ORIGINAL ARTICLE

Does foraging competition drive plumage convergence in three look-alike Atlantic Forest woodpecker species?

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Abstract

Explaining the co-existence of sympatric and ecologically similar species is a central goal in ecology. In woodpeckers (Picidae), co-existence is frequently accompanied by plumage convergence. A particularly striking case concerns three woodpecker species in the Atlantic Forest of South America: Robust Woodpecker (*Campephilus robustus*), Lineated Woodpecker (*Dryocopus lineatus*) and Helmeted Woodpecker (*Celeus galeatus*), which show a remarkable degree of plumage similarity thought to result from convergence due to interspecific social dominance mimicry (ISDM). We studied the foraging ecology and interactions of these three species in old-growth forests and selectively logged forests to test the extent to which these species differ in various aspects of their foraging ecology, and we examined whether particular foraging requirements may help explain the association of the threatened Helmeted Woodpecker with mature forests. The species selected different tree species, tree diameters, foraging heights, decay states of trees and decay states of substrates, resulting in marked niche separation among the three species. Proportionally, the Robust Woodpecker chiselled more, Helmeted Woodpecker used more probing and Lineated Woodpecker used more hammering. Helmeted Woodpecker was the only species that included bamboos as foraging substrates, and it foraged more on dead wood than Lineated or Robust Woodpeckers, but mostly on small dead branches in live trees rather than standing dead trees. Foraging requirements are not the most likely factor explaining the association of Helmeted Woodpecker with mature forests. Limited resource and substrate overlap among the three woodpecker species, lack of interspecific interactions, and rarity of the Helmeted Woodpecker do not match predictions if these species were conforming to a mimicry complex under the hypothesis of ISDM. Instead, plumage convergence may aid in interactions with third species, or impart advantages in intraspecific competition.

Keywords Atlantic Forest · *Campephilus robustus* · *Celeus galeatus* · *Dryocopus lineatus* · Foraging ecology · Helmeted Woodpecker · Lineated Woodpecker · Logging · Mimicry · Plumage convergence · Robust Woodpecker

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Zusammenfassung

Fördert Konkurrenz bei der Nahrungssuche die Konvergenz der Gefiederfärbung dreier ähnlich aussehender Spechtarten im Atlantischen Regenwald?

Die Erklärung der Koexistenz bei sympatrischen und ökologisch ähnlichen Arten ist ein zentraler Gegenstand der Ökologie. Bei Spechten (Picidae) geht die Koexistenz häufig mit einer Konvergenz der Gefiederfärbung einher. Ein besonders auffälliger Fall betrifft drei Spechtarten im Atlantischen Regenwald Südamerikas: Scharlachkopfspecht (*Campephilus robustus*), Linienspecht (*Dryocopus lineatus*) und Wellenohrspecht (*Celeus galeatus*), die ein auffallend hohes Maß an Gefiederähnlichkeit aufweisen. Es wird davon ausgegangen, dass dies aus einer Konvergenz resultiert, die auf der interspezifischen Mimikry der sozialen Dominanz (engl. *interspecific social dominance mimicry*; ISDM) beruht. Wir untersuchten die Nahrungsökologie und Interaktionen dieser drei Arten in Altholzbeständen und selektiv bewirtschafteten Beständen, um zu testen, inwieweit sich diese Arten in verschiedenen Aspekten ihrer Nahrungsökologie unterscheiden. Weiterhin überprüften wir, ob bestimmte Anforderungen an die Nahrungssuche dazu beitragen können, die Assoziation des bedrohten Wellenohrspechts mit ausgewachsenen Waldbeständen zu erklären. Zwei oder jede der Arten wählten bzw. wählte unterschiedliche Baumarten, Baumdurchmesser, Baumhöhen bei der Nahrungssuche sowie Zersetzungszustände der Bäume und Substrate, was zu einer deutlichen Nischentrennung unter den drei Spechtarten führte. Proportional meißelte der Scharlachkopfspecht am meisten, während der Wellenohrspecht häufiger bohrte und der Linienspecht häufiger hämmerte. Der Wellenohrspecht war die einzige Art, die Bambus als Substrat für die Nahrungssuche einschloss. Außerdem nutzte diese Art mehr Totholz für die Nahrungssuche als der Linien- und Scharlachkopfspecht, jedoch handelte es sich hierbei hauptsächlich um kleine tote Äste lebender Bäume und nicht um stehendes Totholz. Die Anforderungen an die Nahrungssuche stellen nicht den wahrscheinlichsten Faktor dar, der die Assoziation des Wellenohrspechts mit ausgewachsenen Waldbeständen erklärt. Geringe Ressourcen- und Substratüberlappungen zwischen den drei Spechtarten, das Fehlen interspezifischer Interaktionen und die Seltenheit des Wellenohrspechtes stimmen nicht mit den Vorhersagen überein, wenn diese Arten gemäß der Hypothese der ISDM einem Mimikry-Komplex entsprechen würden. Stattdessen kann die Konvergenz der Gefiederfärbung bei Interaktionen mit anderen Arten vermitteln oder Vorteile bei intraspezifischer Konkurrenz bringen.

Introduction

The co-existence of ecologically similar species living in the same community is one of the most complex issues that ecologists have tried to understand (Schoener 1974). One familiar theory in ecology proposes the idea that two species cannot have exactly the same niche in a habitat and stably coexist (Gauze 1934). Resource differentiation reduces the amount of niche overlap between potential competitor species, though the mechanisms that may drive this differentiation are open to debate (Wiens 1989; Dhondt 2012). One widely-studied set of ecological dimensions, where species could overlap is foraging ecology. It has been found that co-existing species that belong to the same guild, and share common resources and feeding techniques, show ecological segregation. This is the case, for instance, with warblers (MacArthur 1958; Power 1971; Martin and Martin 2001), and woodpeckers (Williams 1975; Villard 1994) that forage in different strata and rely on different trunk diameters. Interestingly, in the case of woodpeckers, an additional eye-catching aspect of their co-existence is plumage convergence. Proposed mechanisms for phenotypic resemblance include shared ancestry (Short 1982), parallel evolution due to common evolutionary pressures (Winkler et al. 1994), convergence between distantly related taxa (Shakya et al. 2017) and advergent evolution like some types of mimicry (Brower and Brower 1972). Miller et al. (2019) concluded that many woodpecker species form mimicry complexes. This is based on the large number of cases, in many parts of the world, of sympatry between distantly related woodpecker species that share the same colour patterns. Several hypotheses were proposed to explain this mimicry, including predation avoidance (Ruxton et al. 2005), avoidance of interspecific competitive interactions (Diamond 1982), deceiving of third species to gain access to foraging resources (Leighton et al. 2018), or access to a resource in presence of a dominant model species (Prum and Samuelson 2012).

A particularly striking case of woodpecker plumage convergence involves three co-existing South American species: Robust Woodpecker (*Campephilus robustus*, 265 g), Lineated Woodpecker (*Dryocopus lineatus,* 210 g) and Helmeted Woodpecker (*Celeus galeatus*, 127 g). These distantly related species show a startling degree of plumage similarity. All three have black folded wings, black-and-white barred underparts, and conspicuous red crests, with fine-scale differentiation in facial and neck markings (Fig. 1). In flight, Helmeted and Robust woodpeckers exhibit cinnamon spots on the primaries and secondaries and show white backs (lower back and rump in Helmeted Woodpecker), which Lineated Woodpecker does not. Helmeted Woodpecker was long believed to belong in the genus *Dryocopus* (Gray 1845; Peters 1948; Short 1982; Sibley and Monroe 1990; Winkler and Christie 2002), but was then found to belong in *Celeus* in molecular phylogenies (Benz et al. 2015; Lammertink

Fig. 1 Foraging of look-alike Atlantic Forest woodpeckers in Misiones, Argentina. From left to right: Robust Woodpecker (*Campephilus robustus*) extracting a coleopteran larva from the dead trunk of a Paraná pine (*Araucaria angustifolia*); Lineated Woodpecker (*Dryo-copus lineatus*) probing in a foraging excavation in a recently dead branch; Helmeted Woodpecker (*Celeus galeatus*) licking up small ants from a long dead branch Photos by M. Lammertink

et al. 2016). Benz et al. (2015) emphasized plumage convergence between Helmeted and Lineated Woodpecker, whereas Lammertink et al. (2016) pointed out the similarities between Helmeted, Lineated and Robust Woodpeckers as an exceptional case of plumage convergence between three, rather than two, woodpecker species.

Differentiation in foraging ecology between the look-alike Helmeted, Lineated and Robust woodpeckers has not been studied in any detail. Examining this differentiation may bear light on some of the proposed mechanisms of plumage convergence. A recent hypothesis for plumage convergence was postulated by Prum and Samuelson (2012, 2016) and Prum (2014). They proposed that plumage convergence results from a type of mimicry called interspecific social dominance mimicry (ISDM), where a subordinate species evolves to mimic a dominant ecological competitor to avoid attack by the dominant syntopic species. The theory's assumptions include that species are ecological competitors, larger species are socially dominant, subordinate species should exist at higher frequency in the community than model species, and dominant species have more at stake in ecological competition. Based on the sizes of the species in this study we propose Helmeted Woodpecker and Lineated Woodpecker as the potential mimic species and Robust Woodpecker as the dominant species.

The three species occur in the southern Atlantic Forest of Argentina, Brazil and Paraguay, which is considered one of the five most endangered biodiversity hotspots (Myers et al. 2000). Only 10–12% remains (Ribeiro et al. 2009). The globally vulnerable Helmeted Woodpecker is uncommon to rare, associated with old-growth forest (Lammertink et al. 2019), and has a relatively low density in selectively logged forest (Lammertink et al. 2012). In contrast, Robust and Lineated Woodpecker are more

common and have less specific ecological requirements. Both species are fairly common in mature and selectively logged forest and persist in small forest fragments (Krauczuk and Baldo 2004; Krauczuk 2008). The association of Helmeted Woodpecker with old-growth is at least partially explained by its dependence on decay-formed roost cavities in large living trees (Lammertink et al. 2019) and its narrow specialization on large laurel trees (*Nectandra* sp.) for nesting (Lammertink et al. 2020). However, other aspects of its ecology need to be studied for potential additional links to mature forest. The dependence of other old-growth specialist woodpeckers is often related to the availability of foraging resources (Tanner 1942; Czeszczewik 2009; Lammertink et al. 2009; Tremblay et al. 2010). Considering this, it is important to assess whether foraging ecology may be a factor in explaining the association of Helmeted Woodpecker to old-growth forests.

We studied the foraging ecology of the three look-alike woodpecker species in forests, where they co-occur in the Atlantic Forest of Misiones, Argentina. Our study was conducted under two different forest conditions: selectively logged and old-growth forest. Our objectives were to determine how these species differ or overlap in various aspects of their foraging substrates requirements and to compare foraging behaviour of the three species in different forest conditions. We tallied the number of times that individuals of each of the three woodpecker species foraged in close proximity to individuals of another species, and report on interspecific aggressive or associative interactions (or lack thereof). If plumage convergence is being maintained by ISDM, we expect to record competitive interactions between species, either by exploitation (i.e., significant overlap in diet or foraging substrates) or by interference (i.e., aggressive behaviour). We also explored whether use of particular

foraging substrates may help explain the association of Helmeted Woodpecker with mature forests.

Methods

Study areas

Fieldwork was conducted at four Atlantic Forest sites: two old-growth forests each with adjacent selectively logged forest in Misiones province, northeastern Argentina. We define old-growth as a forest with no known history of timber extraction. The sites were within the district of Atlantic mixed forest (Cabrera 1976), with guatambú (*Balfourodendron riedelianum*), laurels (*Nectandra* and *Ocotea* spp.), cancharana (*Cabralea canjerana*), rabo (*Lonchocarpus leucanthus*), cedro (*Cedrela fissilis*) and remnants of the highly exploited Paraná pine (*Araucaria angustifolia*), among a high tree diversity. Woodpeckers were studied in two old-growth sites (1) Parque Provincial Cruce Caballero (PPCC) which supports one of the best preserved remnants of mixed forest with Paraná pine and (2) Reserva Natural Cultural Papel Misionero, as well as in selectively logged forests adjacent to the two old-growth sites. The sites are described in more detail in Lammertink et al. (2020). All four sites are on undulating terrain, at 440–620 m asl. There is a separation of 48–57 km of mosaic landscape including agriculture, forest patches and urban areas between each pair of adjacent selectively logged and old-growth sites.

Field data collection

We captured woodpeckers by luring them into two 6×6 m elevated mist nets placed perpendicular to each other with playing of recorded calls and drums, imitation of double-knock drums on a wooden box to attract Robust Woodpecker, and using decoys. Woodpeckers were marked with a unique combination of coloured leg bands and fitted with Holohil radio transmitters (model PD-2, 3.8 g, for Helmeted and model RI-2C, 5.6 g, for Lineated and Robust Woodpeckers), attached with small zip ties and Gotita instant glue to the base of the central tail feathers. Transmitters were shed with tail feather moult. We relocated birds using a Wildlife Materials TRX-48 receiver mounted on a three-element directional yagi antenna. For reasons not related to this foraging study, we captured male and female of Helmeted Woodpecker pairs (one with playback in late winter, the partner later near the nest) and only one individual of Robust and Lineated Woodpecker pairs.

Two teams of one observer and one trail cutter followed radio-tagged woodpeckers all daytime and recorded foraging observations from 1 h after dawn to ca. 1 h before dusk, from August to December 2012 to 2019, totalling 724 days.

Understory in the study areas was dense, particularly in the selectively logged forest. We used machetes to clear trails to ca. 150 m from foraging woodpeckers and used pruning shears for a more silent final approach. If a woodpecker flushed upon our approach and continued foraging, we did not take an observation at the new, often higher, foraging spot. As woodpeckers often returned to foraging grounds in territories, we could make silent approaches on pre-established trails during later weeks of following an individual.

Variables sampled

Substrate variables

We recorded diameter at breast height (DBH), substrate diameter (branches, trunks or bamboo culms, estimated relative to size of the folded wing), plant species, plant height (m), decay state of substrates and decay state of trees. Decay state of trees and decay state of substrates were defined as: (1) live: full of green leaves; (2) sick: with dead or yellow leaves or fungal presence; (3) recently dead: almost completely covered with bark and with dead branches and twigs; (4) dead for intermediate time: between 80 and 90% bark cover and with small ca. 1 cm diameter branches remaining; and (5) long dead: < 80% bark cover. Foraging surfaces were classified as with or without bark and further classified as: (1) smooth, with < 0.1 cm wide cracks; (2) medium, with 0.1–0.5 cm wide cracks; and (3) rough, with > 0.5 cm wide cracks.

Behavioural variables

Foraging behaviour variables included proportion of foraging techniques used, climbing distance (m) while seeking for prey, moving distance (m) flying between foraging trees, foraging height (m) and foliage cover. Foraging techniques were assigned to the following categories, adapted from Remsen and Robinson (1990): (1) pecking: intermittently striking the bill against the substrate to remove some of the exterior (bark, wood, lichens), ≤ 4 consecutive pecks; (2) chiselling: removing bark or wood layers with bill strikes at an oblique angle, (3) hammering: sustained pecking, digging deep holes, > 4 consecutive pecks; (4) probing: inserting the bill tip in cracks or holes; (5) climbing and seeking: climbing and looking for prey, (6) scanning: looking around; and (7) eating: consuming a prey. We estimated foliage cover within an imaginary 3 m diameter sphere around each foraging woodpecker in five categories: (1) bare: no foliage cover; (2) open: between 1 and 30% foliage cover; (3) medium: 30–60% foliage cover; (4) medium to dense: 60–90% foliage cover; and (5) heavy: > 90% foliage cover. We took ad libitum notes of instances of foraging in close proximity of < 30 m and

interactions (or lack thereof) between any combinations of two of the three species, as an indicator of interference competition.

Data treatment and analysis

Most (80%) of our foraging observations were from radio-tagged woodpeckers (Table 1), specifically, from 17 Helmeted Woodpeckers, 8 Lineated Woodpeckers and 12 Robust Woodpeckers. If an unmarked foraging woodpecker of one of the study species was encountered an observation was made as well. We performed preliminary Levene's test for continuous variables and Chi square test for categorical variables for each species, and found no effect of tagged and untagged individuals for any of the variables ($P > 0.05$), so data of tagged and untagged birds were pooled. We typically recorded one foraging observation per day per individual spaced by several days until the next observation. Thus, we considered them as independent observations. Most foraging observations (59%) had a duration of 60 s as targeted, the remainder had a duration of between 15 and 58 s, after which the woodpecker disappeared from sight.

Differences in DBH, substrate diameter, foraging height and plant height were examined with Kruskal–Wallis tests (α level = 0.05), and differences in foliage cover, foraging surface, decay state of trees and decay state of substrates with Chi square tests. To assess differences in tree diversity used for foraging, we calculated the Shannon–Wiener index (H'). To examine differences in frequency of usage of different foraging techniques between woodpecker species we employed generalized linear models (GLMs) with binomial error distribution and logit link function. Statistical analyses were performed in R 3.3.3 (R Core Team 2017). GLM was performed using the glm function. To check the fit of the models, residuals were tested for normality and homoscedasticity. Measurements are given as mean ± SD.

Table 1 Number of foraging observations of Helmeted, Lineated and Robust Woodpeckers in selectively logged and old-growth forest, for radio-tagged and non radio-tagged individuals

Species	Radio-tagged		Non radio-tagged	
	Logged	Old-growth	Logged	Old-growth
Helmeted	91	100	6	5
Lineated	23	43	12	27
Robust	26	46	17	14
Total	140	189	35	46

Results
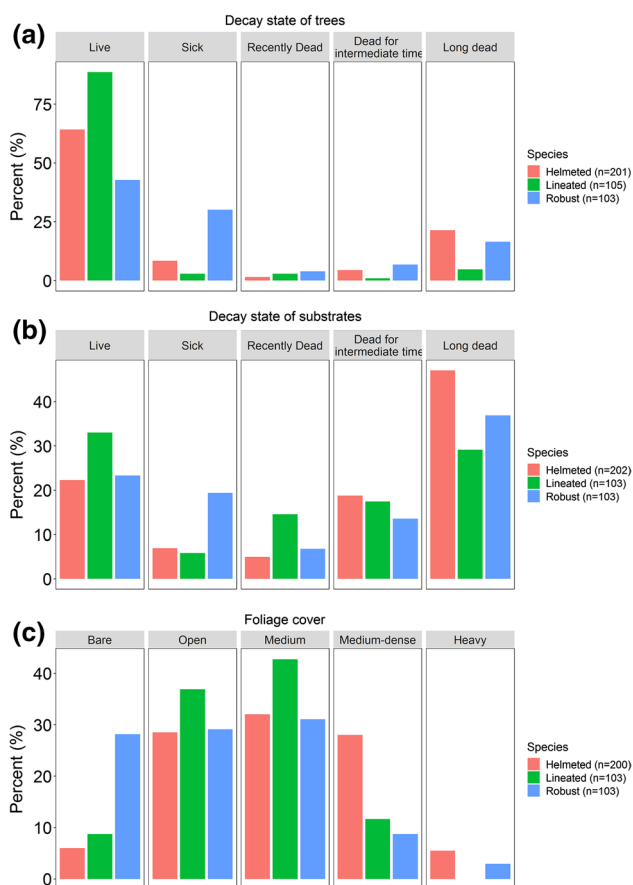
Foraging substrates and trees

Species comparisons

Diameter at breast height (DBH) of trees used for foraging differed among the three woodpecker species ($\chi^2 = 64.4$, $df = 2$, $P < 0.001$). Robust Woodpecker foraged on larger diameter trees (56.9 ± 4 cm, $n = 101$), followed by Lineated Woodpecker (54 ± 3 cm, $n = 103$) and Helmeted Woodpecker (33 ± 2 cm, $n = 194$). Diameter of substrates used for foraging showed a different pattern, in which Robust Woodpecker selected larger diameters (29.6 ± 27.3 cm, $n = 103$) than both Helmeted (14.5 ± 13.3 cm, $n = 200$) and Lineated woodpeckers (14.48 ± 12.7 cm, $n = 105$) that selected similar substrate diameters ($\chi^2 = 46.4$, $df = 2$, $P < 0.001$). Mean plant height selected for foraging was higher in Lineated ($22. \pm 8.1$ m, $n = 101$) and Robust Woodpecker (20.1 ± 8.7 m, $n = 103$), and was significantly lower in Helmeted Woodpecker (14.9 ± 7.7 m, $n = 194$) ($\chi^2 = 66.1$, $df = 2$, $P < 0.001$).

We found a significant difference in the frequency of use of tree species selected for foraging among the three woodpecker species ($\chi^2 = 62.9$, $df = 12$, $P < 0.001$). Robust Woodpecker used Paraná pine frequently (at PPCC). Lineated Woodpecker showed a relatively frequent use of cancharana. Helmeted Woodpecker frequently used laurel trees in the genus *Nectandra* (Table 2), and it was the only species recorded foraging on bamboo stems, which represented 10% of its foraging observations (11 foraging observations on *Guadua trinii* and 6 on *Merostachys claussenii*). Helmeted Woodpecker used the widest diversity of trees ($H' = 3.3$) for foraging, followed by Robust Woodpecker ($H' = 3.0$) and Lineated Woodpecker ($H' = 2.9$). The three woodpecker species differed in decay state of trees ($\chi^2 = 70.8$, $df = 8$, $P < 0.01$). Helmeted Woodpecker showed a frequent use of live trees (64%, $n = 129$), followed by long-dead trees (22%, $n = 43$). Lineated Woodpecker used mostly live healthy trees (90%, $n = 93$) for foraging. Robust Woodpecker most frequently foraged on live trees as well (43%, $n = 44$), and used sick trees more than the other two species (Fig. 2a). We also found a pattern of differentiation of foraging decay state of substrates among species ($\chi^2 = 34.6$, $df = 8$, $P < 0.01$). Helmeted Woodpecker used long-dead substrates, Lineated Woodpecker used live and recently dead substrates, and Robust Woodpecker used sick substrates more than their co-existing species (Fig. 2b). We found no difference among foraging surfaces used by woodpeckers ($\chi^2 = 14.9$, $df = 10$, $P = 0.13$). Foliage cover differed between species ($\chi^2 = 53.3$, $df = 8$, $P < 0.001$). Lineated Woodpecker
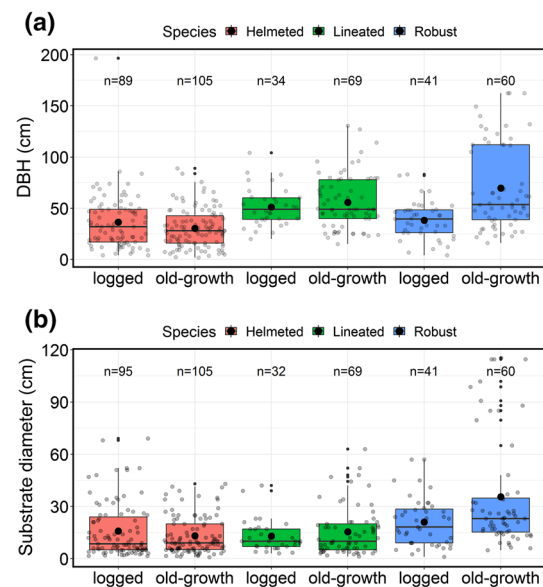
Table 2 Percentage (%) and frequency (*n*) of the most common plant species used for foraging by Helmeted, Lineated and Robust Woodpeckers

Plant species	Common name	Helmeted	*n*	Lineated	*n*	Robust	*n*
Araucaria angustifolia	Paraná pine	0.6	1	5.6	5	19.5	17
Balfourodendron riedelianum	Guatambú	1.8	3	4.4	4	10.3	9
Cabralea canjerana	Cancharana	1.2	2	11.1	10	0	0
Guadua trinii	Yatevó	6.5	11	0	0	0	0
Merostachys claussenii	Takuapí	3.6	6	0	0	0	0
Nectandra lanceolata	Laurel amarillo	12.4	21	10	9	7	6
Nectandra megapotamica	Laurel negro	13.6	23	12.2	11	5.7	5
Prunus subcoriacea	Persiguero	5.9	10	6.7	6	5.8	5
	Liana	4.7	8	2.2	2	4.6	4
	Other	49.7	117	47.8	58	47.1	57
Total			202		105		103

Trees, lianas, bamboo species, and their common names were included

Fig. 2 Comparison of **a** decay state of trees, **b** decay state of substrates and **c** foliage cover between Helmeted, Robust and Lineated Woodpeckers considering both forest conditions

Fig. 3 Comparison of **a** DBH and **b** substrate diameter between Helmeted, Lineated and Robust Woodpecker in old-growth and selectively logged forest. In the boxplot, the box represent the middle 50% of scores (Q1–Q3), the horizontal line represents the median, the mean is represented by the dark black dot and observed values are represented by translucent dots. The lower whisker extends to the lowest sample item not more than $1.5 \times IQR$ (Q3 − Q1) below Q1. The upper whisker extends to the largest sample item not more than $1.5 \times IQR$ above Q3. The individual black points outside the whiskers are the outliers

Robust Woodpecker foraged in spots with medium to bare foliage cover (Fig. 2c).

Old growth vs. logged forest comparisons

DBH of trees used was not related to forest conditions for Helmeted ($\chi^2 = 2.6$, $df = 1$, $P = 0.1$) nor Lineated Woodpecker ($\chi^2 = 0.3$, $df = 1$, $P = 0.6$); however, Robust Woodpecker used larger DBH trees in old-growth forest compared to logged

foraged mostly under medium cover and never foraged under a heavy foliage cover. Helmeted Woodpecker foraged at spots with medium to heavy foliage cover in greater proportion compared to the other two species (Fig. 2c).

forest ($\chi^2 = 13.9$, $df = 1$, $P < 0.001$) (Fig. 3a). Foraging substrate diameters were statistically identical in old-growth and logged forests comparisons within Helmeted ($\chi^2 = 0.02$, $df = 1$, $P = 0.8$), Lineated ($\chi^2 = 2.87$, $df = 1$, $P = 0.09$) and Robust Woodpeckers ($\chi^2 = 1.8$, $df = 1$, $P = 0.1$) (Fig. 3b). Robust Woodpecker foraged on higher trees in the old-growth forest (old-growth: $23.9. \pm 8.5$ m, $n = 60$ vs. logged: 15.9 ± 7.3 m, $n = 43$) ($\chi^2 = 15.9$, $df = 1$, $P < 0.001$), while Helmeted (old-growth: $14.6. \pm 7.8$ m, $n = 89$ vs. logged: 16.3 ± 7.9 m, $n = 66$) ($\chi^2 = 0.5$, $df = 1$, $P = 0.5$) and Lineated Woodpeckers (old-growth: 23.9 ± 8.5 m, $n = 68$ vs. logged: 21.7 ± 7.1 m, $n = 34$) ($\chi^2 = 1.8$, $df = 1$, $P = 0.4$) foraged on trees of similar height in the two forest conditions.

Decay state of substrates ($\chi^2 = 1.6$, $df = 4$, $P = 0.8$) and foraging surface ($\chi^2 = 4.2$, $df = 5$, $p = 0.5$) selected by Helmeted Woodpecker did not differ between old-growth and selectively logged forest. Decay state of trees, on the other hand, reached a nearly significant level ($\chi^2 = 10.6$, $df = 4$, $P = 0.06$), with a higher use of sick trees (12.5%) in selectively logged forest than in old-growth forest (4.8%) and a higher use of trees dead for intermediate time in old-growth forest (6.7%) than in selectively logged forest (2.1%). Robust Woodpecker did not use different foraging surfaces ($\chi^2 = 5.2$, $df = 5$, $P = 0.4$), decay state of trees ($\chi^2 = 5.9$, $df = 4$, $P = 0.2$) or decay state of substrates ($\chi^2 = 3.2$, $df = 4$, $P = 0.5$) between the two forest types. Finally, Lineated Woodpecker did not differ in the use of decay state of substrates ($\chi^2 = 8.8$, $df = 4$, $P = 0.07$) or decay state of trees ($\chi^2 = 2.6$, $df = 5$, $P = 0.6$), but used different foraging surfaces among forest conditions ($\chi^2 = 11.8$, $df = 5$, $P = 0.03$), foraging mostly on medium (30.4%) bark in old-growth forest, compared to selectively logged forest, where it foraged most frequently on smooth bark (45.5%). Foliage cover selection by Helmeted Woodpecker was similar between forest conditions ($\chi^2 = 6$, $df = 4$, $P = 0.2$), but differed for the other two species. Robust Woodpecker foraged mostly at spots (36.7%) with no foliage cover in old-growth forests ($\chi^2 = 10.3$, $df = 4$, $P = 0.03$), while it foraged at spots with medium foliage cover (39.7%) in selectively logged forests. Lineated Woodpecker foraged mostly (47.8%) at spots with medium cover in old-growth forests ($\chi^2 = 11.8$, $df = 3$, $P = 0.007$), while it predominantly (47.1%) foraged at spots with bare foliage cover in selectively logged forests.
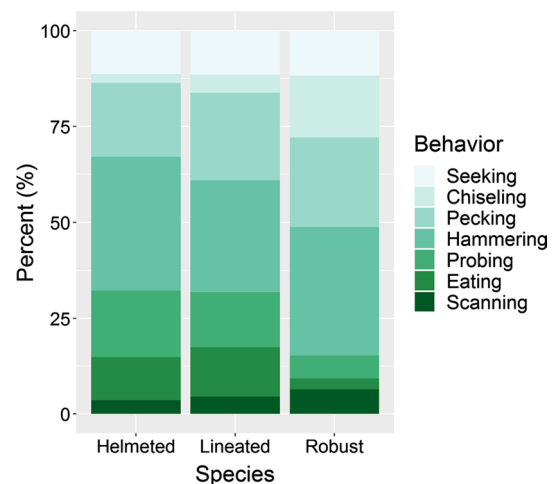
Foraging behaviour

Species comparisons

Foraging behaviour patterns showed some similarities among woodpecker species. Helmeted Woodpeckers spent the highest proportion of their foraging time with hammering (35%), usually quite soft and audible only up to ca. 20 m away, followed by intermittent pecking (19%) and probing

(17%). Lineated Woodpeckers spent most of their time foraging with hammering (29%), usually loud and easy to detect in the forest, followed by intermittent pecking (23%) and probing (14%). Finally, the most common foraging technique for Robust Woodpeckers was hammering (33%), followed by intermittent pecking (23%), both audible from a great distance, and chiselling in third place (16%). Three foraging techniques differed between woodpecker species. Chiselling was used significantly more by Robust Woodpecker and Lineated Woodpecker than by Helmeted Woodpecker (Fig. 4) (Robust Woodpecker: GLM estimate: 2.1, SE: 0.3, $Z = 6.7$, $P < 0.001$; Lineated Woodpecker: GLM estimate: 1.6, SE: 0.3, $Z = 5.5$, $P < 0.001$). Probing was used more by Helmeted Woodpecker than by Robust Woodpecker (Robust Woodpecker: GLM estimate: -0.9, SE: 0.2, $Z = -3.5$, $P < 0.001$; Lineated Woodpecker: GLM estimate: -0.2, SE: 0.2, $Z = -1.1$, $P = 0.3$). Hammering was used more by Helmeted Woodpecker than by Lineated Woodpecker (Robust Woodpecker: GLM estimate: 0.1, SE: 0.2, $Z = 0.2$, $P = 0.8$, Lineated Woodpecker: GLM estimate: -0.6, SE: 0.3, $Z = 2.4$, $P = 0.01$).

We only obtained incidental diet observations, because woodpeckers generally foraged high in the trees and with their bills inside the wood. We recorded 18 *Crematogaster* ant-feeding events and one of a thin worm of ca. 4 cm by Helmeted Woodpeckers, two unidentified ant-feeding events by Lineated Woodpeckers and five wood-boring larvae prey items plus one ant-feeding bout by Robust Woodpeckers.

Analysis of foraging height showed clear differences between the three woodpeckers ($\chi^2 = 107.8$, $df = 2$, $P < 0.001$). Lineated Woodpecker (16.4 ± 6.3 m, $n = 101$) foraged highest, followed by Robust Woodpecker (13.4 ± 7.1 m, $n = 102$) and Helmeted Woodpecker (8.3 ± 4.8 m, $n = 196$). Climbing distances ($\chi^2 = 2.0$, $df = 2$,

Fig. 4 Foraging behaviour comparison between Helmeted, Lineated and Robust Woodpeckers, considering both forest conditions

$P = 0.2$) (Helmeted Woodpecker: 0.7 ± 1.9 m, $n = 193$; Lineated Woodpecker 0.6 ± 2.4 m, $n = 103$; and Robust Woodpecker 0.8 ± 3.1 m, $n = 102$) during observations, and flying distances (Helmeted Woodpecker: 0.9 ± 5.2 m, $n = 193$; Lineated Woodpecker 1.8 ± 7.4 m, $n = 103$; and Robust Woodpecker 0.7 ± 5.5 m, $n = 102$) between foraging substrates were not different between woodpecker species ($\chi^2 = 0.6$, $df = 2$, $P = 0.2$).

Old growth vs. logged forest comparisons

No significant difference was found in foraging height of Helmeted Woodpecker ($\chi^2 = 0.12$, $df = 1$, $P = 0.8$) nor Lineated Woodpecker ($\chi^2 = 0.12$, $df = 1$, $P = 0.7$) between mature and logged forest. On the other hand, Robust Woodpecker foraged higher in the old-growth forest ($\chi^2 = 27.4$, $df = 1$, $P < 0.001$) (Fig. 5).

Lack of interspecific interactions

No interspecific calls, drumming, displays, displacements or following were observed during eight occasions when two of the three woodpecker species were foraging less than 30 m from each other. The occasions involved two cases of Lineated Woodpecker in proximity of Robust Woodpecker, four cases of Lineated Woodpecker in proximity of Helmeted Woodpecker, and two cases of Helmeted Woodpecker in proximity of Robust Woodpecker. In several instances, individuals of two species were even in the same tree, < 3 m away from one another without notable interactions. Considering the low frequency of individuals foraging in proximity of individuals of another species there was no indication that the look-alike species engaged in mixed flocking.
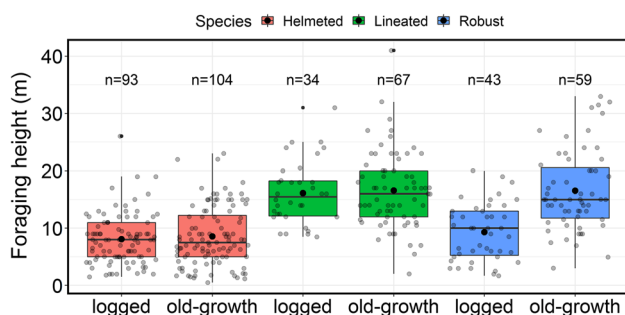
Fig. 5 Foraging height comparison between Helmeted, Lineated and Robust Woodpecker in old-growth and selectively logged forest. Graphic properties are explained in the legend of Fig. 3

Discussion

We found a notable differentiation in the overall foraging ecology of the three largest woodpeckers of the Atlantic Forest. These differences were apparent in both old-growth and selectively logged forests. Except for foraging surface selection, all other measured variables were selected differently by at least one of the species. We found marked niche separation and absence of species interactions, findings that do not agree with predictions if these species were conforming to a mimicry complex under the hypothesis of ISDM. Instead, predictions from alternative hypothesis may better fit our results, as explained below.

Foraging substrates and trees

Species comparisons

Our results clearly demonstrate resource differentiation in relation to diameter and decay state of trees and substrates between the three co-existing woodpeckers. Helmeted Woodpecker foraged on smaller DBH trees and substrate diameters and often used dead branches in live trees. It foraged on entirely dead trees only 26% percent of time. A possible reduction of snags in managed forest may, therefore, not affect the foraging resources of the Helmeted Woodpecker as much as it affects woodpeckers of conservation concern in managed forests elsewhere (Czeszczewik 2009; Imbeau et al. 2001; Tingley et al. 2020). Because of its relatively weak bill (Brooks et al. 1993), the Helmeted Woodpecker often foraged on dead and soft wood that is comparatively easy to excavate. Robust Woodpecker foraged on larger diameter trees and substrates, and showed a frequent use of dead substrates in live and decaying trees, consistent with data reported for the congeneric Magellanic Woodpecker (Vergara and Schlatter 2004; Chazarreta et al. 2012). Finally, Lineated Woodpecker foraged on substrate diameters similar to Helmeted Woodpecker, but in larger diameter trees and used live healthy trees and both live and dead substrates to forage. These results are consistent with studies of Lineated Woodpecker and congeners elsewhere (Rolstad et al. 1998; Newell et al. 2009; Granada-Ríos and Mancera-Rodríguez 2015; Nappi et al. 2015).

Importance of *Nectandra* laurel trees and bamboo for Helmeted Woodpecker

Helmeted Woodpecker frequently used *Nectandra* trees for foraging. For nesting, it uses these trees almost exclusively (Lammertink et al. 2020). Although formerly common in the Atlantic Forest (Ríos 2006) and historically not sought out

for prime timber, these trees are currently under increasing logging pressure. The relevance of *Nectandra* trees for Helmeted Woodpecker to satisfy several important ecological requirements make these tree species an essential factor in understanding its ecology.

Helmeted Woodpecker selected bamboo stems to forage in a relatively high proportion (10% of observations) and it also often used woody substrates within dense bamboo stands. This was unlike Lineated and Robust Woodpeckers, which rarely ventured into bamboo stands. When we tried approaching Helmeted Woodpeckers foraging at low heights in dense bamboo stands we flushed them on multiple occasions before we could get them into view for an observation. We, therefore, estimate that the true frequency of foraging on bamboo by Helmeted Woodpecker lies in the 12–15% range of foraging substrates. The selection of bamboo as a foraging source is well marked in two other *Celeus* species: the Kaempfer´s Woodpecker (*C. obrieni*, Leite et al. 2013) and the Rufous-headed Woodpecker (*C. spectabilis*, Kratter 1997). The mix of bamboo and woody substrates used by Helmeted Woodpecker could be beneficial in avoiding certain risks to which true bamboo specialist birds may be exposed (Areta et al. 2009; Cockle and Areta 2013; Socolar et al. 2013). Nonetheless, during bamboo die offs there probably will be temporary fluctuations in this food source and concomitant reduction of vegetation cover, which could have an impact on foraging microhabitat selection in Helmeted Woodpeckers.

Old growth vs. logged forests

Robust Woodpeckers exhibited the clearest changes between forest treatments, differing in four features: foraging at greater height, choosing trees with a greater DBH, foraging in higher trees and using spots with more open foliage in old-growth forests. The fact that Robust Woodpecker foraged on larger diameter and higher trees in mature forests may correspond to the higher density there of these kind of trees, which are scarce in the selectively logged forests. Our results for substrate and tree use in old-growth forest by Robust Woodpecker are skewed by its frequent use of large Paraná pines at the PPCC site, which holds an important remnant population of these trees. It is of note that although all three species had the same access to the Paraná pine resource at PPCC, only Robust Woodpecker used it in a great proportion. Our results indicate that characterizing foraging habitats of woodpeckers requires extensive geographic sampling. Local features may lead to different resource use by each species. Ecological segregation may differ from place to place for the same set of species depending on local resource availability.

None of the other variables related to trees and substrates use (i.e., decay state of trees, decay state of substrates and foraging surface) differed between forest conditions for each woodpecker species. Prey distribution is related to the characteristics of trees and substrates (Tavakilian et al. 1997). Therefore, if woodpeckers are searching for certain food items, it is expected that woodpecker species will use similar substrate conditions in different forest types.

Foraging behaviour

Helmeted Woodpeckers foraged almost exclusively at lower and middle heights in spots with heavy foliage cover. As the smaller species, it may be at risk from predation from a wider range of predators and may avoid foraging in exposed spots. In contrast, Robust and Lineated Woodpecker were seen foraging at greater heights, although Lineated Woodpecker did not show a clear preference for a foraging height. A larger species such as Robust Woodpecker may be less susceptible to predation risk, and it was usually seen foraging in pairs, which may impart an advantage in detecting predators (Lima 1990), whereas Helmeted Woodpecker almost always foraged solitary. Such behavioural differences undoubtedly contribute to niche partitioning among these sympatric species.

Robust Woodpecker was seen chiselling in a high proportion, in line with congeneric *Campephilus* species (Tanner 1942; Vergara and Schlatter 2004). Chiselling and sustained hard hammering allows Robust Woodpecker to expose wood-boring larvae and beetles that live in cracks and boring holes, which represent their main food source (Winkler et al. 1995). On the other hand, Helmeted and Lineated Woodpecker fed by probing in a considerable proportion. Both *Celeus* and *Dryocopus* genera are known to feed mainly on ants (Winkler and Christie 2002; Newell et al. 2009), which are reached by inserting the tongue into small holes in branches, tree trunks or bamboo stems. These differences in diet (consistent with our observations) and the way woodpeckers capture their prey also play a role in differentiating foraging ecology among species.

Although the Helmeted Woodpecker foraged frequently on certain tree species and substrates, we did not find any remarkable factor in its foraging ecology that explains its association with mature forests, whereas other aspects of its ecology, namely, nesting and roosting sites, provide a clear link to mature forests (Lammertink et al. 2019; Lammertink et al. 2020).

Testing the ISDM hypothesis

Our findings do not correspond to what would be expected if plumage similarities between Helmeted, Lineated and Robust Woodpeckers were driven by ISDM. Prum and Samuelson (2012) proposed that ISDM should occur between ecological competitors. Ecological competition can occur in

two different ways: exploitative competition and interference competition (Schoener 1983). Exploitative competition is an indirect interaction, where one species more efficiently uses a shared limiting resource. Our data on foraging behaviour and characteristics of foraging sites suggests low overlap in both resource and substrate selection between the three woodpeckers, indicating that there is not a strong exploitative competition. Interference competition is a direct interaction, in which species compete for a resource via aggressive behaviours. In our 724 fieldwork days during eight years, we never recorded an agonistic behaviour between any pair of the three woodpecker species in the complex. Instead, we recorded cases, where one species was foraging in the presence of one or two of the other species nearby (within < 30 m) or even within 3 m from one another in the same tree and there were no notable interactions between the look-alike woodpeckers. This is relevant, because the distance of social encounters is an important variable for ISDM, since beyond a certain distance, mimics can deceive the model species, but at a short distance, the model should recognize the mimic and react aggressively to its presence. This lack of interactions, even at short distances, where the model species would no longer be deceived, makes it unlikely that mimicry between species is being maintained by ISDM mechanisms.

Prum (2014) promoted the plausibility of ISDM by citing data on foraging substrate overlap and aggressive behaviour between Hairy (*Dryobates villosus*) and Downy (*D. pubescens*) Woodpeckers (Kisiel 1972), which is contrary to the low overlap in foraging ecology and lack of aggression that we found for the three species in this study. Prum (2014) also suggested that under certain conditions, there could be a significant dietary differentiation, and the model would be preventing access to a resource that is a small component of the diet of the subordinate species but is of high value to the dominant species. If this is the case for Helmeted and Lineated or Robust woodpecker, the low overlap in other aspects of their foraging ecology (i.e., foraging height, substrate diameter, DBH, tree species) indicates that the presumed mimic is not restricted in its access to resources.

The ISDM hypothesis proposes that this type of mimicry would evolve more frequently in species that occupy open habitats that afford longer sight lines, or in smaller species occupying closed habitats (Prum 2014). These predictions do not apply to the case of the Helmeted Woodpecker, the smaller species of the trio, which is strongly forest associated and is a relatively large woodpecker. Finally, ISDM indicates a typical ratio of the mass of mimics to model of ~ 56 to 58% (Prum 2014), which does not match the ratios of the Atlantic Forest woodpeckers, where we found ratios of 48% between Helmeted and Robust Woodpecker, 60% between Helmeted and Lineated Woodpecker, and 79% between Lineated and Robust Woodpecker. However, since there is wide variation

of between 18 and 90% between presumed models and mimics (Prum 2014), this discrepancy from the general pattern alone is not enough to reject the idea of ISDM among the three Atlantic Forest woodpeckers.

Another proposed mimicry mechanism is that mimicry benefits individuals when occurring in mixed flocks with individuals of similar looking species (Beauchamp and Goodale 2011). Willis (1989) noted one instance of a Helmeted Woodpecker occurring near (but not within) a group of Robust Woodpeckers in Brazil and proposed, based on this sparse information, that mixed flocking may drive their plumage convergence. However, Machado (1999) studied mixed flocks at the same site as Willis (1989) and did not observe associations among the three large woodpeckers. Our results from Argentina match those of Machado (1999) and together indicate that mixed flocking is absent among Robust, Lineated and Helmeted Woodpeckers, and it cannot explain their plumage convergence.

Two alternate hypotheses more closely fit our findings: (1) deception of third-party species and (2) deception of conspecifics. Mimicry may be maintained by the advantage of deceiving third-party species into believing they are the socially dominant species, as proposed by Leighton et al. (2018). It is likely that the behaviour of Helmeted Woodpecker, which includes avoidance of foraging in highly exposed spots and remaining silent and hidden for much of the day, is a strategy to avoid detection by potential predators. Considering this is a very striking woodpecker species, with a remarkably large red crest, a raptor could easily detect it. Mimicking larger species could provide an advantage in deceiving potential predators.

Mimicry of co-existing species may also confer advantages in intraspecific competition. In general, individuals experience far stronger competition from conspecifics than from individuals of other species (Dhondt 2012) and thus strong selective pressure exists to alleviate intraspecific competition. Mimicking the plumage of co-existing species results in having look-alike stand-ins around in the territory of an individual, which in turn may help in territorial defence by intimidating and deceiving conspecific interlopers, particularly at longer sight distances (Lammertink 2007). We propose that deceiving conspecifics into mistaking individuals of co-existing species as conspecifics, with resulting advantages in intraspecific competition may be a factor driving plumage convergence.

Helmeted Woodpecker, the smaller and presumably subordinate species, is far rarer than the two larger species. This rejects the prediction of ISDM that the subordinate species should exist at higher frequency in the community than model species (Prum and Samuelson 2016). On the other hand, if plumage convergence is driven by deceiving third species or by deceiving conspecifics, clear advantages exist when individuals of the model species are more common

than those of the mimic, matching the abundance patterns of the three Atlantic Forest woodpeckers.

We recommend several lines of inquiry for future studies into the causes underlying the plumage convergence of the look-alike Atlantic Forest woodpeckers. It would be insightful to quantify the amount of dietary overlap between the three species, through an assessment of the precise diet of each species, for instance by flushing stomachs of mistnetted adults or nestlings, or by analysis of high-resolution images or video of foraging woodpeckers. A study into the prey composition of potential predators (e.g., the raptors *Micrastur* spp., *Accipiter* spp., *Spizaetus* spp.) could assess the frequency of Helmeted Woodpecker as prey, relative to its abundance, and relative to the frequency of prey species of similar size; a lower than expected predation rate would indicate the deceiving of predators succeeds. An assessment of the spatial overlap between home ranges of the three woodpeckers will provide insight in the spatial component of their co-existence. Finally, one testable prediction following from the role of plumage convergence in territory defence against conspecifics is that at sites, where look-alike species are absent, the remaining species would spend more time on territory defence and advertising.

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