We checked for normality using residual Q-Q plots (Quinn and Keough 2002). To identify significant differences among levels of a factor we used *post hoc* tests of least significant differences (l.s.d.).

We performed a principal components analysis (PCA) to explore the relationships between individual plants used for sap-consumption relative to the configuration and size of sap-holes, and plant attributes that may affect the characteristics of sap-holes. We used two GLMs to determine the influence of individual plant attributes on either the diameter of branches and trunks used for sap-holes and the size of sap-holes. In both cases, we began by fitting GLM that ignored the variable species, and then species was added to the model as a categorical variable. Plant health was arcsine-transformed, and the remaining variables were log10-transformed to meet the assumptions of normality and homocedasticity.

To test for differences in the influence of plant attributes in each species on the mean diameter of drilled branches and trunks, and the mean size of sap-holes, we conducted general regression models (GRM) using the forward stepwise selection procedure. Entry and removal probabilities for each step of the stepwise procedure were set at 0.05 and 0.1 respectively. First, we constructed simple correlation matrices to determine which variables were correlated with one another. The variable ‘crown-area’ was correlated mainly with DBH and also with other variables (health

of plants, bark-thickness, health and sap flow) in *Aspidosperma quebracho-blanco*, *Ziziphus mistol*, *Prosopis* spp., *Prosopis ruscifolia* and *Capparis salicifolia* ( $P < 0.01$ ) so we omitted crown-area in GRM analysis for each species.

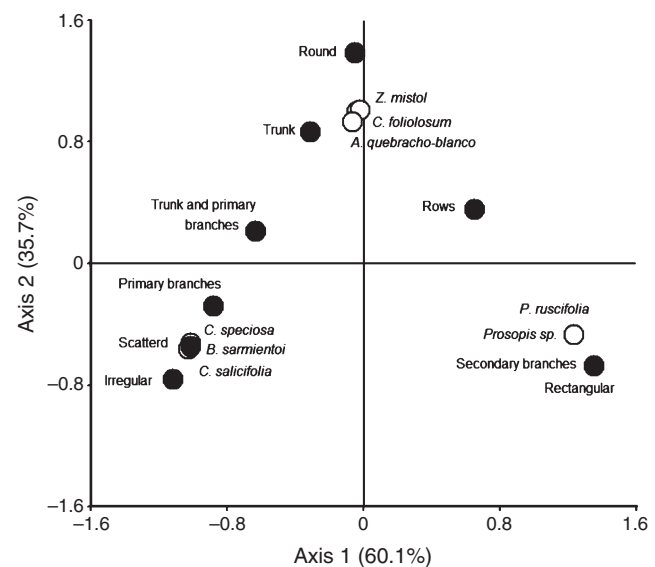
Statistical analyses were performed with InfoStat version 2012 (Di Rienzo *et al.* 2008). We present descriptive statistics as percentages, ranges and means, with significance set at  $P = 0.05$ .

## Results

### Sap-hole configuration, shape and size

Individual plants tended to sort into groups of species in the space defined by Axes 1 and 2 of the CA. These two axes explained 95.8% of among-plant variance in sap-hole configuration and shape (Fig. 2). Most individuals of *B. sarmientoi*, *Capparis salicifolia*, *Capparis speciosa* and *A. quebracho-blanco* had sap-holes in the trunk and primary branches, whereas in *P. ruscifolia* and *Prosopis* spp., individuals had sap-holes only in secondary branches (see Table S1). Sap-holes were arranged in rows in most individuals of *Chloroleucon foliolosum*, *Z. mistol*, *A. quebracho-blanco*, *Prosopis ruscifolia* and *Prosopis* spp.; holes were round in the first three species and rectangular in the latter two. In *B. sarmientoi*, *Capparis salicifolia* and *Capparis speciosa*, sap-holes were irregular and distributed on both trunks and primary branches (see Table S1 and Fig. S1).

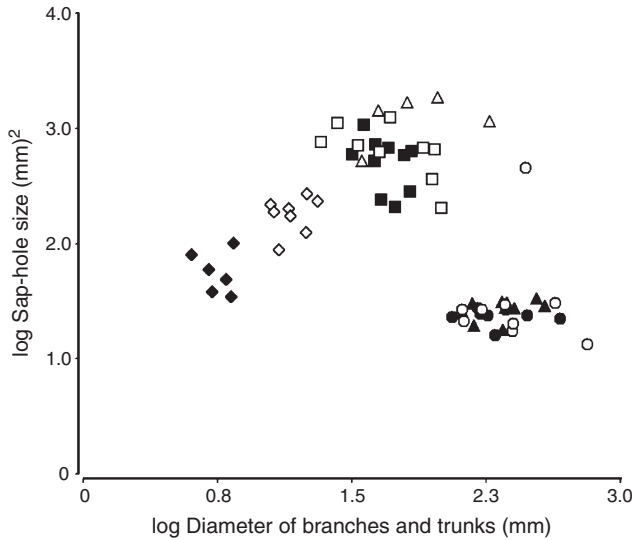
In general, the size of sap-holes increased nearly isometrically ( $b = 0.86 \pm 0.11$  S.E.) with branch diameter in small to medium-sized branches ( $\leq 10$  cm in diameter; simple linear regression,  $R^2 = 0.61$ ,  $n = 38$ ,  $P < 0.001$ ), but not in thick, primary branches or in trunks ( $b = -0.09 \pm 0.28$  s.e.;  $R^2 = 0.005$ ,  $n = 27$ ,  $P = 0.74$ ) (Fig. 3). Individual plants of five species (*B. sarmientoi*, *Prosopis*



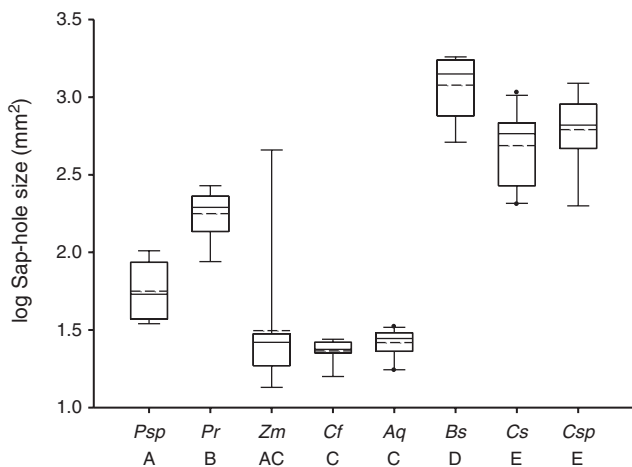
**Fig. 2.** Correspondence analysis of individual plants of eight species used for sap-consumption by White-fronted Woodpeckers, based on location of sap-holes (trunk, trunk and primary branches, primary branches, secondary branches), arrangement of sap-holes (scattered, rows) and their shape (round, rectangular, irregular). Solid symbols indicate variables and empty symbols the species of plants used for sap-consumption.

spp., *P. rusCIFolia*, *Capparis salicifolia* and *Capparis speciosa*) had sap-holes in small to medium-sized branches, but the size of sap-holes was not related to branch diameter for any species ( $P > 0.07$  for all).

The size of sap-holes used for sap-consumption differed among plant species (GLM:  $F_{7,57} = 131.34$ ,  $P < 0.0001$ ), with significant differences among five groups of species (Fig. 4). The



**Fig. 3.** Relationship between the size of sap-holes and diameter of the branch or trunk in which holes were drilled in eight species of shrub and tree.  $\triangle$  *Bulnesia sarmientoi*;  $\bullet$  *Chloroleucon foliolosum*;  $\diamond$  *Prosopis rusCIFolia*;  $\blacklozenge$  *Prosopis* spp.;  $\circ$  *Ziziphus mistol*;  $\blacksquare$  *Capparis salicifolia*;  $\square$  *Capparis speciosa*;  $\blacktriangle$  *Aspidosperma quebracho-blanco*.



**Fig. 4.** Size of sap-holes drilled in by White-fronted Woodpeckers. Plant species: Zm, *Ziziphus mistol*; Bs, *Bulnesia sarmientoi*; Cf, *Chloroleucon foliolosum*; Pr, *Prosopis rusCIFolia*; Psp, *Prosopis* spp.; Cs, *Capparis salicifolia*; Csp, *Capparis speciosa*; Aq, *Aspidosperma quebracho-blanco*. In the plots: boxes comprise 50% of the data (the two centre quartiles); horizontal line and dotted lines within boxes are median and the mean; whiskers represent 90% of the data and points beyond whiskers are outliers. Different letters indicate significant differences in sap-hole size among plant species (*post hoc* test of least significant differences, following a general linear model,  $P < 0.05$ ).

three species with smallest mean sap-hole size ( $\leq 35.7$  mm: *Chloroleucon foliolosum*, *Z. mistol* and *A. quebracho-blanco*) also had the largest mean diameter of branches and trunks with sap-holes (Table 1). *Bulnesia sarmientoi*, *Capparis salicifolia* and *Capparis speciosa* had the greatest mean sap-hole size ( $\geq 655.6$  mm), drilled in branches of intermediate diameter, whereas in *P. rusCIFolia* and *Prosopis* spp., sap-holes were intermediate in size and in branches of small diameter (Table 1).

*Correlates of sap-hole configuration and geometry*

Principal components (PC) 1 and 2 explained 61.1% of the total variance between plants used for sap-consumption (Fig. 5). PC 1 mainly represented an increase in DBH, crown-area and bark-thickness (Table 2), whereas PC 2 represented a gradient of increasing diameter of branches or trunks, sap amount and sugar concentration of sap, as well as a decrease in plant health (Table 2). Individuals of *B. sarmientoi*, *Capparis salicifolia* and *Capparis speciosa* were mainly characterised by low values of DBH, bark-thickness and canopy area; individuals of *P. rusCIFolia* and *Prosopis* spp., by high values of DBH and bark-thickness; and individuals of *Chloroleucon foliolosum*, *Z. mistol* and *A. quebracho-blanco*, by large diameter of branches and trunks with sap-holes, high amount of sap and sugar concentration, and low values of plant health.

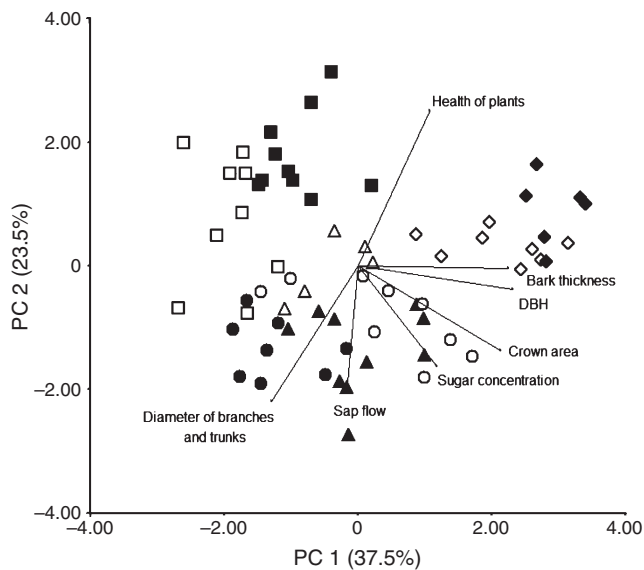
Bark-thickness and plant health were individually correlated with diameter of branches and trunks with sap-holes (Pearson correlation: bark-thickness  $r = -0.40$ , plant health  $r = -0.50$ ;  $P < 0.01$  for both). Both variables were statistically significant in the GLM ( $n = 65$ ,  $R^2 = 0.34$ ,  $F_{3,61} = 15.68$ ,  $P < 0.001$ ). A model including the categorical variable species explained a larger fraction of the variation in diameter of branches and trunks with sap-holes ( $n = 65$ , GLM,  $R^2 = 0.93$ ,  $F_{9,55} = 49.86$ ,  $P < 0.001$ ). In this model, species was the only statistically significant variable ( $F_{7,55} = 55.43$ ,  $P < 0.001$ ). In *Z. mistol* and *A. quebracho-blanco*, bark-thickness (*Z. Mistol*:  $t = 3.05$ ,  $P = 0.02$ ; *A. quebracho-blanco*:  $t = 3.30$ ,  $P = 0.01$ ) explained variation in diameter of branches and trunks with sap-holes (GRM: *Z. mistol*,  $R^2 = 0.57$ ,  $F_{1,7} = 9.33$ ,  $P = 0.02$ ; *A. quebracho-blanco*,  $R^2 = 0.58$ ,  $F_{1,8} = 10.91$ ,  $P = 0.01$ ). In *B. sarmientoi*, only crown-area ( $t = -3.98$ ,  $P = 0.03$ ) explained significant variation of diameter in branches and trunks with sap-holes (GRM,  $R^2 = 0.84$ ,  $F_{1,3} = 15.84$ ,  $P = 0.03$ ). In *Capparis salicifolia*, bark-thickness ( $t = -3.07$ ,  $P = 0.02$ ) and sugar concentration ( $t = -3.34$ ,  $P = 0.01$ ) were the only variables selected by the model (GRM,  $R^2 = 0.79$ ,  $F_{2,7} = 13.07$ ,  $P = 0.004$ ). In all models of those species, the variables entered were retained in the final model (see Table S2). In the remaining plant species, none of the plant variables explained significant variation in diameter of branches and trunks with sap-holes.

Diameter of branches and trunks with sap-holes, crown-area and plant health were individually correlated with the size of sap-holes (Pearson correlation: diameter of branches and trunks  $r = -0.40$ ; crown-area  $r = -0.57$ , plant health  $r = 0.32$ ;  $P < 0.01$  for all). Of these three variables, only diameter of branches and trunks and crown-area were statistically significant in the GLM ( $n = 65$ ,  $R^2 = 0.54$ ,  $F_{3,61} = 23.58$ ,  $P < 0.001$ ). A model including the categorical variable species explained a larger fraction of the variation in sap-hole size (GLM,  $n = 65$ ,  $R^2 = 0.89$ ,  $F_{9,55} = 49.79$ ,

**Table 1. Diameter of branches and trunks with sap-holes, and size of sap-holes drilled by White-fronted Woodpeckers in plant species of the semi-arid Chaco**

For each plant species, the number of plants, branches and trunks, and sap-holes sampled are indicated. Figures are means  $\pm$  s.d.

Plant species	Number of branches and trunks	Diameter of the branches and trunks (mm)	Number of sap-holes sampled	Size of sap-holes (mm <sup>2</sup> )
<i>Bulnesia sarmientoi</i> (n=6)	10	93.5 $\pm$ 91.5	14	1238.1 $\pm$ 1025.4
<i>Chloroleucon foliolosum</i> (n=8)	9	220.1 $\pm$ 105.1	52	25.0 $\pm$ 6.2
<i>Prosopis ruscifolia</i> (n=8)	27	13.9 $\pm$ 3.5	27	203.2 $\pm$ 75.8
<i>Prosopis</i> spp. (n=6)	17	5.5 $\pm$ 1.5	17	60.6 $\pm$ 44.7
<i>Ziziphus mistol</i> (n=9)	13	257.7 $\pm$ 153.4	97	35.7 $\pm$ 105.2
<i>Capparis salicifolia</i> (n=9)	27	50.0 $\pm$ 17.4	33	655.6 $\pm$ 431.9
<i>Capparis speciosa</i> (n=10)	24	57.0 $\pm$ 32.9	38	665.6 $\pm$ 537.5
<i>Aspidosperma quebracho-blanco</i> (n=10)	16	203.2 $\pm$ 78.9	54	27.9 $\pm$ 8.2



**Fig. 5.** Principal components analysis (PCA) of individual plants of eight species used for sap-consumption by White-fronted Woodpeckers, based on variables of sap-holes (diameter of branches and trunks with sap-holes) and plant variables that may affect characteristics of sap-holes (DBH, crown-area, plant health, bark-thickness, and amount of sap).  $\triangle$  *Bulnesia sarmientoi*;  $\bullet$  *Chloroleucon foliolosum*;  $\diamond$  *Prosopis ruscifolia*;  $\blacklozenge$  *Prosopis* spp.;  $\circ$  *Ziziphus mistol*;  $\blacksquare$  *Capparis salicifolia*;  $\square$  *Capparis speciosa*;  $\blacktriangle$  *Aspidosperma quebracho-blanco*.

**Table 2. Eigenvectors of the two first principal components of a PCA for individual plants of eight plant species used for sap consumption by White-fronted Woodpeckers**

Variable	PC 1	PC 2
Diameter of branches or trunks	-0.30	-0.50
DBH	0.53	-0.09
Crown-area	0.49	0.31
Plant health	0.25	0.57
Bark-thickness	0.51	-0.01
Amount of sap	-0.04	-0.43
Sugar concentration	0.27	-0.37

$P < 0.001$ ). In this model, species was the only statistically significant variable ( $F_{7,55} = 26.23$ ,  $P < 0.001$ ). In *Chloroleucon foliolosum*, bark-thickness ( $t = -7.36$ ,  $P = 0.0007$ ) and DBH ( $t = -3.34$ ,  $P = 0.02$ ) explained variation of sap-hole size (GRM,  $R^2 = 0.91$ ,  $F_{2,5} = 27.13$ ,  $P = 0.002$ ), whereas the remaining variables were non-significant. In *Capparis speciosa*, DBH ( $t = -2.85$ ,  $P = 0.02$ ) was the only variable selected by the model (GRM,  $R^2 = 0.54$ ,  $F_{1,7} = 8.12$ ,  $P = 0.02$ ). In all models of those species, the variables entered were retained in the final model (see Table S2). In the remaining plant species, none of the plant variables significantly explained variation in size of sap-holes.

**Discussion**

The shape, size and configuration of sap-holes made by White-fronted Woodpeckers varied between the species of tree and shrub, and suggest different foraging strategies on different sap-plants. The main differences in sap-hole configuration and geometry between plant species were in the shape of the holes, in the arrangement of holes on the tree, and the relationship between the size of sap-holes and the diameter of the branch or trunk. Structural traits of the sap-plants (diameter of branches and trunks used) explained most of the differences in the size of sap-holes. Moreover, the configuration of sap-holes was very similar in structurally similar plant species, suggesting sap-consumption behaviour by Woodpeckers is determined at a supra-specific plant level.

The holes drilled by White-fronted Woodpeckers share similarities with, but also differ from holes drilled by other species of woodpecker. White-fronted Woodpeckers drill small rectangular sap-holes arranged in vertical rows on secondary branches in *Prosopis* species and small round sap-holes, called exploratory holes, arranged in horizontal and vertical rows on thick branches or trunks of large tree species. Further, when drilling in other species of tree and shrub (*Bulnesia sarmientoi*, *Capparis salicifolia* and *Capparis speciosa*), each exploratory hole is enlarged but the holes are scattered on the branches and are never arranged in columns. Sapsuckers (*Sphyrapicus* spp.) drill two main types of hole: primary bands and progressive columns. Primary bands are small horizontal rows of exploratory holes. If these holes are productive, sapsuckers drill holes above them, forming a series of columns of larger holes (Tate 1973; Ehrlich and Daily 1988; Gyug *et al.* 2009). Experiments

on the translocation of organic solutes in plants showed that removing a bark ring from a stem blocks transportation of sucrose and other sugars (from the apical zone to the base), causing accumulation of carbohydrates above the girdled area and depletion below it (Azcón Bieto and Talón 2003). By enlarging holes from the upper edge of the wound and drilling new rows of holes above existing ones, White-fronted Woodpeckers would be gaining access to accumulated carbohydrates. In sapsuckers, the types of sap-holes depends on the plant species and the season (e.g. Tate 1973; Gyug *et al.* 2009), although the species of plants used often varies seasonally, making it difficult to distinguish between effects. In the White-fronted Woodpecker, climate can be excluded as a factor determining the type of sap-hole because the configuration and geometry in each plant species is similar throughout the year (Núñez Montellano 2013).

The size of sap-holes drilled by White-fronted Woodpeckers was related to the branching structure of plants. Sap-holes in trunks and thick branches (>15 cm) were almost always small (<40 mm<sup>2</sup>). There was also a positive relationship between the size of holes drilled in branches of small and intermediate diameter (≤10 cm) of a group of species of trees and shrubs (*B. sarmientoi*, *Prosopis* spp., *P. ruscifolia*, *Capparis salicifolia*, *Capparis speciosa*). In Acorn Woodpeckers, the size of holes drilled in *Quercus agrifolia* was positively related to the diameter of the middle and upper canopy branches that were drilled (MacRoberts 1970). The almost complete absence of large to medium-sized holes in trunks may indicate that White-fronted Woodpeckers are physically unable to dislodge thick pieces of the woody bark of tree trunks. However, the Woodpecker's morphology could not explain the low variability in foraging strategies within a given plant structure (e.g. the absence of sap-holes in secondary branches in most species of sap-tree). A better interpretation might be that, in general, small branches offer smaller quantities of sap but of higher quality, whereas trunks provide a greater amount of diluted sap. The concentration of nutrients (e.g. carbohydrates) is expected to be higher in branches than in trunks owing to the proximity to foliage where sugars are synthesised and exported (Woodruff and Meinzer 2011). However, the diameter of sap-carrying vessels is proportional to stem-size (Olson and Rosell 2013) and the small sap-holes in trunks of large plant species would provide enough sap for consumption (as observed in *Chloroleucon foliolosum*, *Z. mistol* and *A. quebracho-blanco*).

In a few plant species, the configuration and geometry of sap-holes were related to intraspecific variation in plant attributes. As expected, the diameter of branches and trunks drilled by Woodpeckers was negatively related to bark-thickness in *Capparis salicifolia*. However, White-fronted Woodpeckers drilled sap-holes in primary branches and trunks in large *Z. mistol* trees, which also had thick bark, and the diameter of drilled branches and trunks was positively related to bark-thickness in *A. quebracho-blanco*. These latter results run counter to the prediction that bark-thickness would hinder access to phloem vessels. However, the bark of both *Z. mistol* and *A. quebracho-blanco* has fissures where the thickness is reduced and where Woodpeckers can drill holes to obtain access wide sap-carrying vessels. White-fronted Woodpeckers made larger holes in *Chloroleucon foliolosum* plants with thin bark and also as in *Capparis speciosa*, in small plants. Small trees and shrubs would

have less well-developed outer bark, which would allow White-fronted Woodpeckers to drill larger holes to extract sap while reducing energy and time expenditure. Indeed, Kozma (2010) suggested that White-headed Woodpeckers consumed sap of smaller ponderosa pine (*Pinus ponderosa*) trees because it may be easier to drill into the thinner bark of small trees than in the thicker bark of larger trees.

In summary, the White-fronted Woodpecker shows great plasticity in its ability to exploit sap, an unusual behaviour in the family Picidae, and one that allows them to cope with the seasonality typical of semi-arid temperate regions. This plasticity is manifested in the exploitation of shrubs and trees differing in structural and textural attributes that influence the drilling of sap-holes. Woodpeckers switch between foraging strategies according to differences in the characters of different plant species, notably, differences in the configuration and geometry of holes associated with the dichotomy between drilling in main trunks or in primary and secondary branches. This flexibility of drilling behaviour may be an important adaptive trait, which could enable individuals to utilise a wide range of habitats, often with extreme environmental conditions and wide changes in food availability. Future studies should aim to elucidate the most relevant interpretation of our results, namely the White-fronted Woodpecker drill sap-holes trying to maximise sap-harvesting, in a trade-off between gains in sap quantity and sap quality. Given the difficulty in accurately quantifying the sap consumed in the wild, we recommend experimental laboratory trials as the best way to achieve this.

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