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Comparison of nesting ecology of three co-existing Atlantic Forest woodpeckers reveals narrow specialization in the Helmeted Woodpecker *Celeus galeatus*

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Abstract. The Atlantic Forest in southeastern South America is a biodiversity hotspot with high species richness and high forest loss. Three large to medium-sized woodpecker species (Robust Woodpecker *Campephilus robustus*, Lineated Woodpecker *Dryocopus lineatus*, and the globally threatened Helmeted Woodpecker *Celeus galeatus*) coexist in the south of the ecoregion, and show remarkable convergence in plumage patterns and colouration, possibly driven by interspecific interactions. We assessed differentiation in nest tree species, nest substrates, and timing of breeding and evaluated whether nesting ecology may be a factor explaining an association with mature forests in the Helmeted Woodpecker. Robust and Lineated Woodpeckers excavated cavities in nine and eight nest tree species, respectively, whereas Helmeted Woodpeckers specialized narrowly on laurel trees (88% of nest cavities in two species in genus *Nectandra* of 52 ± 14 cm DBH). Helmeted Woodpecker is further distinguished by a more frequent use of living, partially decayed trees and by more frequent re-use of nest cavities. When nesting in selectively logged forest (vs. old-growth), Robust and Lineated Woodpeckers used trees with smaller DBH and Robust Woodpeckers excavated lower in trees. Helmeted Woodpeckers selected nest trees with similar dimensions in both environments, indicating lesser flexibility. Helmeted Woodpeckers bred 20–23 days later in the year than Lineated and Robust Woodpeckers, potentially allowing them to avoid nesting near the two larger species. The narrow specialization of Helmeted Woodpecker on nesting in *Nectandra* trees of large sizes at the onset of decay is a possible factor in making it sensitive to selective logging effects. To stop declines of Helmeted Woodpecker we recommend (1) sparing large trees from selective logging (including *Nectandra* and tree species used for roosting), and (2) restoring more forested areas to mature forest conditions.

Key words: *Campephilus robustus*, *Dryocopus lineatus*, *Celeus galeatus*, nests, logging, Argentina, plumage convergence, *Nectandra*

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INTRODUCTION

The Atlantic Forest in southeastern South America is a biodiversity hotspot with high species richness and a high percentage, and high rate, of forest loss (Galindo-Leal & Câmara 2003, Ribeiro et al. 2011). Some of the best preserved tracts of Atlantic Forest are found in the south, especially in Misiones province, Argentina (Giraudo 2003). The occurrence of disturbed and old-growth forests in adjacent tracts in Misiones allows for studies comparing the ecology of model organisms in forest treatments. In studies of forest biodiversity, woodpeckers (Picidae) are a frequent focal group, because they are intimately linked to forest structure and forest conditions by foraging,

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nesting and roosting requirements (Virkkala 2006). Among the rich biodiversity of the southern Atlantic Forest are 11 woodpecker species, 9 of which are forest interior species. The three largest woodpeckers of this assemblage are Robust Woodpecker *Campephilus robustus* (241–276 g), Lineated Woodpecker *Dryocopus lineatus* (192–232 g) and Helmeted Woodpecker *Celeus galeatus* (115–145 g). These three species show a startling degree of plumage convergence: all three have black folded wings, black-and-white barred underparts, and conspicuous red crests, with only minor differentiation in facial and neck markings (Fig. 1). Despite the considerable differences in body weights, the overall size of the three species is very similar (Fig. 1). Their plumage similarity fits in a pattern of plumage convergences in woodpeckers (Prum 2014, Miller et al. 2019), involving species in at least 18 of the 35 genera in the Picidae (Gill & Donsker 2019). The convergence between Robust, Lineated and Helmeted Woodpeckers is among the closest resemblances in woodpecker plumages observed and it is the clearest example of convergence between three, rather than two, woodpecker species, from three genera (Lammertink et al. 2016). The plumage convergence between these woodpeckers is most likely caused by interspecific mimicry because the degree of convergence is beyond what is expected based on the influences of habitat, climate, and evolutionary relatedness (Miller et al. 2019). The mimicry may be driven by resource competition between species (Prum 2014), though the precise interactive mechanisms driving woodpecker mimicry remain poorly understood and speculative (e.g. Prum & Samuelson 2012). Leighton et al. (2018) showed that Downy Woodpecker *Dryobates pubescens*, an apparent mimic of the larger Hairy Woodpecker *Leuconotopicus villosus*, gains some dominance over third species in conflicts at bird feeders, but it remains to be determined whether this advantage is found in natural settings and drives mimicry.

A niche dimension where the three largest Atlantic Forest woodpeckers potentially overlap, or may avoid overlapping by narrow differentiation, is nest substrates. All three species excavate nest cavities in dead or decaying wood and all require, because of body size, large diameter trunks or branches to excavate nest cavities (Fig. 1). As access to suitable nest sites is often a determining factor in the reproductive success of birds (Dhondt 2012), the nesting ecology of the Atlantic Forest woodpeckers is an important aspect of their co-existence and in need of a comparative study. An additional reason to examine the nesting ecology of Robust, Lineated and Helmeted Woodpeckers is that the three species differ in their responses to selective logging and forest fragmentation. Robust and Lineated Woodpecker remain fairly common in logged and fragmented landscapes (Krauczuk & Baldo 2004, Krauczuk 2008), whereas Helmeted Woodpecker is associated with well preserved, mature forest (Lammertink et al. 2012). The association of Helmeted Woodpecker with old-growth is at least partly due to its roosting in decay-formed cavities in large living trees (Lammertink et al. 2019), but other aspects of its ecology need to be studied for potential additional links to mature forest.

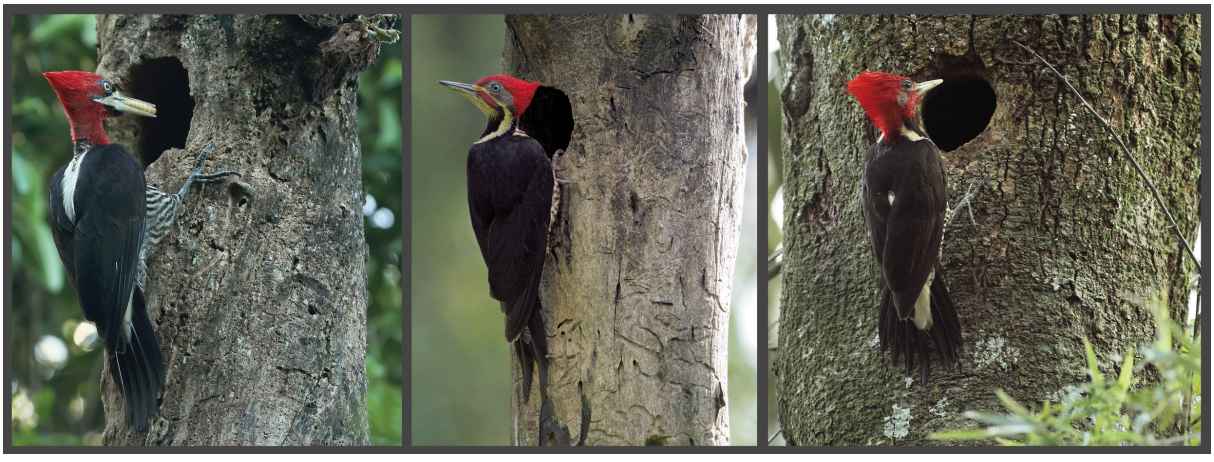

Fig. 1. Robust, Lineated and Helmeted Woodpeckers (from left to right) at their nest cavities in Cruce Caballero Provincial Park, Misiones, Argentina. The photos have been scaled using wing length to a uniform scale, showing the relative sizes of the three woodpeckers, and the relative sizes of their nest substrates. Photos by M. Lammertink.

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To assess differentiation in nest niche dimensions and to evaluate whether nesting ecology may be a factor explaining an association with mature forests in the Helmeted Woodpecker, we examine nest tree species, nest substrates, and timing of breeding of Robust, Lineated and Helmeted Woodpeckers in old-growth and selectively logged forests of Misiones province, Argentina, where the three species co-exist.

STUDY AREAS

Woodpecker nests were studied in Misiones province, Argentina, at four Atlantic Forest sites, two of which were old-growth forests (defined as a forest with no known history of logging), and two of which were selectively logged forests. Forest policy in Misiones stipulates minimum diameter cutting limits of 35–55 cm diameter at breast height (DBH) depending on tree species (Ministerio de Ecología y Recursos Naturales Renovables 1987), and consequently there are fewer large trees in selectively logged forests than in old-growth. The four study sites were: Site 1 — Parque Provincial (PP) Cruce Caballero (26.5199°S, 53.9973°W), a 600 ha protected area including 405 ha of old-growth forest with numerous large old trees (30 trees/ha > 60 cm DBH, Cockle et al. 2010); Site 2 — Valle del Arroyo Alegría (26.5037°S, 54.0021°W), a 8,550 ha private forest property adjacent to PP Cruce Caballero. The forest was selectively logged until ca. 1981, and currently consists of a mosaic dominated by intensively logged regenerating forest, with a few lightly logged patches and a few old forest patches in steep stream valleys; Site 3 — Lote 13 (26.9178°S, 54.1437°W), a 4,850 ha private property within the 253,773 ha Yaboty Biosphere Reserve. Selective logging is ongoing in patches on a 5–10 year rotating cycle, often targeting different tree species in successive cycles; Site 4 — Reserva Natural Cultural Papel Misionero (26.9896°S 54. 2007°W), a 10,000 ha private property within the Yaboty Biosphere Reserve, adjacent to Lote 13. It contains ca. 9,000 ha of old-growth forest, the largest existing remnant in the southern Atlantic Forest, with numerous large trees.

Sites 3 and 4 are separated from the other two sites by 48–57 km of forests, agriculture and urban areas. All four sites are on undulating terrain, at 440 to 620 m asl, within the district of subtropical semi-deciduous Atlantic mixed forest with laurels (*Nectandra* and *Ocotea* spp.), guatambú *Balfourodendron riedelianum* and Paraná pine *Araucaria angustifolia* (Cabrera 1976). Because of variations in soils and elevation, Paraná pines are common at site 1, rare at sites 2 and 3, and absent at site 4. Relatively common canopy trees that occur at all four sites include laurels, guatambú, cancharana *Cabralea canjerana*, grapia *Apuleia leiocarpa*, ceibo *Erythrina falcata*, timbó de campo *Ateleia glazioveana*, and cedro *Cedrela fissilis*.

METHODS

Between 2006 and 2018 during July–November we searched for nests by listening for excavation or contact calls and by looking for fresh cavities or wood chips, and between 2013 and 2018 also by following adult radio-tagged woodpeckers that were lured with playback and decoys into mist nets and fitted with Holohil radio transmitters (model PD-2 for Helmeted and model RI-2C for Lineated and Robust Woodpeckers (Cockle et al. 2011, Lammertink et al. 2019). We confirmed nests (presence of eggs or nestlings) using small video cameras mounted on extendable poles (up to 15 or 22 m), and in three cases of high nests, by observing adults taking food to the cavities. We measured height of nest cavities with extendable poles, measuring tape, or laser rangefinder. The width of the branch or trunk at cavity height were measured using single-rope climbing and a tape measure, or using Photoshop CS3 software from photos showing a cavity camera or folded wings of woodpeckers for size reference. We measured tree diameter at breast height using a tape measure.

Body weights of woodpecker species (ranges provided in the Introduction) were measured from individuals captured for radio-tagging at the study sites: Robust Woodpecker mean 265 ± 11 g, n = 16; Lineated Woodpecker mean 210 ± 7 g, n = 14; Helmeted Woodpecker mean 127 ± 8 g, n = 24. Wood densities of nest tree species (Table 1) follow Melo et al. (2013) for *Prunus subcoriacea*, Richter & Dallwitz (2019) for *Lonchocarpus leucanthus* and *Erythrina falcata*, and Cockle et al. (2017) for remaining tree species. We scored time of year of breeding activity (from egg laying to fledging) per 1-week intervals for all nests combined of each species, including first and second nesting attempts, and derived the median date of this aggregate breeding activity for each species. For nests found after the laying of the first egg, we estimated the start date using mean egg laying, brooding and nestling periods derived from following other nests of each of the three species.

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To examine the effects of woodpecker species and habitat on nest site characteristics, we used the glm function in R 3.5.3 (R Core Team 2019) to fit generalized linear models (Gamma family, identity link) that predicted DBH, cavity height and diameter at cavity height from the predictor variables woodpecker species (Helmeted, Lineated, or Robust), habitat (old-growth vs. logged), and their two-way interaction. Gamma family models were appropriate for our non-negative, right-skewed, continuous response variables, and the identity link reflected the additive relationship between predictors and outcome variables. (Models using a log-link produced qualitatively similar results). We used the package DHARMa (Hartig 2019) for model diagnostics.

RESULTS

We followed 60 nesting attempts (15 of Robust, 26 of Lineated, 19 of Helmeted Woodpecker) in 56 cavities, of which 21 cavities were found through following radio-tagged woodpeckers and 35 through cavity searches or by chance findings. The 56 cavities were located in 56 different trees, 45 of which could be identified to species and 11 could not, usually because these trees were long dead. Robust and Lineated Woodpeckers excavated nest cavities in a variety of nine and eight nest tree species, respectively (Table 1). In contrast, Helmeted Woodpeckers specialized narrowly on laurel trees, with 88% of nest cavities in two species in the laurel genus *Nectandra*, one cavity in a laurel of the genus *Ocotea*, and only one cavity in a tree other than a laurel (Table 1). The mean wood density of trees (with species identification) used for excavating nest cavities tended highest for Robust and lowest for Helmeted Woodpecker (Table 1), though these differences were not significant (Mann-Whitney $U = 121.5$, $Z = -0.04$, $p = 0.97$ for Helmeted vs Lineated, $U = 115.5$, $Z = -0.12$, $p = 0.90$ for Helmeted vs Robust, $U = 105.5$, $Z = 0$, $p = 1$ for Lineated vs Robust). Helmeted Woodpecker frequently excavated nest cavities in living (but partially decayed) trees, with 69% of cavities, contrasted with 13% use of living trees by Robust Woodpecker and 32% by Lineated Woodpecker. Similarly the nest substrates (tree trunk or primary branch) in which Helmeted Woodpecker excavated nest cavities were more often alive with 31%, versus 7% in Robust Woodpecker and 0% in Lineated Woodpecker. Helmeted Woodpecker more frequently re-used nest cavities from previous years, in 32% of nests, versus 0% for Robust Woodpecker and 4% for

Table 1. Species diversity and wood density (following Cockle et al. 2017, Melo et al. 2013 and Richter & Dallwitz 2019) of nest trees of Robust, Lineated and Helmeted Woodpeckers.

Tree species		Wood density	N nest trees		
Common name	Scientific name	(g/cm^3)	Robust	Lineated	Helmeted
Laurel negro	*Nectandra megapotamica*	0.52		3	10
Laurel amarillo	*Nectandra lanceolata*	0.48	2		4
Laurel ayuí	*Ocotea diospyrifolia*	0.54	2		1
Laurel guaica	*Ocotea puberula*	0.42	1		
Grapia	*Apuleia leiocarpa*	0.83	2	3	
Paraná Pine	*Araucaria angustifolia*	0.46	3		
Persiguero	*Prunus subcoriacea*	0.80	1	1	1
Mora blanca	*Alchornea triplinervia*	0.49	1	2	
Cedro	*Cedrela fissilis*	0.50		2	
Fumo bravo	*Solanum granuloso-leprosum*	0.40		2	
Maria preta	*Diatenopteryx sorbifolia*	0.74	1		
Rabo itá	*Lonchocarpus leucanthus*	0.90	1		
Ceibo	*Erythrina falcata*	0.38		1	
Cambará	*Gochnatia polymorpha*	0.76		1	
unknown tree			1	10	
N nest trees total			15	25	16
N nest trees with species identification			14	15	16
N tree species			9	8	4
Shannon-Weaver H' diversity index of identified nest trees			8.22	7.33	2.68
% in *Nectandra* trees			14	20	88
Mean wood density of nest trees (g/cm^3)			0.60	0.58	0.53

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Table 2. Sample size (*N*) and ranking of generalized linear models (Gamma family) in three sets, predicting diameter of nest tree at breast height (DBH, cm), cavity height (m), and tree diameter at cavity height (DCH, cm) for three species of woodpeckers in the Atlantic Forest of Misiones, Argentina. For each model, we indicate number of parameters (*k*), difference in Akaike's Information Criterion (corrected for small sample size) between each model and the lowest AIC_c model in the set (ΔAIC_c), and Akaike weight (w_i). Lowest AIC_c values for each model set were: DBH 489.3, cavity height 325.9, diameter at cavity height 428.4.

Response variable	N	Model	k	ΔAICc	wi
DBH	56	Species × Forest type	7	0.0	0.986
		Species	4	10.0	0.007
		(Null)	2	10.0	0.007
Cavity height	56	Species × Forest type	7	0.0	0.814
		Species	4	3.6	0.134
		(Null)	2	5.5	0.053
DCH	53	(Null)	2	0.0	0.585
		Species	4	1.36	0.297
		Species × Forest type	7	3.19	0.119

Lineated Woodpecker. One Helmeted Woodpecker nest cavity was used three years in a row with three successful nests.

We found significant interactions between woodpecker species and forest type in generalized linear models predicting diameter at breast height (DBH) and cavity height, but no significant predictor variables in the model predicting diameter at cavity height (Tables 2 and 3). Helmeted Woodpeckers used nest trees of similar DBH and excavated at similar heights regardless of forest type (Fig. 2). In contrast, Lineated and Robust Woodpeckers used smaller DBH trees, and Robust Woodpeckers nested lower, in selectively logged forest (vs. old-growth; Fig. 2).

Timing of breeding was similar for Robust and Lineated Woodpeckers (Fig. 3), with a median date of 24 September for Robust Woodpecker and 27 September for Lineated Woodpecker. The breeding activity distribution of Helmeted Woodpecker was similar in shape and spread to those of the two larger woodpeckers, but was later in the year, with a median date of 17 October (Fig. 3). Breeding activity was spread over 20 weeks in Robust Woodpecker, 17 weeks in Lineated Woodpecker, and 21 weeks in Helmeted Woodpecker.

The closest distance we observed between simultaneously active nests of Helmeted and Robust Woodpecker was 230 m. The closest distance between simultaneously active nests of Helmeted and Lineated Woodpecker was 115 m, with dense vegetation between the two nests, meaning nests were not in line of sight and not on the frequently travelled routes of the neighbouring woodpeckers. Between active Robust and Lineated Woodpecker nests the closest observed distance was 91 m. Because we probably did not find all woodpecker nests in our study areas, we cannot provide mean distances and ranges of interspecific spacing of nest trees.

Table 3. Parameter estimates (b) ± standard error (SE), test statistic (t) and associated p-values (p) for top generalized linear models predicting nest tree diameter at breast height (DBH, cm) and cavity height (m) for three species of woodpeckers in the Atlantic Forest of Misiones, Argentina. Reference levels for categorical predictors were: forest type = logged, species = Helmeted Woodpecker. The top model predicting diameter at cavity height was the intercept-only (null) model, and none of the parameters in the other models for diameter at cavity height differed significantly from 0 (all $p > 0.1$).

Response variable	Predictor variable	b ± SE	t	p
DBH	Species – Lineated Woodpecker	-15.9 ± 8.1	-1.98	0.054
	Robust Woodpecker	-1.4 ± 8.7	-0.2	0.874
	Forest type (old-growth)	2.9 ± 8.5	0.34	0.732
	Lineated × old-growth	23.8 ± 11.0	2.16	0.036
	Robust × old-growth	28.1 ± 13.8	2.03	0.047
Cavity height	Species – Lineated Woodpecker	0.96 ± 2.4	0.40	0.689
	Robust Woodpecker	-0.2 ± 1.9	-0.11	0.910
	Forest type (old-growth)	0.8 ± 1.9	0.44	0.662
	Lineated × old-growth	1.1 ± 3.0	0.38	0.706
	Robust × old-growth	7.2 ± 3.3	2.18	0.034

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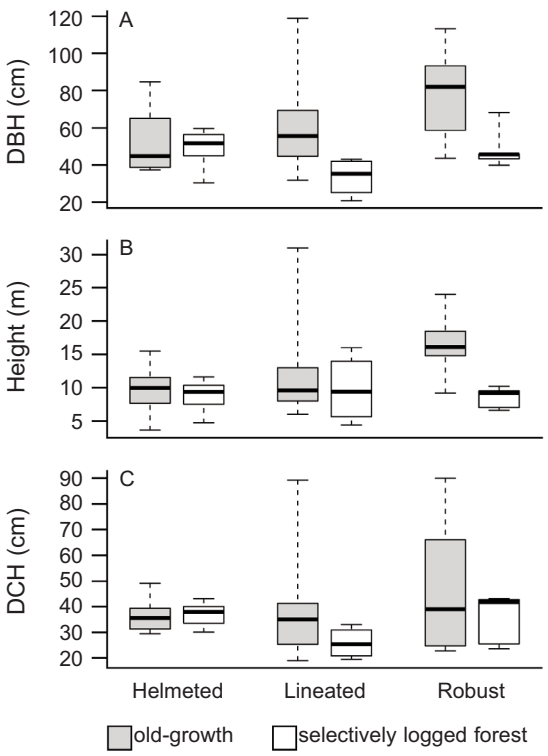

Fig. 2. Dimensions of nest trees and nest substrates of Helmeted, Lineated and Robust Woodpecker in old-growth forests and in selectively logged forests: A — diameter of nest tree at breast height (DBH); B — height of nest cavity; C — diameter of nest substrate (branch or trunk) at cavity height (DCH). Thick horizontal lines are the medians, boxes represent 25th and 75th percentiles, and whiskers are the ranges.

DISCUSSION

The nest niche of Helmeted Woodpecker was narrower than that of Lineated or Robust Woodpeckers, and appeared less flexible in response to selective logging. Whereas Robust Woodpecker used at least eight tree species and Lineated Woodpecker at least nine tree species for nest cavities, Helmeted Woodpecker narrowly specialized on two tree species in the genus *Nectandra* (laurel negro, *N. megapotamica*, 63% of nest cavities, and laurel amarillo *N. lanceolata*, 25% of nest cavities). Whereas Robust and Lineated Woodpeckers adjusted their use of nest sites (lower, in smaller DBH trees) in selectively-logged forest (vs. old-growth), Helmeted Woodpeckers exhibited no such plasticity.

Helmeted Woodpecker specializes on *Nectandra* for nest trees

The older *Nectandra* trees (52 ± 14 cm DBH) in which we found nests of Helmeted Woodpeckers often had fungi and moist spots on trunks and limbs, properties that may cause wood decay and facilitate cavity excavation. *Nectandra* trees are of an intermediate wood density (Table 1), meaning they may provide an attractive balance between providing structurally sound wood for a cavity and ease of excavating. *Nectandra* is used by

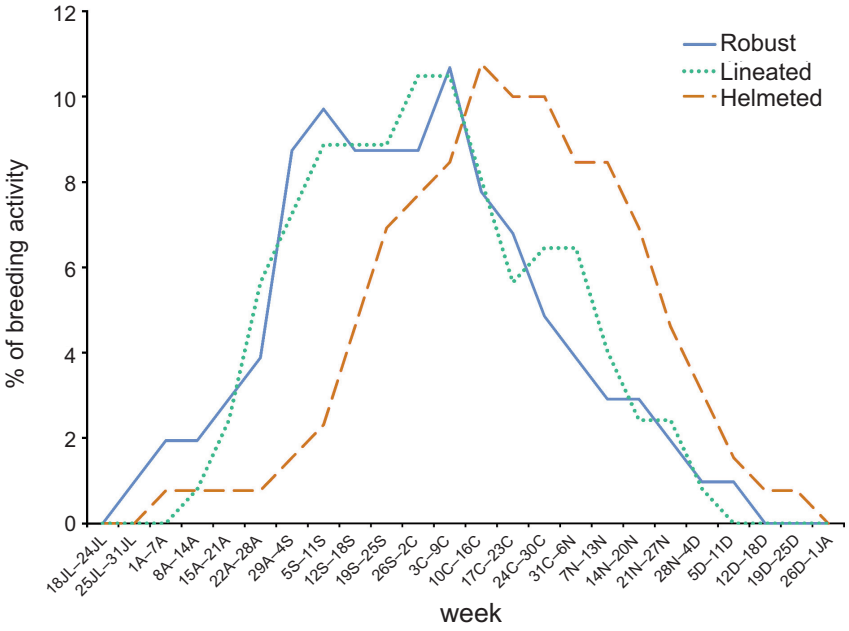

Fig. 3. Time of year of breeding of Robust, Lineated and Helmeted Woodpeckers, with percentage of breeding activity (the aggregate activity of all nests of each species) scored per one-week intervals between 18 July and 1 January, for October the abbreviation C is used.

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Helmeted Woodpeckers for nesting not only in our study region in central Misiones province, Argentina, but also in Iguazú department in northern Misiones, 120 km NE of our study region, where a nest was found in *N. angustifolia*, and in Intervales State Park in São Paulo, Brazil, 635 km NW of our study area, where two nests were found in *N. megapotamica* (Lammertink et al. 2012). The only two cavities excavated by Helmeted Woodpeckers we found in trees other than *Nectandra* were one in laurel ayuí *Ocotea diospyrifolia*, a tree species closely related to *Nectandra* and with similar appearance and wood structure, and one in persiguero *Prunus subcoriacea*, a tree occasionally used for nest cavities by each of the three woodpeckers (Table 1).

Helmeted Woodpeckers appear to be relatively weak excavators: their foraging hammering is soft and inconspicuous (Lammertink et al. 2012), their bill base is narrow (Brooks et al. 1993), and for roosting, they exclusively use decay-formed cavities (Lammertink et al. 2019). In accordance with this profile, Helmeted Woodpeckers excavated nest cavities in trees of species with, on average, a lower wood density than Lineated and Robust Woodpeckers (Table 1), which are large-billed woodpeckers that frequently hammer powerfully when foraging. It is somewhat surprising that Helmeted Woodpeckers more frequently excavated nests in relatively sturdy live trees and live substrates than Lineated and Robust Woodpeckers. Probably because of their more frequent placing of nest cavities in live trees and live substrates, which have a longer life span (Cockle et al. 2017), Helmeted Woodpeckers more frequently re-used cavities from previous years. Helmeted Woodpecker is similar in these aspects to the Green Woodpecker *Picus viridis* of Europe, which only rarely and weakly excavates in wood for foraging but often excavates nest cavities in live trees, including in oaks *Quercus* sp. of high wood density, and often re-uses nest cavities (Blume 1996, Gorman 2004).

Nest niche differentiation among Helmeted, Robust and Lineated Woodpeckers

Despite the attractiveness of *Nectandra* trees to Helmeted Woodpeckers, with 88% of their nest cavities in these trees, Robust and Lineated Woodpeckers used *Nectandra* trees only for 14% and 20%, respectively, of their nest cavities. The specialization by Helmeted Woodpecker on *Nectandra* thus accounts to a large degree for the ecological separation in breeding ecology between it and the two co-existing large woodpeckers. Helmeted Woodpecker further differs from Robust Woodpecker in old-growth forest by excavating lower in trees, from Lineated Woodpecker in selectively-logged forest by excavating in trees with larger DBH, and from both by more frequently excavating in live trees and live substrates, and by breeding later in the year.

Robust and Lineated Woodpeckers, while well separated from Helmeted Woodpecker in breeding ecology, showed little separation among each other in nest placement. They showed some differentiation in cavity height in old-growth forest and in DBH in selectively logged forest, but these differences were not consistent between the two forest types (Fig. 2). Their periods of breeding activity were similar (Fig. 3). They may differentiate in the tree species they use for nesting, as there were several tree species in which we found nests of only one or the other species. However, because tree species use was diverse in both species (Table 1) sample sizes per tree species were small, and it will take a much larger sample of nests to assess whether there is a real separation between the two in tree species use. Apart from nest placement, an ecological dimension in which these two species are well separated, and which may facilitate their co-existence during the breeding season, is nestling diet. Robust Woodpeckers bring large prey items, mostly beetle larvae, in the bill, making frequent feeding visits with one food item at a time (Fig. 1). Lineated Woodpeckers (as well as Helmeted Woodpeckers) bring large numbers of small items, such as ants, ant eggs, and termites, which are regurgitated to nestlings during infrequent visits to the nest (Manegold & Töpfer 2012).

The median date of breeding activity of Helmeted Woodpecker was 23 days later in the year than that of Robust Woodpecker, and 20 days later in the year than that of Lineated Woodpecker. Because breeding activity is spread over 17–21 weeks in each of the species, there was still considerable overlap in breeding activity of the three (Fig. 3). However, by starting later in the year, Helmeted Woodpeckers are, in principle, able to excavate nests in trees away from active Lineated and Robust Woodpecker nests, and we did not find nests of Helmeted Woodpecker near the nests of the larger woodpeckers. This way, encounters between the look-alike species may be avoided, and the risk of nest predation on Helmeted Woodpecker by one of the larger woodpeckers may be reduced (Wiktander et al. 2001, Ojeda & Chazarreta 2006, Charman et al. 2012).

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An alternative explanation that may be considered for the later breeding of Helmeted Woodpecker is a difference in nestling diet, but this does not seem likely given the broad similarities of its diet with Lineated Woodpecker (Winkler et al. 1995, Lammertink et al. 2012).

Impact of selective logging on nest sites

In accordance with reduced availability of large trees in selectively logged forests, Robust and Lineated Woodpeckers adjusted to smaller DBH trees, and Robust Woodpeckers excavated nests lower in trees (Fig. 2). Helmeted Woodpeckers showed no such flexibility, and kept excavating in trees of the same large DBH, and similar other dimensions, in selectively logged forests as in old-growth forest (Fig. 2). The narrow specialization by Helmeted Woodpeckers on nesting in large DBH trees, at the onset of decay, of mainly two tree species in the genus *Nectandra* may make an important contribution to their reduced abundance in selectively logged forests (Lammertink et al. 2012, 2019). Robust and Lineated Woodpeckers each have rather similar densities in old-growth and selectively logged forest at our study sites (unpublished data), reflecting more ecological flexibility.

Nectandra trees are fairly common in the Atlantic Forest region. For instance, at one of our study sites in PP Cruce Caballero, *Nectandra* trees make up 3.4%, 1.1%, and 5.4% of trees on three different soil types, in a community of 116 tree species (Ríos 2006). Historically, *Nectandra* trees have been less desirable timber trees, coming in a third category behind durable hardwoods as grapia or lighter timber for construction and furniture as Paraná Pine and cedro *Cedrela fissilis*. As prime timber trees of harvestable sizes have been exhausted in recent decades, and as *Nectandra* can be used for laminated wood (Gérard et al. 2011), these trees are currently being harvested at an increased frequency. The minimum allowed DBH for logging of 35 cm for *N. lanceolata* and 40 cm for *N. megapotamica* (Ministerio de Ecología y Recursos Naturales Renovables 1987) takes out trees well below the mean DBH of trees sought out by Helmeted Woodpeckers for nesting (Fig. 2). Conservation measures for the Helmeted Woodpecker should include maintaining a sufficient supply of older *Nectandra* trees in forested landscapes, to provide suitable trees for nesting.

Apart from older *Nectandra* trees for nesting, another factor tying Helmeted Woodpecker to old-growth forests is their year-round use of decay-formed cavities for overnight roosting (Lammertink et al. 2019). The tree species most frequently used for roosting are highly sought after as timber trees, are only slightly more common than *Nectandra* (Ríos 2006), and only in certain conditions cavities of suitable dimensions are formed by decay in some of the older trees of these species. It thus seems probable that trees with suitable roost cavities are an even more limiting resource for Helmeted Woodpeckers than nest trees, in which Helmeted Woodpeckers actively can excavate their nest cavities. To stop declines of Helmeted Woodpecker we recommend sparing large trees — *Nectandra* trees and tree species used for roosts (Lammertink et al. 2019) — from selective logging, and restoring more forested areas to mature forest conditions. This will increase the available forest area with the roost trees and nest trees that Helmeted Woodpeckers require, and will also improve conditions for a diverse community of cavity nesting animals (Cockle et al. 2011, 2019, Lammertink et al. 2019).

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STRESZCZENIE

[Porównanie ekologii lęgowej trzech współwystępujących dzięciołów w lesie atlantyckim w Argentynie wykazuje wąską specjalizację dzięcioła hełmiastego]

Las atlantycki (Mata Atlântica) rozciągający się w południowo-wschodniej części Ameryki Południowej jest ważnym obszarem bioróżnorodności biologicznej z dużym bogactwem gatunkowym. Jednocześnie w ostatnich czasach obserwuje się postępującą utratę tych cennych siedlisk. W południowej części lasu atlantyckiego żyje 11 gatunków dzięciołów, wśród których największe to dzięcioły: jasnogrzbiety (średnia masa 265 g), czerwonoczuby (średnia masa 210 g) oraz globalnie zagrożony dzięcioł hełmiasty (średnia masa 127 g). Gatunki te wykazują niezwykłe morfologiczne podobieństwo w ubarwieniu upierzenia (Fig. 1), prawdopodobnie będące przykładem mimikry powstałej na skutek konkurencji o zasoby. Wszystkie trzy gatunki wykuwają dziuple w martwym lub rozkładającym się drewnie i wszystkie wymagają do tego celu (ze względu na duży rozmiar ciała) pni lub gałęzi o dużej średnicy. Ponadto gatunki te odmiennie reagują na selektywny wyrąb oraz fragmentację lasu. Dzięcioły jasnogrzbiety i czerwonoczuby występują dosyć powszechnie w lasach poddanych wyrębowi oraz pofragmentowanych, natomiast występowanie dzięcioła hełmiastego ogranicza się najczęściej do dojrzałych drzewostanów. Jednym z powodów jest wybór przez ten gatunek na miejsca noclegu dziupli naturalnych powstałych w dużych, żywych drzewach. W pracy porównano miejsca gniazdowe tych trzech gatunków, a dodatkowo zbadano, czy ekologia gniazdowania dzięcioła hełmiastego odpowiada za jego brak występowania na terenach poddanych presji gospodarki leśnej lub o silniejszej fragmentacji.

Badania prowadzono na czterech powierzchniach leśnych w prowincji Misiones w północno-wschodniej Argentynie. Dwa z tych terenów są lasami naturalnymi, bez historycznych danych o prowadzonym na ich terenach wyrębie, na pozostałych prowadzony był wyrąb selektywny, przez co na ich powierzchni mniej jest drzew o dużej pierśnicy. W okresie od lipca do listopada 2006–2018 wyszukiwano dzięcioły kujące dziuple, kontrolowano zawartość dziupli, opisując następnie miejsca lęgowe — m.in. gatunek drzewa, pierśnicę, wysokość nad ziemią, grubość pnia lub gałęzi na wysokości dziupli.

Łącznie analizami objęto 60 lęgów: 15 dzięcioła jasnogrzbietego, 26 czerwonoczubego i 19 hełmiastego. Dzięcioły jasnogrzbiety i czerwonoczuby wykuwały swoje dziuple odpowiednio w dziewięciu i ośmiu gatunkach drzew, natomiast dzięcioł hełmiasty specjalizował się w gniazdowaniu w drzewach z rodziny wawrzynowatych (w tym 88% gniazd znajdowało się w dwóch gatunkach z rodzaju *Nectandra* (Tab. 1)). Gęstość drewna drzew wybieranych na dziuple nie różniła się pomiędzy gatunkami dzięciołów. Dzięcioł hełmiasty częściej niż pozostałe gatunki wykuwał dziuple w żywych, choć częściowo obumierających drzewach oraz częściej użytkował swoje dziuple w kolejnych sezonach (32% dziupli). Analizy wykazały, że pierśnica drzew wykorzystywanych do wykucia dziupli oraz wysokość dziupli na ziemią zależy od gatunku dzięcioła i charakteru drzewostanu (poddany wyrębowi lub naturalny) (Tab. 2, 3). W przypadku gniazdowania w lasach z wyrębem selektywnym dzięcioły jasnogrzbiety i czerwonoczuby wykorzystywały drzewa o mniejszej pierśnicy, a dodatkowo dzięcioły jasnogrzbiete gniazdowały niżej niż w drzewostanach naturalnych (Fig. 2). Z kolei dzięcioły hełmiaste wykuwały dziuple w drzewach o podobnej pierśnicy oraz na podobnej wysokości w obu typach środowisk, co wskazuje na ich mniejszą plastyczność. Okres lęgowy dzięciołów jasnogrzbietego i czerwonoczubego przypadał w podobnym terminie, natomiast lęgi dzięcioła hełmiastego rozpoczynały się o 20–23 dni później (Fig. 3). Prawdopodobnie pozwala im to uniknąć gniazdowania w pobliżu dwóch większych gatunków.

Autorzy sugerują, że wąska specjalizacja dzięcioła hełmiastego do gniazdowania w dużych, żywych drzewach z rodziny wawrzynowatych, jest możliwym czynnikiem powodującym jego wrażliwość na wyrąb selektywny. W celu powstrzymania spadku liczebności tego gatunku autorzy rekomendują wyłączenie z gospodarki leśnej z wyrębem selektywnym dużych drzew z rodzaju *Nectandra* oraz dużych drzew gatunków wykorzystywanych do nocowania, a także przywracanie większej powierzchni terenów leśnych charakteru dojrzałych drzewostanów.

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