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Tree use, niche breadth and overlap for excavation by woodpeckers in subtropical piedmont forests of northwestern Argentina

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Abstract. Studies dealing with the selection of tree species and characteristics for cavity-nesting birds are important to evaluate the abundance and quality of available resources in the environment. The aim of this study is to characterize the use of trees by woodpecker species in the subtropical piedmont forests of northwestern Argentina by using the analysis of niche selection, breadth and overlap in a total of five woodpecker species of different body size found in these subtropical forests: White-barred Piculet *Picumnus cirratus* (small woodpeckers), Golden-olive Woodpecker *Colaptes rubiginosus*, Golden-green Woodpecker *Piculus chrysochloros*, Dot-fronted Woodpecker *Veniliornis frontalis* (medium-sized woodpeckers), and Cream-backed Woodpecker *Campephilus leucopogon* (largest woodpeckers). From a total of 54 tree species, only 15 were used by these woodpecker species. Primary excavator species were moderate specialists in tree use (Levin's index), and they showed selection according to their availability (Ivlev's index) of four of the fifteen tree species (*Calycophyllum multiflorum*, *Amburana cearensis*, *Cedrela balansae*, *Astronium urundeuva*) and snags. There was a high overlap (Morisita's overlap index) in the use of tree species between *Picumnus cirratus* and medium-sized woodpeckers, while less overlap was found between *Campephilus leucopogon* and other woodpecker species. Both living trees and snags were used by the woodpeckers, although snags were more important for small and medium-sized woodpeckers, whereas living trees were more important for *Campephilus leucopogon*. Both snags and living trees had a large diameter at breast height (DBH) in > 50 cm. Results show the existence of different cavity-excavation niches for woodpecker species in subtropical forests of Argentina, and they allow us to identify the important relationships between these birds and the available tree species. Thus, the results of this work may be useful to develop sustainable forest management guidelines for this group of birds.

Key words: cavity-nesting birds, Neotropics, niche breadth, overlap, subtropical forest, tree cavities, woodpeckers

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INTRODUCTION

Studies on niche breadth and overlap are used to examine possible mechanisms associated with the use and selection of resources (Swihart et al. 2003, Slatyer et al. 2013). Generalist species use a wide range of resources and specialists use a comparatively narrow range of resources. As they are at the two opposite ends of a resource gradient of use, differences in the niche breadth may be determined (Julliard et al. 2006, Clavel et al. 2011, Le Viol et al. 2012). The availability and characteristics of different kinds of resources may determine the abundance, breeding, and survival of animal species (Bernstein et al. 1991, Pulliam 2000, Johnson et al. 2006).

Woodpeckers (Picidae family) are considered primary excavators since they create their own cavities (Gibbons & Lindenmayer 2002, Martin et al. 2004). The cavities made by these excavators are then used by other animal species; thus, they are often considered keystone "ecosystem engineers", increasing cavity availability within forests (Gibbons et al. 2002, Aitken & Martin 2007, Cornelius et al. 2008, Robles & Martin 2013). For excavating, each woodpecker species has particular resource requirements and characteristics, such as particular tree species, diameter at breast height, height or wood decay. Therefore, not all available trees are suitable for use (Martin et al. 2004, Cockle et al. 2011, Edworthy & Martin 2013). Consequently, bird species may differ in their selection of tree species (Politi et al. 2009, Cockle et al. 2011, Lorenz et al. 2015, Ruggera et al. 2016). The selection of different types of substrate (and their characteristics) might turn certain woodpeckers´ species into specialists for excavating (Nappi & Drapeau 2009, Stillman et al. 2019). Hence, information on cavity tree use may be essential to propose guidelines for the conservation and management of forest´s bird species (Lindenmayer et al. 2000, Marzluff et al. 2004, Manly et al. 2007).

The piedmont forest of NW Argentina is currently subject to a very intense selective forest extraction with little or no planning designed to ensure the maintenance of the forest's economic and ecological value (Grau & Brown 2000, Pacheco & Brown 2006). Thus, it is necessary to understand the resource requirements of primary excavating birds and to develop forest management schemes to ensure the conservation of these species, particularly of woodpeckers, which are very sensitive to environmental change due to their specific ecological requirements (Ojeda & Chazarreta 2014, Vergara-Tabares et al. 2018). Despite the studies carried out in the last decade in these forests (Politi et al. 2009, 2010, 2012, Albanesi et al. 2016, Ruggera et al. 2016), further specific studies of tree use need to be carried out. The aim of this study is to characterize tree use, niche breadth and overlap in the use of tree species for excavation by woodpeckers. Different species of woodpeckers of variable body size were studied. Consequently, differences in usage, selection, and characteristics of the trees could be expected, in addition to differences in niche breadth and overlap. With this information we hope to provide help and guidance in the conservation of woodpeckers in this ecoregion.

METHODS

Study area

The piedmont forest is located in the subtropical forests of northwestern Argentina, between 400 and 900 m a.s.l. and it constitutes a phytogeographic unit of the seasonal forests in South America (Prado 2000). It is characterized by seasonal weather and an annual rainfall ranging between 800 and 1000 mm, concentrated in the summer. Mean annual temperature averages 21.1 °C (Arias & Bianchi 1996). The dominant tree species in the piedmont forest are *Calycophyllum multiflorum*, *Phyllostylon rhamnoides*, *Anadenanthera colubrina*, *Myroxylon peruiferum* and *Astronium urundeuva* (Brown et al. 2001). Around 90% of the original area of the piedmont forest has been transformed into agricultural and urban areas (Brown & Malizia 2004). Forest extraction is performed in a large extent of the remaining forest. Only a few hundred hectares have been preserved for at least 45 years and can be considered reference sites (Politi et al. 2009). This study was carried out in three reference sites of the piedmont forest, located in the province of Jujuy, Argentina (23°28′11.43″S–64°35′22.86′′W; 23°45′37.10″S–64°48′57.30′′W; 23°56′10.14″S–64°54 44.83′′W). At each site, an area of 100 ha was selected for fieldwork.

Tree measurements and search for excavated cavities

Fieldwork took place from July to February (during the woodpeckers´ breeding season), during 2014–2015, 2015–2016, and 2016–2017 and 2017–2018. In order to obtain the data on tree availability for excavation by woodpeckers, 60 plots of 50 × 50 m (0.25 ha) were randomly placed inside a 100-ha study area and separated by at least 150–200 m. Within each plot, all trees >10cm diameter at breast height (DBH) were identified and their DBH measured. The number of snags (standing dead trees) was also registered together with their DBH but species were not identified.

The searching and inspection of excavated cavities were carried out within the plots and also in transects within each study area: six linear transects of 1.2 km long × 50 m width were arranged, at least 150 m apart. This allowed us to find a greater number of cavities comparable with the available trees (unused trees) since the plots were close to the examined transects. All excavated cavities in these transects were inspected with a mini video camera attached to an extensible pole which reached a maximum of 16 m (Richardson et al. 1999). The excavated cavities in transects were georeferenced and the tree species housing the cavity was identified (snags were considered as a different category) together with its DBH value. In addition, the cavity height above the ground (with an extensible pole), the tree height (visually estimated) and the location of the cavity in the tree (i.e., trunk or branch) were recorded. Concerning the cavities found in the branches of living trees, we distinguished living from dead branches.

Woodpeckers were grouped into small, medium and large species according to body sizes and the diameter of the cavity entrance that they excavate using prior knowledge of the species in the study area (Ruggera et al. 2016, Schaaf et al. 2020). Thus, we inferred that cavity entrances with a diameter lesser for smaller than 5 cm were excavated by the smallest woodpecker in the area, the White-barred Piculet *Picumnus cirratus*; cavity entrances with a diameter between 5 and 10 cm were excavated by medium-sized woodpeckers, such as the Golden-olive Wooodpecker *Colaptes rubiginosus*, the Golden-green Woodpecker *Piculus chrysochloros*, and the Dot-fronted Woodpecker *Veniliornis frontalis*, and cavity entrances equal or greater than 10 cm in diameter were excavated by the largest woodpecker species in the area, the Cream-backed Woodpecker *Campephilus leucopogon*. In all cases, cavities had been excavated recently or in previous seasons, with no traces of enlargement by another animal enlarged. Therefore, cavities belonging to different woodpecker species were easily identified.

Statistical analyses

We calculated mean (± SD) tree density, DBH, and tree height of all the trees present in the plots (the complete dataset). We compared the mean DBH and tree height between unused and the excavated trees, for each of group of woodpeckers, using a non-parametric Wilcoxon test (W). In addition, DBH, cavity height and tree height were compared among three woodpecker groups using non-parametric Kruskal-Wallis tests (H). All analyses were performed using the Infostat software (Di Rienzo et al. 2008).

We evaluated the selection of trees by woodpecker species using the Ivlev's index (E) (Jacobs 1974, Bhusal et al. 2015). The selection formula used is E = (r - p)/(r + p); in which r is the total percentage of nests, shelters or roosts, and p is the percentage of tree species available (unused tree). The Ivlev's index varies between -1 (maximum negative selection, they avoid it), +1 (maximum positive selection) and 0 is the central value of the non-selection. Due to the fact that it is not possible to evaluate the degree of significance with this index, a value greater than 0.6 was considered to indicate selection, from 0 to 0.6 to indicate the non-selective use (species use resources according to availability), and negative values mean avoidance (Atienza 1994). Tree species with a low frequency of use were grouped in the category "other tree species" in this analysis (see Fig. 1 for details).

To examine whether woodpecker groups are specialists or generalists, the niche breadth was calculated for each group, using Levin's standardized index (Colwell & Futuyama 1971). This index is calculated according to the following equation: $B_a = B\text{-}1/n\text{-}1$ where B_a is the Levin's standardized index, n is the number of total tree species which are used by woodpeckers and B is the Levins Index. B results from $B = 1/\Sigma\ p_j^2$ where p_j is the proportion of each excavated tree species and ranges from 0 to 1. For values near 0, species are considered specialists as this indicates that the species uses a relatively low amount of items (resources) and particular tree species. Species with intermediate values, between 0.3 and 0.6, are considered moderate specialists, while species with values greater than 0.6 are treated as generalists (Krebs 1998).

We also calculated the overlap (O) in the use of tree species among the woodpecker groups using the Morisita's overlap index (Krebs 1989):

$$M_{ab} = \frac{2\Sigma p_{ai} p_{bi}}{\Sigma p_{ai}\left(\frac{n_{ai}\text{-}1}{\Sigma\ n_{ai}\text{-}1}\right) + \Sigma p_{bi}\left(\frac{n_{bi}\text{-}1}{\Sigma\ n_{bi}\text{-}1}\right)}$$

where p_{ai} is the proportion of woodpeckers of the species a which excavates the tree species i, p_{bi} is the proportion of woodpeckers of the species b which excavates the tree species i, n_{ai} is the number of woodpeckers of the species a which excavates the tree species i and n_{bi} is the number of woodpeckers of species b in the tree species i. This index ranges from 0 to 1, where 0 indicates no overlap and 1 indicates a total overlap in the resource use (Horn 1966).

In these analyses, tree species, minimum DBH and tree height used by each species were taken into account, according to the results obtained: the White-barred Piculet and medium-sized woodpeckers excavated trees with a DBH greater than 10 cm, and height > 3 m; while Cream-backed Woodpecker excavated tree species with DBH values higher than 35 cm, and tree height > 13 m (see Table 1 for details).

RESULTS

Tree density was approximately 401.2 ± 79.32 individuals/ha and the trees belonged to 54 species, with an average DBH value of 27.53 ± 8.39 cm and a height of 14.12 ± 1.91 m. The dominant species were *Phyllostylon rhamnoides* (34.40% of the individuals with a DBH greater than 10 cm), *Anadenanthera colubrina* (28.50%) and *Calycophyllum multiflorum* (11.60%). The less abundant tree species were *Cedrela balansae* (4.40%), *Astronium urundeuva* (4.30%) and *Amburana cearensis* (0.40%); snags were also a relatively rare item (0.80%, 12.80 ± 7.41 individuals/ha).

We found 211 excavated cavities in living individuals of 15 tree species, as well as in snags (Fig. 1). Seventy-eight cavities were excavated by *Picumnus cirratus* (small woodpeckers), mostly in dead substrates (42% — snags and dead branches), 16% in *A. colubrina*, 11% in *C. multiflorum* and 10% in *A. cearensis*. We found 52 cavities excavated by medium-sized woodpeckers, in dead substrates (42% — snags and dead branches), 24% in

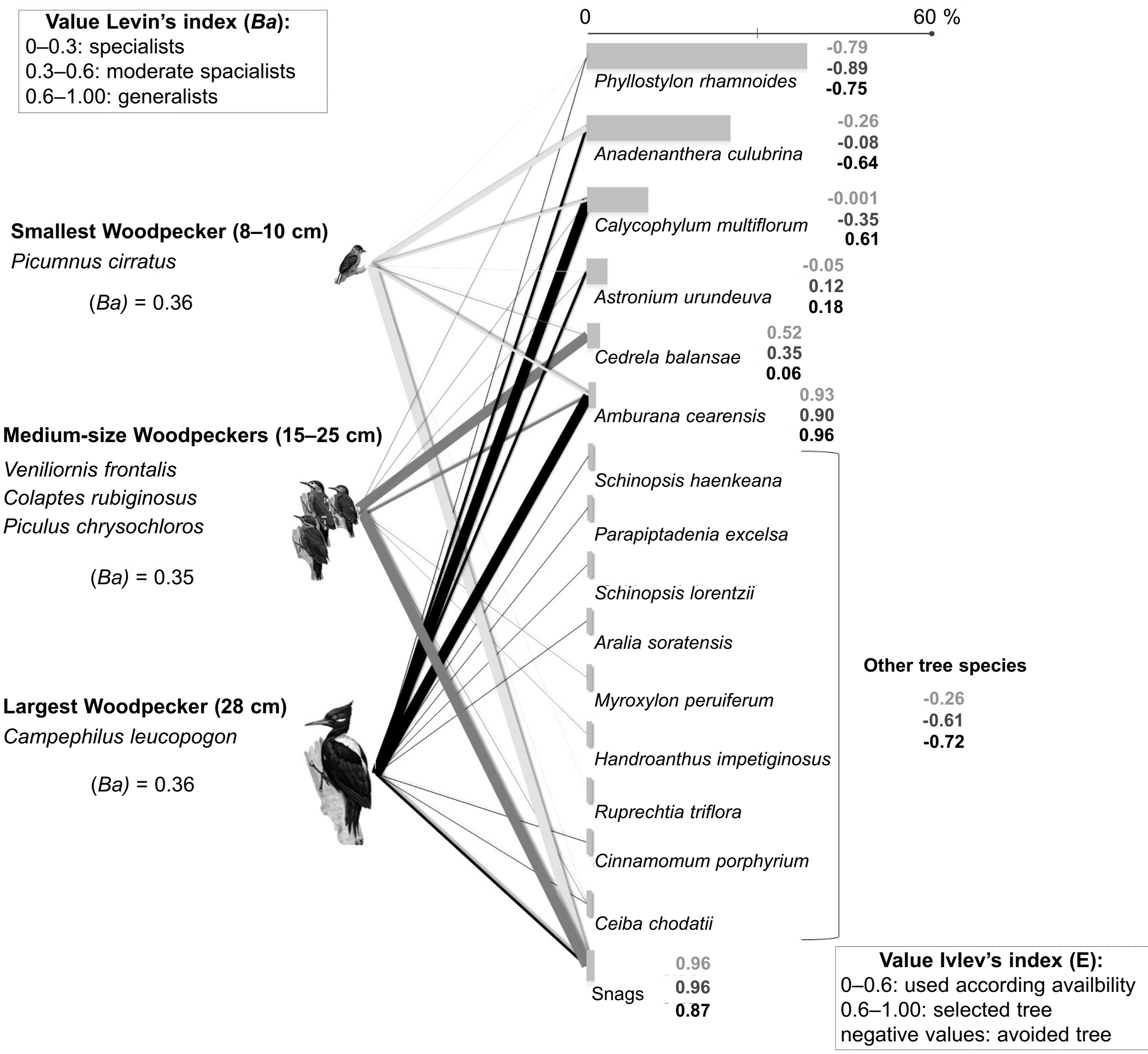

Fig. 1. Tree species used by woodpeckers in the Piedmont forest of northwestern Argentina. Lines indicate the tree species in which woodpecker groups excavated their cavities (thick lines: > 40%, medium lines: 10–40% and thin lines: < 10%). Bars show data on tree abundance. Light grey, grey and black values describe the Ivlev's selectivity values (E) for each woodpecker species.

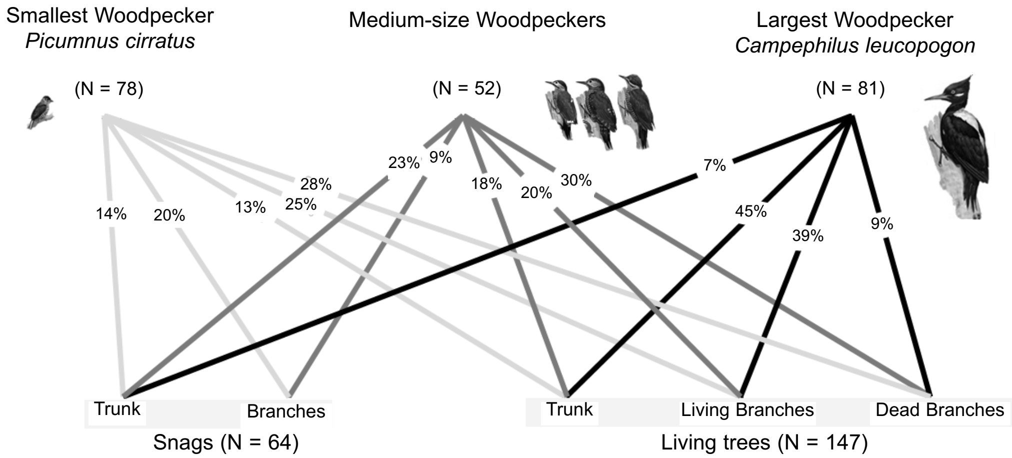

Fig. 2. Percentage of use of the living tree species and snags, in trunks and branches (living or dead) for the three woodpecker groups from Piedmont forest in northwestern Argentina.

A. colubrina and 9% in *C. balansae*. Large woodpeckers excavated 81 cavities in trees of *C. multiflorum* (39%), 19% in *A. cearensis* and 12% in dead substrates (snags and dead branches) (Fig. 1, Fig. 2).

The available trees (unused trees) were shorter and with smaller DBH when compared with the species of trees excavated by woodpeckers, except for medium-sized woodpeckers, for which there were no significant differences between the height of the available trees and that of trees excavated by these group (Table 1). We also found significantly larger DBH, cavity height and tree height in the cavities excavated by *Campephilus leucopogon* than in the cavities excavated by the other two woodpecker groups. We found no significant differences in DBH, cavity height and tree height among cavities excavated by *Picumnus cirratus* and medium-sized woodpeckers (Table 1).

Table 1. Average values ± SD, range (in brackets), and the Wilcoxon test parameter (W) of traits measured in available unused trees and in woodpecker-excavated trees. Kruskall Wallis test parameter (H) for cavity height between excavated trees by the woodpecker species. Different letters indicate significant differences ($p < 0.05$) for the K-W test.

	Available unused trees	Excavated trees	W	p
DBH (cm)				
Picumnus cirratus	32.80 ± 15.97 (10.70–135.61)	48.61 ± 21.32^{a} (11.40–89.49)	47496	p < 0.001
Medium-sized woodpeckers	32.80 ± 15.98 (10.70–135.61)	47.93 ± 25.66^{a} (12.41–108.11)	30962	p < 0.001
Campephilus leucopogon	50.16 ± 15.89 (35.01–135.60)	61.54 ± 15.33^{b} (35.15–123.57) H = 30.59, p < 0.001	19139	p < 0.001
Tree height (m)				
Picumnus cirratus	15.78 ± 7.270 (3.00–28.00)	18.80 ± 6.23^{a} (3.48–26.00)	38217	p < 0.001
Medium-sized woodpeckers	15.78 ± 7.270 (3.00–28.00)	16.89 ± 6.07^{a} (3.92–27.00)	22474	p = 0.077
Campephilus leucopogon	19.41 ± 15.20 (13.20–28.00)	22.59 ± 4.39^{b} (13.80–28.00) H = 11.40, p < 0.001	6546.5	p < 0.001
Cavity height (m)				
Picumnus cirratus		11.83 ± 4.64^{a} (2.15–16.5)		
Medium-sized woodpeckers		11.21 ± 3.68^{a} (2.27–18.00)		
Campephilus leucopogon		13.08 ± 3.94^{b} (4.10–19.00) H = 15.89, p < 0.001		

For all woodpecker species, similar results were found in the selection of tree substrates (*A. cearensis* and snags), in the use according to their availability (*C. balansae*) and the avoidance of abundant tree species, such as *A. colubrina* and *P. rhamnoides*. For details about the tree species selected, avoided, or used in proportion to their availability see Fig. 2 (E, Values Ivlev's index).

The three woodpecker groups were specialists in the use of a few tree species (B_a= 0.35 and 0.36) (Fig. 1). Overlap in the use of tree species was high between White-bared Piculet and medium-sized woodpeckers (O = 0.96) while less overlap was found between the Cream-backed Woodpecker and White-barred Piculet (O = 0.58) and medium-sized excavators (O = 0.46).

DISCUSSION

Our results suggest that woodpeckers from the piedmont forest of northwestern Argentina are largely reliant on a rather small number of tree species and indicate that there are differences in the use of tree species (and their characteristics) among woodpeckers. This confirms the existence of different ecological niches for excavation, which allows us to identify the important relationship between these bird species and the available tree species (Virkkala 2006, Vierling et al. 2009, Nappi et al. 2015). We found that woodpecker species do not select and rarely use the tree species *P. rhamnoides*, one of the most abundant species in these forests, suggesting that excavation is not necessarily related to tree abundance in the landscape. The avoidance of *P. rhamnoides* may occur due to the unsuitability of this species for excavation (species of low height and small DBH), possibly due to the lack of an appropriate degree of hardness for excavation or because it breaks easily and does not last in time (Schepps et al. 1999, Lorenz et al. 2015).

The largest woodpecker species, *Campephilus leucopogon*, excavates in larger trees (>DBH) and at a higher height when compared with the other woodpecker species. Additionally, *Campephilus leucopogon* mainly used trunks of living trees which was expected as they have greater excavation strength (Kosinski & Winiecki 2004, Sandoval 2008, Lorenz et al. 2015, Albanesi et al. 2016). Other studies showed that living trees with harder wood and thicker walls had higher nest success (Albano 1992, Christman & Dhondt 1997, Martin et al. 2004). The use of snags and dead branches by *Picumnus cirratus* and medium-sized woodpecker species may be explained by their body size and excavating strength. Excavation may be energetically expensive; therefore, species with relatively low excavation strength might have higher benefits due to the lower energy expenditure in excavation (Schepps et al. 1999, Martin et al. 2004, Lorenz et al. 2015).

For the three groups of excavators in this study, DBH and tree height were significantly larger in cavity trees than in unused trees, suggesting that large trees are a key resource for excavators in piedmont forests. Thus, tree species is not only considered a priority for this group of birds, but also their individual characteristics, such as snags with DBH of 40–50 cm (for small and medium-sized woodpeckers) and living trees with a DBH > 60 cm (for large woodpeckers). Moreover, the niche overlap analysis showed that *Picumnus cirratus* and medium-sized woodpeckers have similar use of tree species, but differ from the tree species used by *Campephilus leucopogon*. Therefore, between the smaller and medium-sized excavators, there may be competition for the use of available tree species (Kosinski & Winiecki 2004, Pasinelli 2007, Ónodi & Winkler 2016). The intermediate values from Levin's analyses suggest that woodpeckers do not use a single tree species, but instead specialize in use of several tree species (Krebs 1998). Specialist species are more sensitive to habitat disturbances, like forest logging, which may affect their abundance or even their occurrence (Boyce & McDonald 1999, Marzluff et al. 2004).

These results are important for land managers in order to protect woodpecker groups. A viable recommendation is to retain the living tree species with high forest economic value which are selected by woodpeckers (such as *Calycophyllum multiflorum*, *Amburana cearensis*, *Cedrela balansae* and *Astronium urundeuva*) as well as snags with a DBH > 50 cm. In particular, *A. cearensis* (used by the three excavator groups) which is an endangered tree species (IUCN Red List of Threatened Species) with a low population density (Politi et al. 2015). Moreover, *C. balansae* is a tree species highly extracted in the study area and its abundance has dramatically decreased throughout the 20th century (Minetti 2006). The results of this work, together with previous research (Politi et al. 2009, 2010, 2012, Albanesi et al. 2016, Ruggera et al. 2016) may be useful in developing sustainable forest management guidelines to ensure the conservation of woodpeckers. These management strategies will not only benefit woodpeckers, but they will also benefit other components of the biodiversity present in these subtropical forests (Imbeau et al. 2000, Gibbons et al. 2002, Lindenmayer & Likens 2010).

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STRESZCZENIE

[Charakterystyka drzew wybieranych do wykucia dziupli oraz szerokość niszy gniazdowej i jej nakładanie się u pięciu gatunków dzięciołów w subtropikalnych lasach podgórskich północno-zachodniej Argentyny]

Badania dotyczące wyboru przez dziuplaki pierwotne drzew do wykucia dziupli są ważne dla oceny zasobności i jakości dostępnych w środowisku potencjalnych miejsc lęgowych dla tej grupy ptaków. Celem badań był opis wykorzystania przez pięć gatunków dzięciołów drzew poszczególnych gatunków w subtropikalnych lasach podgórskich północno-zachodniej Argentyny. Badania prowadzono na terenie trzech powierzchni referencyjnych. Na każdej z nich wyznaczono 60 powierzchni o wymiarach 50 × 50 m i w ich obrębie określono gatunek oraz zmierzono pierśnicę wszystkich drzew o pierśnicy >10 cm. Dodatkowo określono liczbę martwych stojących drzew (bez identyfikowania gatunku) oraz zmierzono ich pierśnicę. W ten sposób oszacowano dostępność drzew do wykucia dziupli. Drzewa zawierające dziuple dzięciołów opisywane były pod względem gatunku drzewa, jego pierśnicy i wysokości. Opisano także wysokość dziupli nad ziemią, jej położenie (w pniu lub

konarze) oraz kondycję fragmentu drzewa, w którym była wykuta (żywy lub martwy). Na tej podstawie określono wybiórczość dzięciołów względem gatunków drzew oraz szerokość niszy gniazdowej i jej nakładanie się u badanych gatunków dzięciołów. Dzięcioły podzielono na trzy grupy ze względu na wielkość ciała oraz średnicę otworu wejściowego ich dziupli: 1) małe — dzięciolnik zebrowany, 2) średniej wielkości — dzięcioły: oliwkowy, złotowąsy i falisty, oraz 3) duże — dzięcioł płowogrzbiety.

Spośród 54 gatunków drzew stwierdzonych na powierzchniach badawczych, tylko 15 było wykorzystywanych do wykucia dziupli przez badane gatunki dzięciołów. Na podstawie współczynnika Levina badane gatunki dzięciołów zostały zakwalifikowane jako umiarkowani specjaliści pod względem wybiórczości gatunków drzew. Wskaźnik Ivleva wykazał, że wyraźne preferowane były *Amburana cearensis* oraz martwe stojące drzewa (Fig 1). Wysoki stopień pokrywania się nisz (wskaźnik pokrywania się Morisita) zaobserwowano w wykorzystaniu gatunków drzew pomiędzy dzięciolnikiem a dzięciołami średniej wielkości, natomiast mniejszy wystąpił pomiędzy dzięciołem płowogrzbietym i pozostałymi gatunkami dzięciołów. Zarówno żywe drzewa, jak i martwe były wykorzystywane przez dzięcioły, chociaż drzewa martwe lub ich martwe fragmenty były ważniejsze dla małych i średnich dzięciołów, natomiast żywe drzewa były ważniejsze dla największego dzięcioła płowogrzbietego (Fig 2). Drzewa nie wykorzystywane przez dzięcioły były mniejsze i cieńsze niż te zawierające dziuple (Tab. 1). Dziuple dzięcioła płowogrzbietego znajdowały się w drzewach grubszych i wyższych oraz wyżej niż dziuple dwóch pozostały grup dzięciołów. Z kolei dziuple dzięciolnika zebrowanego i dzięciołów średniej wielkości nie różniły się pod względem grubości i wysokości drzewa oraz wysokości, na której znajdowała się dziupla (Tab. 1).

Uzyskane wyniki wskazują na istnienie różnych nisz gniazdowych dzięciołów zasiedlających lasy subtropikalne Argentyny i pozwalają zidentyfikować zależności pomiędzy tymi ptakami a dostępnymi gatunkami drzew. Wyniki badań mogą być przydatne do opracowania wytycznych zrównoważonej gospodarki leśnej dla tej grupy ptaków.