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Research Paper

Home range patterns of Helmeted Woodpecker (*Celeus galeatus*), Lineated Woodpecker (*Dryocopus lineatus*), and Robust Woodpecker (*Campephilus robustus*) in Misiones, Argentina, in a global perspective

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ABSTRACT. Home range mapping studies of birds inform about area requirements and responses to land management as reflected by home range sizes and by resource selection within home ranges. Tracking studies of woodpeckers (*Picidae*) so far have been concentrated in temperate regions. In the subtropical Atlantic Forest of northeast Argentina, we assessed interspecific differences in home range sizes in old-growth forests and selectively logged forests of Helmeted Woodpecker (*Celeus galeatus*, a globally threatened species), Lineated Woodpecker (*Dryocopus lineatus*), and Robust Woodpecker (*Campephilus robustus*). Helmeted Woodpecker had larger breeding home ranges in selectively logged forests, averaging 105 ± 39 ha for pairs, versus 60 ± 13 ha in old-growth forests. Lineated Woodpecker breeding home ranges of pairs averaged 56 ± 22 ha, and those of Robust Woodpecker 43 ± 22 ha, with no differences between forest types. Helmeted Woodpeckers had an unusual separation between the home ranges of males and females in breeding pairs, with a mean area overlap of only 8% ± 9% near the nest tree, resulting in large home ranges for pairs. Helmeted Woodpecker and Robust Woodpecker individuals that were followed into the post-breeding stage had marked expansions of their home range sizes relative to breeding home ranges. To place our findings with Atlantic Forest woodpeckers in perspective we reviewed whether woodpecker home range sizes increase with latitude and body mass globally. For 29 populations of 22 woodpecker species, a power regression model with these factors explained 24.1% of variation in breeding home range sizes, with 17.1% of variation explained by latitude alone. Woodpecker species with larger home ranges than predicted values were three species of North American woodpeckers of coniferous forests, as well as the Helmeted Woodpecker. Our results of smaller home ranges in old-growth forests for the Helmeted Woodpecker affirm an association of this species with such forests. We urge the conservation of the few remaining tracts of old-growth Atlantic Forest and more restoration of logged forests to mature conditions.

Modèles de domaines vitaux du pic casqué (*Celeus galeatus*), du pic ouentou (*Dryocopus lineatus*) et du pic robuste (*Campephilus robustus*) à Misiones, en Argentine, dans une perspective globale

RÉSUMÉ. Les études de cartographie des domaines vitaux des oiseaux informent au sujet des exigences territoriales et des réponses à la gestion des terres telles qu'elles sont reflétées par la taille des domaines vitaux et par la sélection des ressources au sein des domaines vitaux. Les études de suivi portant sur les pics (*Picidae*) se sont jusqu'à présent concentrées sur les régions tempérées. Dans la forêt atlantique subtropicale du nord-est de l'Argentine, nous avons évalué les différences interspécifiques en termes de taille du domaine vital dans les forêts anciennes et les forêts exploitées de manière sélective du pic casqué (*Celeus galeatus*, une espèce menacée à l'échelle mondiale), du pic ouentou (*Dryocopus lineatus*) et du pic robuste (*Campephilus robustus*). Le pic casqué présentait un domaine de reproduction plus étendu dans les forêts exploitées de manière sélective, avec en moyenne 105 ± 39 ha pour les couples, contre 60 ± 13 ha dans les forêts anciennes. Les domaines de reproduction du pic ouentou pour les couples étaient en moyenne de 56 ± 22 ha, alors qu'ils étaient de 43 ± 22 ha pour le pic robuste, quel que soit le type de forêt. Chez les pics casqués, on constate une séparation inhabituelle entre les domaines vitaux des mâles et des femelles des couples reproducteurs, avec un chevauchement moyen de ces zones de seulement 8 à 9 % à proximité de l'arbre où se trouve le nid, de sorte que le domaine vital des couples est très étendu. Les pics casqués et les pics robustes individuels qui ont été suivis au cours de la phase post-reproduction présentaient des extensions nettes de la taille de leur domaine vital par rapport à celle de leur domaine de reproduction. Pour mettre en perspective nos résultats concernant les pics de la forêt atlantique, nous avons essayé de savoir si la taille du domaine vital des pics augmente avec la latitude et la masse corporelle à l'échelle mondiale. Pour 29 populations de 22 espèces de pics, un modèle de régression de puissance prenant en compte ces facteurs a expliqué la variation de 24,1 % de la taille des domaines de reproduction, une variation de 17,1 % étant expliquée par la seule latitude. Les espèces de pics possédant des domaines vitaux plus étendus que les valeurs prévues étaient trois espèces de pics nord-américains habitant les forêts de conifères, ainsi que le pic casqué. Nos résultats concernant les domaines vitaux plus petits dans les forêts anciennes pour le pic casqué confirment l'association de cette espèce avec ces forêts. Nous incitons à la conservation des quelques territoires restants de forêt atlantique ancienne et à une restauration supérieure des forêts exploitées jusqu'à maturité.

Key Words: *Atlantic Forest; body mass; home range size; latitude; old-growth forest; radio-tracking; selective logging; woodpeckers*

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INTRODUCTION

Home range mapping studies of birds have various purposes, including conservation purposes, such as to inform about area requirements of birds and their responses to land management, as reflected by home range sizes and resource selection within home ranges. Many species in the woodpecker family (*Picidae*) are associated with forest conditions such as mature stands and naturalness of forests by their specific requirements of tree resources for foraging, nesting, and roosting (Roberge et al. 2008, Vergara-Tabares et al. 2018). Starting in the 1970s, woodpecker home ranges have been mapped by following color-banded individuals (Baker 1971) or by radio-tracking individuals (Nesbitt et al. 1978). Woodpecker tracking studies generally aim to assess area requirements, and responses to forest management or forest fires as reflected by home range sizes, space use, and tree selection within home ranges (e.g., Rolstad et al. 1998, Pasinelli et al. 2001, Rota et al. 2014, Tingley et al. 2014, Campion et al. 2020). The bulk of such radio-tracking or color-banding studies to map home ranges of woodpeckers have been carried out in temperate areas of North America and Europe, with the exceptions of Corrêa (2012) and Da Silva et al. (2012). A lack of published radio-tracking studies of woodpeckers from subtropical or tropical areas reflects the general paucity of ecological studies of woodpeckers from these regions. This stands in contrast to high woodpecker species diversity in (sub)tropical regions and high pressures from deforestation and logging that woodpeckers there experience, and the resulting clear need for detailed information on their ecological requirements (Mikusiński 2006, Lammertink 2014, Vergara-Tabares et al. 2018). Moreover, few radio-tracking studies of woodpeckers, anywhere in the world, have reported on tracking of multiple species in the same study sites, even though such work will yield the clearest understanding of interspecific differences in area use in response to forestry practices.

The Helmeted Woodpecker (*Celeus galeatus*) is a rare, globally threatened, medium-sized woodpecker of the Atlantic Forest of southeastern South America, a biodiversity hotspot in a highly deforested region with ongoing loss of mature forests (Galindo-Leal and Câmara 2003, Ribeiro et al. 2011, Rosa et al. 2021, Andreacci and Marenzi 2020, BirdLife International 2022). The Helmeted Woodpecker can be found in well-preserved forest areas and is more frequently encountered in the few remaining Atlantic Forest areas with old-growth conditions (Bodrati et al. 2010, Lammertink et al. 2020a). Plausible links that explain the association of this species with mature forests include its use of decay-formed cavities in mature trees, in tree species that are sought-after for timber, for year-round overnight roosting (Lammertink et al. 2019) and its use of large, decaying laurel (*Nectandra* sp.) trees for nest cavity excavation (Lammertink et al. 2020b). Although the dependence on mature forests in other specialist woodpeckers is often related to the availability of foraging resources (Tanner 1942, Czeszczewik 2009, Lammertink et al. 2009, Tremblay et al. 2010), Helmeted Woodpeckers forage mostly in younger, medium-sized trees and on bamboo substrates (Fernández et al. 2020). The Helmeted Woodpecker co-exists throughout its range with the larger Lineated Woodpecker (*Dryocopus lineatus*) and still larger Robust Woodpecker (*Campephilus robustus*). The three species are strikingly similar in plumage colors and patterns, and in spite of considerable differences in body mass they are rather similar in overall size, in part because of the increasingly larger crests of Lineated and Helmeted Woodpeckers (Lammertink et al. 2020b). The plumage convergence of the three species has been proposed to be driven by interference competition for foraging resources (Prum and Samuelson 2016). However, the three species occupy markedly different foraging niches and do not exhibit interspecific aggression (Fernández et al. 2020). Plumage convergence may instead aid in deceiving predators, and provide advantages in intraspecific competition by deceiving conspecific territory interlopers into mistaking the co-existing species for conspecifics (Fernández et al. 2020). Lineated Woodpecker and Robust Woodpecker are more flexible than Helmeted in adapting to smaller trees in logged forests for cavity excavation (Lammertink et al. 2020b), use both excavated and decay-formed cavities for roosting (M. Lammertink and J. M. Fernández, *unpublished data*), generally are more common than Helmeted Woodpecker (see https://ebird.org/home), and often persist in selectively logged forests and fragmented forests (Krauczuk and Baldo 2004, Krauczuk 2008).

We mapped home ranges of radio-tagged Helmeted, Lineated, and Robust Woodpeckers in old-growth forests and selectively logged forests in the Atlantic Forest region of Misiones province, northeast Argentina. In view of the reported association of Helmeted Woodpecker with old-growth forest and the reported persistence of Robust and Lineated Woodpecker in disturbed or fragmented forests, we expected Helmeted Woodpecker to be impacted more by selective logging and have larger home range sizes in selectively logged forests than in old-growth forests, whereas we expected the other two species to have no such differences, or to have them to a lesser extent. We aimed to assess (1) whether the Helmeted, Lineated, and Robust Woodpeckers have larger home ranges in selectively logged forests than in old-growth forests, (2) whether there are interspecific differences in home range sizes, (3) whether breeding home range sizes of woodpecker individuals expand in the post-breeding stage, and (4) whether the three species differ in separation (or overlap) of home ranges of males and females of breeding pairs, with resulting interspecific differences in the area requirements of pairs versus individuals.

Our radio-tracking of Atlantic Forest woodpeckers provides among the first detailed home range mapping of subtropical woodpeckers. Comparing and contrasting our results with radio-tracking studies from other regions is, however, not straightforward, because home range sizes of woodpecker populations potentially correlate with latitude and body mass, and interspecific differences in the degree of separation in the ranges of breeding partners need to be taken into account as well. Within species with extensive geographical ranges, such as the Black Woodpecker (*Dryocopus martius*) of Eurasia and Pileated Woodpecker (*Dryocopus pileatus*) of North America, home range sizes are larger at higher latitudes (Cramp 1985, Tomasevic and Marzluff 2018). An effect of latitude on home range size may exist between species at different latitudes as well. At the same time, as a general pattern, larger bird species tend to have larger home ranges (Jenkins 1981). However, there are exceptions in woodpeckers. In Sweden, the Lesser Spotted Woodpecker (*Dryobates minor*) with a body mass of ca. 24 g had mean winter home ranges of 742 ha (Wiktander et al. 2001), whereas on the Sweden–Norway border the much larger Black Woodpecker, with

a body mass of ca. 310 g, had smaller mean year-round home ranges of 223 ha (Rolstad et al. 1998). We reviewed radio-tracking or other home range mapping studies of woodpeckers from around the world, including our Atlantic Forest results, with the additional aims of (5) assessing the variation in the percentage of overlap between home ranges of breeding partners in woodpecker species, (6) determining what percentage of variation in breeding home range sizes of woodpeckers is explained by latitude and body mass of populations, and (7) assessing which woodpeckers world-wide deviate furthest in home range size from the size predicted by the latitude and body mass model. This review allows for placing our home range results from Atlantic Forest woodpecker species in a global perspective.

METHODS

Study areas and woodpecker capturing

Woodpecker home ranges were studied at four Atlantic Forest sites in Misiones province, Argentina, each embedded in extensively forested regions of the province. Two of the sites, separated by a distance of 55 km, are the largest old-growth forest remnants of the southern Atlantic Forest. Old-growth forest is defined here as forests that were never logged for timber, though at one site some trees had been toppled for honey collection, and minor sections of these forests were younger because of wind damage. Two sites were selectively logged forests adjacent to each of the old-growth sites. The four study sites were the following: (1) Parque Provincial (PP) Cruce Caballero (26.52°S, 54.00°W), a 600 ha protected area including 405 ha of old-growth forest; (2) Valle del Arroyo Alegría (26.50°S, 54.00°W), an 8550 ha private forest property adjacent to PP Cruce Caballero. Valle del Arroyo Alegría was selectively logged until ca. 33 years before our fieldwork, and currently consists of a forest mosaic dominated by intensively logged regenerating forest, with a few lightly logged patches and a few old forest patches; (3) Reserva Natural Cultural (RNC) Papel Misionero (27.00°S, 54.20°W), a 10,000 ha private property including ca. 9000 ha of old-growth forest, within the 253,773 ha Yaboty Biosphere Reserve; and (4) Lote 13 (26.92°S, 54.14°W), a 4850 ha private property within the Yaboty Biosphere Reserve and adjacent to RNC Papel Misionero. Selective logging is ongoing in Lote 13 in patches on a 5–10 year rotating cycle, often targeting different tree species in successive cycles. All four sites are at 440 to 620 m above sea level in undulating terrain, 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). By studying adjacent old-growth and selectively logged sites we excluded geographical variation in soil, elevation or vegetation composition from influencing comparisons. Woodpeckers were captured, after extensive scouting for their calling and drumming sites, with mist nets, a decoy lure of each species, playback of vocalizations and drums, and imitations of Robust Woodpecker double knock drums. The woodpeckers were color-banded and outfitted with Holohil Ltd. (Carp, Ontario) radio-tags of < 3% body mass, zip-tied and glued to the central tail feathers. Study sites, capture methods, radio-tagging and woodpecker body masses were described in more detail in Fernández et al. (2020) and Lammertink et al. (2019, 2020b). Between scouting, trapping, and radio-tracking our effort was 724 field days during July–December of 2012 through 2019.

Radio-tracking sampling

For comparisons of home ranges between logged and old-growth forests, and between woodpecker species, we assessed the home ranges of individuals or pairs during nesting, because this is the period of the yearly cycle with peak food demands and demands for nest cavity trees, when home range sizes are most expected to reflect habitat quality and interspecific differences. A focus on the breeding season was also determined by logistical constraints, because woodpeckers could only be captured with playback when they were territorial early in the breeding season, and radio tags had a life span of three to four months. We mapped tracking locations with a hand-held GPS receiver and compass from locations with a visual or aural confirmation (vocalizations, drums, foraging noise, or close-range radio signals) of the location of the tagged bird. For a degree of independence between tracking locations, we used tracking locations separated by at least two hours or at least 200 m from the previous location; at most five locations were collected on a day; and nest and roost locations were only included once. We considered an alternative sampling scheme with locations taken at short intervals and analyzed with a Brownian bridge kernel method (Horne et al. 2007, Tingley et al. 2014) but found this not feasible in our study areas, where hilly terrain and dense undergrowth meant 40 minutes to three hours or more were required to approach a woodpecker for a location reading.

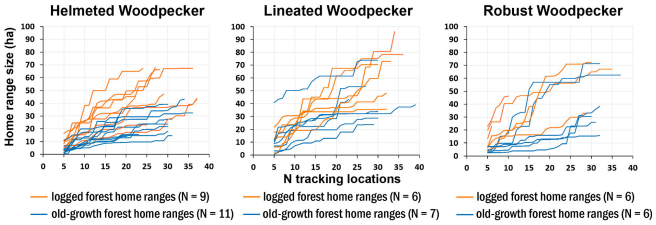
In radio-tracking studies of home ranges of birds, a sample of about 30 tracking locations often yields a stabilized home range size (Kenward 2001) and 25–30 tracking locations is a sample size often used in woodpecker radio-tracking studies (e.g., Renken and Wiggers 1989, Rolstad and Rolstad 1995, Pasinelli et al. 2001, Wiktander et al. 2001, Camprodon et al. 2015, Tremblay et al. 2020). We based comparisons of breeding home range sizes between forest types and between species on a standardized sample of 27 locations per individual (Table 1), because this sample was complete for 35 individuals. For another five individuals with 22–25 locations during breeding, we completed 27 locations with the first locations from post-breeding tracking. Out of a total of 45 radio-tagged woodpeckers, five individuals with between six and 18 points during breeding were discarded for statistical analysis because the acquired number was far below the target of 27, and home range size curves increased in accumulation rate after breeding (three individuals), or because tags were lost early (two individuals). These five individuals were included with their partial, breeding period accumulation curves in Figure 1. We tested whether ranges reached an asymptote at 27 points following the method and criteria of Gupta et al. (2020) that an asymptote was reached if the final 20% of points (i.e., points 22–27) added < 10% of home range size at 27 points.

Early in our project we became aware that for the Helmeted Woodpecker, males and females of pairs have widely separated home ranges. In order to be able to map and measure Helmeted Woodpecker pair home ranges we attempted to capture one individual with playback in late winter, and the partner at 20–40 m from the nest cavity in a flight from the nest during the nestling feeding period. We mapped breeding home ranges of both partners of seven pairs this way (Fig. 2). For each of these 14 individuals we calculated the ratio between the size of the individual home range and the size of the pair home range, and then used the average of these 14 ratios to estimate the home range

Table 1. Home range sizes of individuals of three Atlantic Forest woodpecker species during nesting, at 27 point locations per individual.

Study site	Forest type	N home ranges	Mean ± SD (ha)	Range (ha)
Helmeted Woodpecker (*Celeus galeatus*)				
PP Cruce Caballero	old-growth	3	24 ± 4.6	20–29
RNC Papel Misionero	old-growth	6	23 ± 10.6	11–37
Valle Alegría	33-yr-old logged	3	64 ± 5.9	57–68
Lote 13	active logging	6	45 ± 18.1	19–70
old-growth forests combined		9	24 ± 8.7	11–37
logged forests combined		9	51 ± 17.3	19–70
Lineated Woodpecker (*Dryocopus lineatus*)				
PP Cruce Caballero	old-growth	3	42 ± 16.2	24–53
RNC Papel Misionero	old-growth	4	42 ± 21.5	29–74
Valle Alegría	33-yr-old logged	2	55 ± 28.0	35–75
Lote 13	active logging	4	59 ± 13.4	42–70
old-growth forests combined		7	42 ± 17.8	29–74
logged forests combined		6	58 ± 16.4	35–75
Robust Woodpecker (*Campephilus robustus*)				
PP Cruce Caballero	old-growth	2	59 ± 2.8	57–61
RNC Papel Misionero	old-growth	4	25 ± 7.3	15–30
Valle Alegría	33-yr-old logged	1	61	61
Lote 13	active logging	2	50 ± 29.0	30–71
old-growth forests combined		6	36 ± 18.5	15–61
logged forests combined		3	54 ± 21.4	30–71

Fig. 1. Accumulation of home range sizes (100% minimum convex polygons) of individuals of three Atlantic Forest woodpecker species (Helmeted WP, *Celeus galeatus*; Lineated WP, *Dryocopus lineatus*; Robust WP, *Campephilus robustus*) versus number of radio-tracked locations, during nesting, in selectively logged forests and old-growth forests.



sizes of another four Helmeted Woodpecker pairs where only one individual was mapped (Table 2). For the Lineated Woodpecker, we tagged both the male and female of one pair, and of two pairs for the Robust Woodpecker. In these species, there was a great amount of overlap in the home ranges of breeding partners (Fig. 2). Except when incubating or brooding small nestlings, Robust and Lineated Woodpeckers were nearly always encountered in pairs, and the observed degree of overlap within pairs likely extended to pairs of these species where we tagged only one individual. Such a degree of home range overlap between partners is common in woodpeckers (e.g., Bonar 2001, Pasinelli et al. 2001, Elchuk and Wiebe 2003, Höntsch 2004). For efficient sampling, of the remaining Lineated Woodpecker and Robust Woodpecker pairs we radio-tagged only one partner. We used the same procedure as with Helmeted Woodpecker to estimate pair home range sizes when only one partner was mapped, in order to make interspecific comparisons of pair home range sizes.

Fig. 2. Home ranges of radio-tagged pairs of three Atlantic Forest woodpecker species (Helmeted WP, *Celeus galeatus*; Lineated WP, *Dryocopus lineatus*; Robust WP, *Campephilus robustus*). Home range 100% minimum convex polygons are presented based on a sample of 27 tracking locations per individual during nesting, except for the Robust Woodpecker pair in Lote 13, which was mapped primarily during post-breeding. One Helmeted Woodpecker home range in Parque Provincial (PP) Cruce Caballero is not convex in shape because a meadow clearing was excluded from the otherwise forested home range.

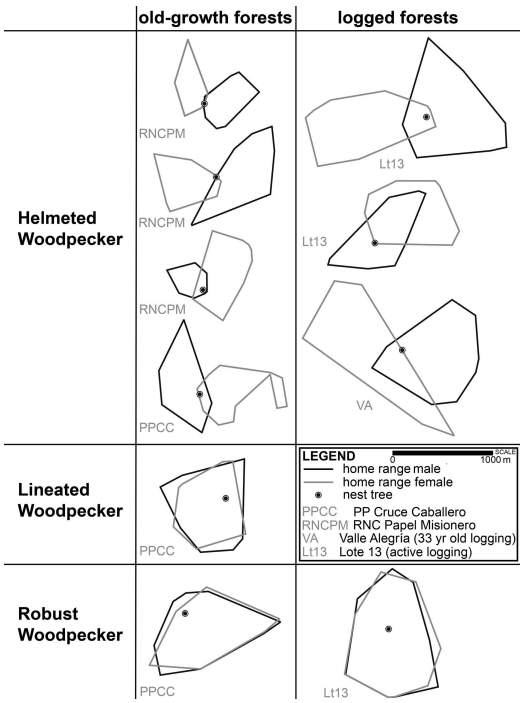


Table 2. Home range sizes of pairs of three Atlantic Forest woodpecker species during nesting, at 27 point locations per individual.

Study site	Forest type	N home ranges[†]	Mean ± SD (ha)	Range (ha)
Helmeted Woodpecker (*Celeus galeatus*)				
PP Cruce Caballero	old-growth	2(1)	62 ± 9.3	55–68
RNC Papel Misionero	old-growth	3(0)	59 ± 16.5	48–78
Valle Alegría	33-yr-old logged	2(1)	133 ± 10.0	126–140
Lote 13	active logging	4(2)	91 ± 40.9	53–148
old-growth forests combined		5(1)	60 ± 12.6	48–78
logged forests combined		6(3)	105 ± 38.7	53–148
Lineated Woodpecker (*Dryocopus lineatus*)				
PP Cruce Caballero	old-growth	2(1)	42 ± 21.3	27–57
RNC Papel Misionero	old-growth	4(4)	48 ± 24.7	33–85
Valle Alegría	33 yr old logged	2(2)	63 ± 32.2	41–86
Lote 13	active logging	4(4)	68 ± 15.4	38–81
old-growth forests combined		6(5)	46 ± 21.6	27–85
logged forests combined		6(6)	66 ± 18.8	38–86
Robust Woodpecker (*Campephilus robustus*)				
PP Cruce Caballero	old-growth	1(0)	65	65
RNC Papel Misionero	old-growth	4(4)	27 ± 7.9	17–34
Valle Alegría	33 yr old logged	1(1)	66	66
Lote 13	active logging	2(2)	54 ± 31.2	32–76
old-growth forests combined		5(4)	34 ± 18.5	17–65
logged forests combined		3(3)	58 ± 23.1	32–76

[†] In parentheses is the number of pair home range sizes estimated from the home range size of one radio-tagged partner.

Review of woodpecker home range studies

With the aim of interpreting our Atlantic Forest results against tracking studies of woodpeckers from elsewhere, we examined the relation between mean breeding home range size, body mass, and latitude of woodpecker populations from around the world, and assessed the variation in the percentage overlap of home ranges of males and females in pairs, by reviewing 58 studies of woodpeckers that used radio-tracking or followed marked individuals. These studies were found by searching the online Web of Science database (https://apps.webofknowledge.com), in All Databases mode, for the key words "woodpecker home range" and "woodpecker territory," by reviewing the references in the found studies, and by reviewing the references in Birds of the World species accounts (https://birdsoftheworld.org). To keep studies of home range sizes comparable for analysis, we narrowed the studies to home range sizes during nesting and based on 100% minimum convex polygon (MCP) figures. A 100% MCP polygon is constructed as the smallest possible convex polygon around the point locations of an animal, pair, or group. It is one of the oldest methods of home range analysis (Burt 1943) and is still widely used. The 100% MCP method is considered to allow the most straightforward comparisons between studies (Harris et al. 1990). Of the reviewed woodpecker studies, nine did not report on home range sizes, 21 reported on home ranges outside of the breeding season (or on year-round home ranges), and three reported on home ranges during breeding but did not include 100% MCP figures. That left 25 studies, of 19 woodpecker species (or 28 studies of 22 species, including our own), that provided information on 100% MCP home ranges during nesting and were included in our analysis. Ten studies of 7 woodpecker species (or 13 studies of 10 species including our own) included information on the percentage overlap between home ranges of males and females in pairs. For scientific names of the reviewed woodpecker species we follow Gill et al. (2021) instead of the source publications.

Analysis

We calculated woodpecker home range sizes using the 100% MCP method (e.g., Harris et al. 1990), considering this the most objective measure of the forest areas actually used by individuals, as contrasted with kernel methods that exclude peripheral point locations, and extend modelled polygons into areas not used by individuals (figures in Dudley and Saab 2007, Tingley et al. 2014). We calculated mean ranges, standard deviation (SD) and size range of home ranges for each of our study sites for each woodpecker species. For analysis, because values for home range sizes were similar at the two old-growth sites and values at the 33-year old logged forest were similar to those of the forest with active logging, particularly for Helmeted and Lineated Woodpeckers (Table 1), and because samples at separate sites were small, we grouped in two categories and tested old-growth forests versus selectively logged forests. Five woodpecker individuals in the adjacent PP Cruce Caballero and Valle Alegría study areas had home ranges that were between 88% and 99.5% in either old-growth forest or 33-year-old logged forest, and with the remainder of the home range in another forest type. In these cases, we grouped the home ranges with the predominant forest type for analysis. We used two-sided t-tests with unequal variance (Welch t-tests) to contrast home range sizes between forest categories for each of the three species, and One-Way ANOVA tests to contrast home ranges of the three species within forest categories. For the overlap of the 100% MCP home ranges of males and females in pairs (both from our own data and the literature review), we plotted a 100% MCP range for their area of overlap, as well as a 100% MCP pair home range with their combined locations, and derived the percentage overlap between these final two ranges. We tested the overlap of pair home ranges in Helmeted against Robust Woodpecker with a two-sided t-test with unequal variance. We tested the overlap of pair home ranges in Helmeted Woodpeckers against one Lineated Woodpecker pair, and the mean home range

overlap in Helmeted Woodpecker pairs against the mean home range overlap in pairs of nine other woodpecker populations of six species reported in the literature, with two-sided one sample t-tests. For the relationship between individual breeding home range size, body mass, and latitude of woodpecker populations we explored linear multiple regression models as well as nonlinear power regression models and selected the model with the lowest AICc value (Akaike's information criterion with small sample correction; Burnham and Anderson 2002). We calculated the ratio between predicted home range sizes from the model and observed values for each population, and highlight species with the furthest deviations from predicted home range sizes, that is, those with observed home ranges over three times larger or smaller than expected. Tests were performed in R 3.5.3 (R Core Team 2019), often with code provided by https://www.statskingdom.com/. For all tests, significance was accepted when $p < 0.05$.

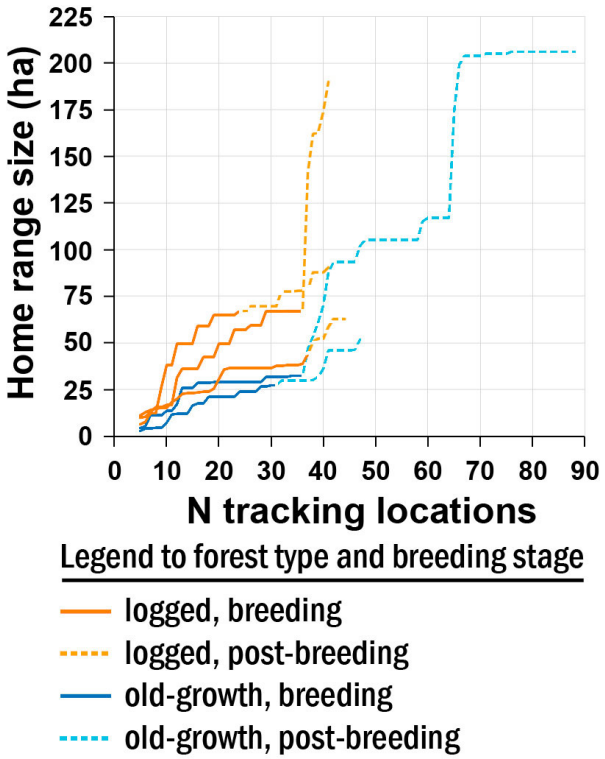
RESULTS

Home range sizes of individuals of Atlantic Forest woodpeckers

Accumulation curves of breeding home range sizes versus the number of tracking locations had no clear distinction between logged forests or old-growth forests for Lineated and Robust Woodpecker individuals (Fig. 1). In Helmeted Woodpecker, however, the accumulation curves separated in two distinct groups, with markedly larger home ranges in logged forests (Fig. 1). According to the asymptote criteria of Gupta et al. (2020), at 27 point locations, 50% of Helmeted Woodpecker individuals, 46% of Lineated Woodpecker individuals, and 44% of Robust Woodpecker individuals were at an asymptote, with similar proportions of individuals at an asymptote in selectively logged forests as in old-growth forests. We compared the relative home range sizes at this standardized effort of 27 points. Home range sizes (Table 1) did not differ between logged forests and old-growth forests for Lineated Woodpeckers ($t_{10.9} = -1.7$, $p = 0.12$) or Robust Woodpeckers ($t_{3.6} = -1.2$, $p = 0.29$). For Helmeted Woodpeckers there was a difference in breeding home range sizes between logged forests and old-growth forests ($t_{11.8} = -4.3$, $p = 0.001$). Mean Helmeted Woodpecker home range sizes in logged forests were over twice as large (2.2 times as large) as in old-growth forests. Although larger home ranges may be expected in species with larger body mass, there were no differences in home range sizes between the three woodpecker species either in logged forests (ANOVA, $F_{2,15} = 0.2$, $p = 0.80$) or old-growth forests (ANOVA, $F_{2,19} = 3.1$, $p = 0.06$), which is also recognizable in the broadly similar spread of accumulation curves of home range sizes of the three species (Fig. 1).

Five Helmeted Woodpecker individuals were tracked over longer periods, with between 41 and 88 tracking locations, during first breeding and then post-breeding stages (Fig. 3). For all individuals, home range sizes during post-breeding expanded to well beyond breeding season home range sizes, often with a sharp increase in home range size accumulation rate after breeding. In logged forest, one individual that had a breeding home range size of 67 ha at 36 tracking locations jumped to a post-breeding home range size of 190 ha with 41 tracking locations (an increase by a factor of 2.9), and was still accumulating home range size at that stage (Fig. 3). In old-growth forest, one individual that had a breeding home range size of 32 ha with 36 tracking locations reached a plateau of a 206 ha post-breeding home range size between 76 and 88 tracking points (an increase by a factor of 6.4; Fig. 3). Also in old-growth forest, one individual was tracked in two consecutive years. In the first year, it had a breeding range of 27 ha at 31 tracking points. It expanded to a post-breeding range of 52 ha at 47 points. In the second year, it had a breeding range of 27 ha at 20 points, when the nest fledged, slightly expanding to a post-breeding range of 29 ha at 29 points. The overlap between the breeding ranges of the two years was 34%, and the overlap between the post-breeding ranges of the two years was 39%. The total area used by this individual over two years was 71 ha, further expanded to 80 ha with a re-sighting in year five. Among our tracked Lineated Woodpeckers and Robust Woodpeckers there was one Robust Woodpecker with prolonged monitoring, an individual in logged forest with a breeding range of 33 ha at 29 tracking points, expanded to a post-breeding range of 83 ha at 47 points (an increase by a factor of 2.5). Another Robust Woodpecker in logged forest had a nest that fledged when six points were collected, and it then reached a post-breeding home range of 112 ha at 30 points, a larger range than any of the breeding ranges we measured. These cases show that in Helmeted and Robust Woodpeckers the home ranges in a single breeding season were only a portion of the long-term home ranges of individuals.

Fig. 3. Accumulation of home range sizes (100% minimum convex polygon) of five individuals of Helmeted Woodpecker (*Celeus galeatus*) versus number of radio-tracked locations, during nesting and post-breeding stages, in selectively logged forests and old-growth forests.



Home range sizes of pairs of Atlantic Forest woodpeckers

Males and females of Helmeted Woodpeckers consistently had breeding home ranges well separated from their partners, generally showing only a small area of overlap around the nest (Fig. 2). Specifically, the area of overlap between partners constituted only 8% ± 9% (range 0.3%–26%, n = 7) of their combined home range. There was no difference in the percentage of overlap between home ranges of breeding partners in old-growth forests and logged forests ($n_1 = 4$, $n_2 = 3$, $t_{2.1} = -2.1$, $p = 0.16$). Because of the large separation in home ranges of breeding partners, and because a MC polygon around the diverging home ranges added additional area, the home ranges of breeding pairs of Helmeted Woodpeckers were markedly larger than those of individuals (Tables 1 and 2). Specifically, in old-growth forests breeding home ranges of pairs averaged 60 ha, compared to 24 ha of individuals, and in logged forests, home ranges of pairs averaged 105 ha, compared to 51 ha of individuals. As with individual home ranges, pair home ranges of Helmeted Woodpeckers were larger in logged forests than in old-growth forests ($n_1 = 6$, $n_2 = 5$, $t_{6.1} = -2.7$, $p = 0.03$).

In Robust Woodpeckers and Lineated Woodpeckers, pair members had a great amount of overlap with the home ranges of their partners, in sharp contrast with the separated home ranges of Helmeted Woodpecker partners. In a tagged pair of Lineated Woodpeckers, the area of overlap between the partners constituted 72% of their combined nesting home range, a larger overlap than in Helmeted Woodpecker ($t_6 = -18.2$, $p < 0.0001$). In a breeding pair of Robust Woodpeckers, the overlap was 83%, and in another tagged pair that was followed primarily after nesting, the area of overlap between the partners constituted 87% of their combined post-breeding home range (Fig. 2), a larger overlap than in Helmeted Woodpecker ($t_{6.7} = -19.3$, $p < 0.0001$). Because of the large amount of overlap between pair members, home ranges of Robust and Lineated Woodpecker pairs were only slightly larger than of individuals. Whereas for individuals, Helmeted Woodpecker home ranges averaged the smallest of the three species, both in old-growth and logged forests (Table 1), for pairs the reverse was true: Helmeted Woodpecker pairs averaged the largest home ranges in both environments (Table 2). However, as for individuals, the differences in home ranges between the three species did not reach a significant level (ANOVA, $F_{2,13} = 2.5$, $p = 0.12$ in old-growth forests, ANOVA, $F_{2,12} = 3.7$, $p = 0.06$ in logged forests).

Atlantic Forest woodpecker home range overlap of breeding partners compared to that of other woodpecker species

The mean overlap of 8% in home ranges of paired male and female Helmeted Woodpeckers during breeding was lower than that found for other radio-tagged woodpecker species world-wide. For species with home range data based on 100% MCP polygons during breeding, mean home range overlap between breeding partners was 89% (n = 1) in Great Spotted Woodpecker (*Dendrocopos major*) in Japan (Mori 2005), 61% (n = 4) in Lesser Spotted Woodpecker (*Dryobates minor*) in Germany (Höntsch 2004), 68% (n = 2) in Middle Spotted Woodpecker (*Dendrocoptes medius*) in Switzerland (Pasinelli et al. 2001), and 81% (n = 6) in Pileated Woodpecker (*Dryocopus pileatus*) in Canada (Bonar 2001). Three other studies of Pileated Woodpecker in the United States, also reporting 100% MCP ranges but not (only) during breeding, found mean overlap between partners of 88% (n = 7) during post-breeding in Oregon (Bull and Holthausen 1993), 50% (n = 6) during post-breeding in Oregon (Mellen et al. 1992), and 68% (n = 3) in year-round ranges in Washington (Tomasevic and Marzluff 2018). For two species with ranges based on 95% kernel methods, mean overlap in the breeding home ranges of partners was 37% (n = 2) in Lilford's White-backed Woodpecker (*Dendrocopos leucotos lilfordi*) in Spain (Campion et al. 2020) and 67% (n = 10) in Eurasian Three-toed Woodpecker (*Picoides tridactylus*) in Germany (Pechacek 2004). An outlier of only 3% overlap was found in the 100% MCP home ranges of one pair of Green Woodpeckers (*Picus viridis*) in England, tracked mostly during post-breeding (Alder and Marsden 2010). However, Rolstad et al. (2000) mapped 100% MCP home ranges of four pairs of Green Woodpeckers in Norway and reported that "male and female ranges overlapped extensively within pairs," without quantifying the overlap, but indicating that the low overlap in the pair in England is not universal for this species. Excluding the ambiguous Green Woodpecker results, the overall mean overlap in home ranges between males and females of woodpecker pairs, in nine studies of six woodpecker species, was 68%, with a range of 37%–89%. Clearly, Helmeted Woodpeckers show exceptionally low overlap in home ranges of pairs at a mean of 8% ($t_8 = 10.5$, $p < 0.0001$). The overlap in a Lineated Woodpecker pair we found of 72%, and the overlap of a mean 85% in two pairs of Robust Woodpeckers, were above the mean reported in other woodpecker radio-tracking studies, though within the range reported in other studies.

Home range sizes of woodpeckers as a function of latitude and body mass

For the relationship between latitude, body mass, and the size of individual breeding home ranges of woodpeckers from 29 populations of 22 species, from latitudes 5.50° to 60.17° N or S (Table 3), we found the best-fitting model was a power regression model:

$$HR_{size} = 0.1709 \cdot Latitude^{0.9002} \cdot BodyM^{0.4299} \qquad (1)$$

($r = 0.49$, $p = 0.03$), which explained 24.1% of variation, with 17.1% of variation explained by latitude alone. Home range sizes related positively with both latitude and body mass (Fig. 4). The three Atlantic Forest woodpecker species we studied conformed fairly closely to the individual home range sizes predicted by the model (Table 3). However, as explained above, for most woodpecker species individual home ranges are a ca. 68% approximation for those of pairs, but in the case of Helmeted Woodpecker the ranges of breeding partners are widely separated, and their combined range should be considered for interspecific comparisons against the predicted home range size. The mean observed home range of a pair of Helmeted Woodpeckers in Misiones was 3.23 times larger than predicted. Only four woodpecker populations had individual breeding home ranges that diverge greater than three times from the predicted sizes (Table 3): American Three-toed Woodpecker (*Picoides dorsalis*) in Quebec (Tremblay et al. 2020), Black-backed Woodpecker (*Picoides arcticus*) in Quebec (Tremblay et al. 2009), Black-backed

Table 3. Relation between body mass, latitude, and 100% minimum convex polygons breeding home range sizes of woodpeckers from around the world. Obs HR is the reported mean home range size in each source. Pred HR is the predicted home range size according to the best fitted model $HRsize = 0.170924 \cdot Latitude^{0.900164} \cdot BodyM^{0.429915}$. D obs-pred is the factor of the difference between observed and predicted home range sizes, with home ranges over three times larger than predicted shown in bold font.

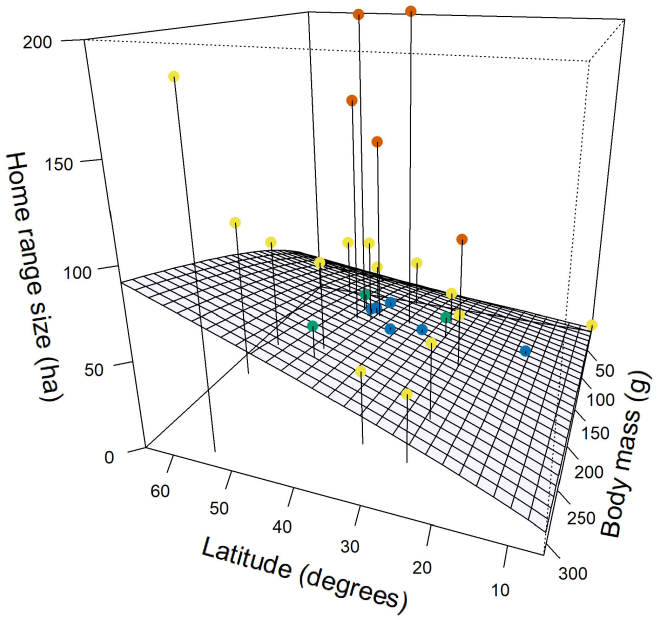
Species	Source	Body M (g)	Latitude	Obs HR (ha)	Pred HR (ha)	D obs-pred (factor)
Ochraceous Piculet (*Picumnus limae*)	da Silva et al. (2012)	11	5.50 S	4.4	2.2	1.98
Lesser Spotted WP (*Dryobates minor*)	Camprodon et al. (2015)	21	41.47 N	33.7	17.9	1.88
Lesser Spotted WP	Höntsch (2004)	23	50.15 N	27	22.3	1.21
Lesser Spotted WP	Wiktander et al. (2001)	24	56.67 N	43	25.4	1.69
Eurasian Wryneck (*Jynx torquilla*)	Weisshaupt et al. (2011)	35	46.23 N	4.8	24.8	0.19
Red-cockaded WP (*Dryobates borealis*)	Hooper et al. (1982)	49	33.10 N	27.8	21.3	1.31
Red-cockaded WP	Wood et al. (2008)	49	32.26 N	24.1	20.8	1.16
Red-naped Sapsucker (*Sphyrapicus nuchalis*)	Walters (1996)	50	50.63 N	13.2	31.4	0.42
American Three-toed WP (*Picoides dorsalis*)	Tremblay et al. (2020)	55	50.57 N	201	32.8	**6.14**
Middle Spotted WP (*Dendrocoptes medius*)	Pasinelli et al. (2001)	58	47.62 N	7.2	31.6	0.23
Red-breasted Sapsucker (*Sphyrapicus ruber*)	Manning and Shepard (1999)	58	48.78 N	5.9	32.4	0.18
White-headed WP (*Dryobates albolarvatus*)	Lorenz et al. (2015)	61	46.75 N	125	31.9	**3.92**
Black-backed WP (*Picoides arcticus*)	Tingley et al. (2014)	66	39.92 N	204	28.6	**7.12**
Hairy WP (*Dryobates villosus*)	Ripper et al. (2007)	70	47.96 N	58	34.6	1.68
Black-backed WP	Tremblay et al. (2009)	74	50.57 N	151.5	37.2	**4.08**
Acorn WP (*Melanerpes formicivorus*)	Hooge (1995)	79	36.38 N	5.2	28.4	0.18
Golden-fronted WP (*Melanerpes aurifrons*)	Husak and Husak (2002)	81	31.52 N	17.4	25.2	0.69
Great Spotted WP (*Dendrocopos major*)	Mori (2005)	82	42.77 N	2.64	33.4	0.08
Guadeloupe WP (*Melanerpes herminieri*)	Villard and Rousteau (1998)	83	16.01 N	4.2	13.7	0.30
Helmeted WP ind. (*Celeus galeatus*)	this study	127	26.51 S	37.5	26.2	1.43
Helmeted WP pair	this study	127	26.51 S	84.8	26.2	**3.23**
Gray-headed WP (*Picus canus*)	Schneider (2018)	142	51.54 N	62	50.0	1.24
Gray-headed WP	Rolstad and Rolstad (1995)	150	60.17 N	73.3	58.9	1.24
Northern Flicker (*Colaptes auratus*)	Elchuk and Wiebe (2003)	158	51.87 N	25	52.6	0.47
Green WP (*Picus viridis*)	Rolstad et al. (2000)	203	60.17 N	98	67.1	1.46
Lineated WP (*Dryocopus lineatus*)	this study	210	26.51 S	49.2	32.5	1.51
Pileated WP (*Dryocopus pileatus*)	Noel (2011)	257	34.07 N	45.7	44.5	1.03
Robust WP (*Campephilus robustus*)	this study	265	26.51 S	42.1	36.0	1.17
Pileated WP	Bonar (2001)	303	53.56 N	186.4	71.8	2.60

Woodpecker in California (Tingley et al. 2014), and White-headed Woodpecker (*Dryobates albolarvatus*) in Washington (Lorenz et al. 2015), all species present in coniferous forests of North America. Populations with markedly small individual home ranges of under 1/3 the size predicted by the model are Eurasian Wryneck (*Jynx torquilla*) in Switzerland (Weisshaupt et al. 2011), Middle Spotted Woodpecker in Switzerland (Pasinelli et al. 2001), Red-breasted Sapsucker (*Sphyrapicus ruber*) on Vancouver Island, Canada (Manning and Shepard 1999), Acorn Woodpecker (*Melanerpes formicivorus*) in California (Hooge 1995), and Guadeloupe Woodpecker (*Melanerpes herminieri*) on the Caribbean islands of Basse-Terre and Grande-Terre (Villard and Rousteau 1998).

DISCUSSION

The Helmeted Woodpecker is generally perceived to have greater associations with mature forests than the co-existing Lineated Woodpecker and Robust Woodpecker (Lammertink et al. 2020a, BirdLife International 2022). Until now, the possibility existed that this was a false perception originating from a greater observer

Fig. 4. The relationship between latitude, body mass, and individual home range sizes of the 28 populations of woodpeckers from Table 3. The regression surface shows predicted values of home range size. Orange points are for populations with mean home ranges over three times as large as predicted. The four orange points in the upper left of the cube are for American Three-toed (*Picoides dorsalis*), Black-backed (*Picoides arcticus*; two populations), and White-headed Woodpeckers (*Dryobates albolarvatus*), and the orange point to the right is for Helmeted Woodpecker (*Celeus galeatus*) pairs. Yellow points are populations with home range sizes up to three times larger than predicted, green points for populations with home ranges up to 1/3 smaller than predicted, and blue points for populations with home ranges under 1/3 smaller than predicted.



effort in protected areas and the generally low detectability of the scarce, usually silent Helmeted Woodpecker. However, our results demonstrate that the association of Helmeted Woodpecker with old-growth forest is real: the species has consistently, markedly smaller home ranges in old-growth forests than in selectively logged forests, both for individuals and for pairs. This difference indicates that ecological requirements of the threatened Helmeted Woodpeckers are more readily met in old-growth forests, allowing it to range over smaller home ranges, and that more individuals can be conserved in an area of old-growth forest than in a similar area of selectively logged forest. In contrast, Lineated Woodpeckers and Robust Woodpeckers had no significant differences in home range size between old-growth forests and selectively logged forests.

Magnitude of home range size differences between old-growth forests and disturbed forests

We found that mean Helmeted Woodpecker breeding ranges in selectively logged forest were 2.2 times larger than in old-growth forests for individuals and 1.8 times larger for pairs. For individuals, the smallest measured home range was 11 ha and was in old-growth forest, and the largest measured home range was 70 ha and was in forest with active logging, a seven-fold difference over the range of measured home ranges. For pairs, the smallest measured home range was 48 ha and was in old-growth forest, and the largest measured home range was 148 ha and was in forest with active logging, a five-fold difference over that range. In previous studies that tracked woodpeckers in old-growth and selectively logged forests, for Red-cockaded Woodpecker (*Dryobates borealis*), Engstrom and Sanders (1997) found among clans with varying percentages of old growth in the forested portions of their home ranges a two-fold difference between the smallest (32.4 ha, with 76% old-growth forest) and largest (78.5 ha, with 11% old-growth forest) home ranges. For Pileated Woodpecker, Bull and Holthausen (1993) found a four-fold range of 196–876 ha home ranges where old-growth forest area percentages of home ranges varied from 41% for the smallest home ranges to 4% for the largest home ranges. Compared to these cases, Helmeted Woodpeckers in our study exhibited a larger difference of larger home range sizes in selectively logged forests compared to old-growth forests. In studies of effects of forest fires on woodpecker home range sizes, the smallest ranges occurred in recently burnt areas, and home range size differences with older burnt forests were very large: a 13-fold difference over a range of home range sizes of Black-backed Woodpeckers at sites that burnt two to five years previous to the study (Tingley et al. 2014) and a 19-fold difference in home ranges of Hairy Woodpeckers (*Dryobates villosus*) in forests burnt two years versus seven years previously (Covert-Bratland et al. 2006). The favorable conditions for such woodpecker populations in recently burnt areas last usually not more than two years (Murphy and Lehnhausen 1998, Covert-Bratland et al. 2006), whereas for woodpecker populations or species that find favorable conditions in old-growth forests, these conditions are in principle permanent.

Separation of home ranges of breeding partners

One of our most surprising results is the extremely low overlap of home ranges of male and female Helmeted Woodpeckers in breeding pairs, unprecedented in eight other woodpecker species for which such overlap information is available, and unlikely to occur in many other woodpecker species that live in pairs or family groups. One possible explanation for this pattern is that suitable roost cavities for Helmeted Woodpeckers are a scarce resource. Cavities used by Helmeted Woodpeckers for year-round overnight roosting are highly specific: decay-formed cavities in large living trees with sufficient space, above the entrance, for an adult and dependent juvenile to roost together during several months of the year. Such cavities can be used for many years, including by successive territory holders. Males and females of breeding pairs occupy roost cavities that are usually far apart at 1071 ± 427 m (Lammertink et al. 2019). Possibly, suitable roost cavities are so sparsely distributed across the landscape that this results in the separated home ranges of males and females of Helmeted Woodpecker pairs. In contrast, most other woodpecker species roost in excavated cavities, alternate between several roost cavities, and several species, including Robust Woodpecker, roost in pairs or family groups in a shared cavity (Bodrati et al. 2015, Chazarreta and Ojeda 2020). An alternative explanation that can be considered for the separated ranges of breeding partners in

Helmeted Woodpecker is that foraging resources are limited, and by separating, more resources are available for each individual. However, Helmeted Woodpeckers forage on medium-sized substrates of 15 ± 13 cm diameter, mostly (72%) on dead substrates in mostly (74%) living trees of medium, 33 ± 2 cm diameter at breast height, and also forage ca. 12–15% of foraging occasions on bamboo (Fernández et al. 2020), resources that are not particularly scarce or specific to either old-growth or selectively-logged forests in Misiones, and that are unlikely to force strong separation of male and female home ranges. Finally, it should be noted that the Helmeted Woodpecker, even with its large, red bushy crest, is a highly inconspicuous bird that seeks out dense foliage or dense bamboo stands, where it remains hidden and silent most of the time, perhaps to avoid attention from predators. The separation of the home ranges of breeding partners could be yet another way of remaining inconspicuous. These three potential drivers of home range separation in Helmeted Woodpecker pairs are not mutually exclusive and may operate at the same time.

Although pairs of Helmeted Woodpeckers have larger mean home ranges than pairs of either Lineated Woodpeckers or Robust Woodpeckers, the difference is not large and not significant. The mean breeding home range size of Helmeted Woodpecker pairs is 1.3 and 1.8 times as large in old-growth forests, and 1.6 and 1.8 times as large in selectively logged forests, compared to Lineated and Robust Woodpecker pairs, respectively. This means that the difference in home range size alone cannot explain the generally much lower abundance of the Helmeted Woodpecker at a landscape level. A marked spacing, and scattered occurrence, of home ranges also contributes to the low density of the Helmeted Woodpecker, a topic we will address elsewhere.

Home range size relationship with latitude and body mass

About half of our tracked Atlantic Forest woodpecker individuals were not an asymptote for home range size at the standardized effort of 27 points we considered, and thus the comparisons we made among species and habitats at that sample concern relative home ranges rather than total home ranges. Not reaching an asymptote at 27 points could be an effect of undersampling, or it could reflect the continuous expanding of the home range throughout the breeding period from within the larger year-round home range of these woodpeckers, so that breeding home ranges genuinely do not reach an asymptote. We consider it valid to make global comparisons of our results with other woodpecker radio-tracking studies because a sample of 25–30 points is often used in other studies, usually without a formal asymptote analysis. Differences in home range sizes between species often surpass the potential 10–20% underestimate of home range sizes for individuals that are not at an asymptote.

Both latitude and body mass correlated positively with breeding home range sizes of a wide range of woodpecker species (Fig. 4), though in conjunction only explained a modest 24.1% of variation in the home range sizes. Latitude explained most (17.1%) of the variation in home range sizes. Likely, the shorter growing season, the less diverse forest structure, and lesser plant diversity at higher latitudes result in fewer food resources for woodpeckers, and combined with the probably higher energy demands of woodpeckers in colder climates result in larger home ranges at higher latitudes. Of the three Atlantic Forest woodpeckers, the Robust Woodpecker and the Lineated Woodpecker had home ranges close to the sizes predicted by the best-fitted power regression model, whereas Helmeted Woodpecker pairs had remarkably large home ranges relative to body mass and latitude. The only other woodpecker populations with markedly large home ranges relative to model-predicted sizes (Table 3) are of three North American species present in coniferous forests at higher latitudes or high elevations. A less diverse forest structure and low tree diversity in coniferous forests, likely resulting in fewer niches for insect prey, may drive these large woodpecker home ranges. Populations of Black-backed Woodpecker in northern California and White-headed Woodpecker in Washington were studied at high elevations (Tingley et al. 2014, Lorenz et al. 2015), and predicted home range sizes from latitude will have been underestimates relative to the local, colder high elevation climates. In contrast, the finding that the Helmeted Woodpecker is a woodpecker with markedly large home ranges in structurally rich, subtropical forests is another indication that its large home ranges may not be driven by foraging resource availability. Woodpecker populations of five species with markedly small home ranges (Table 3) do not appear to have a unifying characteristic, and may have small ranges for species-specific or local reasons.

Inclusion of studies in Table 3 was based on the narrow criteria of studies with 100% MCP home ranges during the breeding season. Relaxing these criteria allows for a wider pool of woodpecker tracking studies with the possibility to make comparisons between our Atlantic Forest woodpeckers and congeneric species. The only other *Celeus* species, besides Helmeted Woodpecker, for which tracking information is available is Kaempfer's Woodpecker (*Celeus obrieni*), a rare, threatened bamboo specialist of the Cerrado region of northeast Brazil. Corrêa (2012) reported on five home ranges of Kaempfer's Woodpecker, mapped with a 95% kernel method during breeding and post-breeding stages, with between 10 and 63 tracking locations, with an average size of 211 ± 208 ha. This is similar to the ca. 200 ha ranges we found for two Helmeted Woodpeckers followed into the post-breeding period (Fig. 3). Regarding *Dryocopus*, the breeding home-range sizes we found for Lineated Woodpecker individuals at 26.51° S (Table 1) are similar to those found for Pileated Woodpecker at 34.07° N by Noel (2011; Table 3). Regarding *Campephilus*, Ojeda and Chazarreta (2014) mapped with a 95% fixed kernel method, during the post-breeding stage, the home ranges of eight family groups of two to five individuals of Magellanic Woodpecker (*Campephilus magellanicus*) in old-growth deciduous forests in the Patagonian Andes of Argentina, with between 39 and 228 locations, and found home ranges (within one post-breeding season) of 39 ± 14 ha. This is similar to our values for breeding home ranges of Robust Woodpecker pairs in old-growth Atlantic Forest, of 34 ± 19 ha (Table 2). The home ranges of Magellanic Woodpecker would be expected to be larger: with a body mass of 315 g and 41.09° S latitude location of the studied population, the modeled breeding home range size is 57 ha, and this would be expected to further increase for the post-breeding period and for family groups instead of pairs. Indeed, when followed over multiple years, the Magellanic Woodpecker families in this study expanded to cumulative home ranges of 63 ± 12 ha (Ojeda and Chazarreta 2014). Radio-tracking and GPS tracking studies were undertaken of tree selection and habitat

selection of another population of Magellanic Woodpeckers, in Chile, but no home-range sizes were reported (Vergara et al. 2016, Soto et al. 2017). Tanner (1942:38) in a study of the Ivory-billed Woodpecker (*Campephilus principalis*) in the mostly old-growth bottomland forests of the Singer Tract, Louisiana, mapped seven home ranges defined as "In the recent history of the tract, Ivory-bills have almost always ranged in these areas," thus presumably equivalent to 100% MCP year-round home ranges areas, and which measured 1010 ± 395 ha. These are extremely large home ranges, because the modelled value for breeding home range size of this population, with a body mass of 510 g at 32.33° N latitude, is 57 ha.

CONCLUSIONS AND NEXT STEPS

We have demonstrated that among three species of co-existing Atlantic Forest woodpecker species, breeding home range sizes of Helmeted Woodpeckers are markedly larger in selectively logged forests than in old-growth forests, whereas Lineated Woodpeckers and Robust Woodpeckers show no home range size difference between these forests. This affirms an association of Helmeted Woodpecker with mature forests. The Helmeted Woodpecker has large breeding home ranges relative to its body mass and the latitude at which it occurs, and home ranges expand after the breeding season. The conservation implications of our findings are: (1) because the Helmeted Woodpecker is associated with mature forests, it is more impacted by ongoing loss of such forests in the Atlantic Forest region (Rosa et al. 2021) than other woodpeckers, and its IUCN red list status is justified, and (2) because of its large home ranges and association with old-growth forests, the area requirements of Helmeted Woodpecker call for the availability of large mature forest tracts to contain viable populations. We urge land managers and governments in Argentina, Brazil, and Paraguay to conserve the few remaining areas of mature forest in the southern Atlantic Forest region and to restore more logged native forests to mature conditions.

Future tracking studies of the Helmeted Woodpecker should assess the variation in home range sizes throughout the year, in old-growth forest areas and disturbed forests, and include study sites with forests more disturbed and fragmented, including secondary forests, than the relatively intact selectively logged forests we compared with old-growth forests, for a more complete understanding of Helmeted Woodpeckers' spatial requirements in the current spectrum of land uses in the Atlantic Forest. To assess year-round home ranges, long-lasting or solar-charged radio-tags are needed, ideally with location data collected by GPS readings that can be downloaded remotely without the need to recapture the tagged woodpecker. Such technology is not yet available for a bird with the body mass of a Helmeted Woodpecker, but it may be soon (Campion et al. 2020).

Responses to this article can be read online at:
https://www.ace-eco.org/issues/responses.php/2277

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