Area-restricted search in Magellanic Woodpeckers: importance of tree senescence, forest composition and open habitats

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Abstract
Animals with stable territories, specialized diets and narrow habitat choices, such as some woodpecker species, should concentrate foraging activity in areas of higher quality, a behavior consistent with the area-restricted search (ARS) behavior. The assessment of ARS behavior in specialized woodpeckers contributes to identify feeding areas important for not only their conservation but also habitats negatively affecting their foraging behavior. We addressed the effects of tree senescence, forest succession, stand composition and open habitats on the adoption of ARS behavior in Magellanic Woodpecker (Campephilus magellanicus) in a heterogeneous landscape in southern South America. Using GPS relocations from 24 woodpeckers, we estimated the First-Passage Time (FPT), a measure of the time individuals remain in a given area, with longer FPT values indicating the adoption of an ARS behavior. We determined the effects of habitat variables on FPT using a methodological framework based on Linear Mixed Effect models and a randomization procedure intended to reduce spatial autocorrelation. Averaged model coefficients showed that woodpeckers spent less time in sites dominated by the Antarctic beech (Nothofagus antarctica) and partially covered by open habitats. Conversely, FPT increased in stands and home ranges where tree senescence was higher. Thus, the ARS behavior in Magellanic Woodpecker is explained by forest composition, avoidance of open habitats and tree senescence. Our results suggest the conservation of Magellanic Woodpeckers in heterogeneous landscapes involves retention of senescent trees and maintenance of canopy continuity.

Keywords Foraging · First-passage time · Tree senescence · Open habitats

Zusammenfassung
Konzentrierte Nahrungssuche bei Magellanspechten: Die Bedeutung von Baumalter, Waldzusammensetzung und Offenhabitaten

Tiere mit stabilen Revieren, spezialisierter Ernährung und enger Habitatwahl, wie beispielsweise einige Spechtarten, sollten ihre Nahrungssuche auf Gebiete höherer Qualität konzentrieren, was mit dem Verhalten der konzentrierten Nahrungssuche („area-restricted search“, ARS) vereinbar ist. Die Abschätzung von ARS-Verhalten bei spezialisierten Spechten trägt dazu bei, Nahrungsgebiete zu identifizieren, die für den Schutz der Art wichtig sind, aber auch Habitats, die das Nahrungserwerbsverhalten negativ beeinflussen. Wir haben den Einfluss von Baumalter, Waldsukzession, Zusammensetzung des Baumwuchses und Offenhabitat auf die Annahme von ARS-Verhalten beim Magellanspecht (Campephilus magellanicus) untersucht.

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in einer heterogenen Landschaft im südlichen Südamerika untersucht. Mittels GPS-Daten von 24 Spechten haben wir die „first-passage time“ (FPT), ein Maß der Zeit, die Individuen in einem bestimmten Gebiet verbringen, abgeschätzt, wobei längere FPT-Werte die Annahme von ARS-Verhalten zeigten. Wir haben die Effekte verschiedener Habitatvariablen auf die FPT ermittelt, indem wir ein methodologisches Bezugsystem verwendeten, das auf linearen gemischten Effektmodellen und einer Randomisierungsprozedur, die darauf abzielte, räumliche Autokorrelation zu reduzieren, basierte. Die gemittelten Modellkoeffizienten zeigten, dass die Speche weniger Zeit in Bereichen, die von der Antarktischen Scheinbuche (Nothofagus antarctica) dominiert wurden und teilweise von Offenhabitat bedeckt waren, verbrachten. Umgekehrt nahm die FTP in Beständen und Aktionsgebieten mit höherem Baumalter zu. Daher lässt sich das ARS-Verhalten von Magellanspechten mit der Waldzusammensetzung, dem Vermeiden von Offenhabitaten und dem Baumalter erklären. Unsere Ergebnisse deuten darauf hin, dass der Schutz von Magellanspechten in heterogenen Landschaften die Erhaltung alter Bäume und ein durchgängiges Kronendach beinhaltet.

**Introduction**

Animals with stable territories, specialized diets and narrow habitat choices, such as some woodpecker species, are known to adjust their space use and movements based on the spatio-temporal heterogeneity of habitat resources (Nappi et al. 2015; Vergara et al. 2015). Those animal species concentrate their movements in the habitats of higher foraging quality (Farris et al. 2004; Vergara and Schlatter 2004; Saab et al. 2007; Macey et al. 2016; Schütz et al. 2017; Matseur et al. 2018), a behavior known as area-restricted search (ARS) that, in many cases, involves the use of spatial memory to return to suitable sites within territories (Fagan et al. 2013, 2019). Determining the areas where animals concentrate their movements and foraging activity not only contributes to understand decision-making behavior or foraging efficiency but also to the identification of feeding areas important for the conservation of vulnerable species (Robinson et al. 2010; Carter et al. 2016; Lascelles et al. 2016; Ironside et al. 2017). The assessment of ARS behavior has been, for instance, carried out in marine species, including sharks (Meese and Lowe 2020), seals (Bras et al. 2017), whales (Palacios et al. 2019), dolphins (Bailey et al. 2019), sea turtles (Freitas et al. 2018), puffins (Bennison et al. 2019), boobies (Somerfeld et al. 2013) and albatrosses (Conners et al. 2015). Although the ARS behavior has been tested in terrestrial species like carnivores (Lode 2000; Ironside et al. 2017), small mammals (Le Borgne and Fortin 2020), marsupials (Orlando et al. 2020), lizards (Eifler et al. 2012) and spiders (Patt and Pfannenstiel 2009), less attention has been paid to study it in specialized forest birds with spatially uneven distribution of foraging resources, such as woodpecker species. Determining habitat conditions under which forest specialized woodpeckers adopt an ARS behavior may contribute to sustainable landscape planning and forest management intended to increase habitat quality and connectivity.

The assessment of finer scale movement patterns within territories provides a mechanistic basis for understanding the foraging decisions, which is especially evident in specialized animals (Fagan et al. 2013). In this sense, Hidden Markov Models (HMM) and State-space Models (SSM) have been used to distinguish between discrete modes of movement in woodpecker territories (McKellar et al. 2015; Vergara et al. 2019), where each behavioral mode is interpreted to represent a distinct behavior (e.g., foraging vs. traveling). Those discrete-time modelling approaches assume that, while moving across its home range, a woodpecker can either remain in a same mode or switch to a different mode between two successive time intervals (Jonsen et al. 2005). Foraging woodpeckers, however, may stay for relatively long periods in the foraging mode when using forest stands or forest sites of high quality, as found in animals adopting an area-restricted search (ARS) strategy (Kareiva and O’dell 1987; Fauchald and Tveraa 2003). Although HMM and SSM capture the fine-grained step-by-step movement patterns, these approaches are usually difficult to implement and do not provide spatially explicit inference about the habitat area that animals use when moving. Alternative methodological approaches, such as First-Passage Time (FPT) (Fauchald and Tveraa 2003) and residence time (Barraquand and Benhamou 2008), provide statistical frameworks for the quantification of habitat areas where animals remain more times, thus allowing for testing associations between ARS behavior and habitat conditions (Freitas et al. 2008). Indeed, FPT and residence time are useful approaches to evaluate habitat preferences and movement ecology of species that occupy spatially heterogeneous habitats (Byrne and Chamberlain 2012; Le Corre et al. 2014; Zhang et al. 2014).

In this study, we address the movement strategies adopted by Magellanic Woodpeckers (Campephilus magellanicus) in a heterogeneous forested landscape. The Magellanic Woodpecker is an indicator of old-growth forest conditions and a large primary excavator providing tree cavities to forest-dwelling species (Vergara and Schlatter 2004; Ojeda et al. 2007). Field observations suggest that Magellanic Woodpeckers move between neighboring trees by selecting and adjusting residence times in each visited tree based on its attributes, spending more time at trees that are highly decayed (Vergara et al. 2016). The tree decay-stage serves as a cue of habitat quality for woodpeckers, offering them with
information about the presence of their prey inside trees, such as the larvae of long-horned beetles (*Microplophorus magellanicus*) (Vergara and Schlatter 2004; Vergara et al. 2016, 2017, 2019; Soto et al. 2017). Although movement decisions of Magellanic Woodpeckers have been shown to depend on the availability of senescent and dead trees (Vergara et al. 2016, 2019), to date, no studies have determined how the ARS behavior of woodpeckers varies across a heterogenous landscape. Magellanic Woodpeckers are known to be highly territorial, with males behaving agonistically when encountering same-sex individuals (Soto et al. 2016). Depending on forest disturbances, home ranges of Magellanic Woodpeckers may include forest stands that vary in tree species composition and age (old-growth vs. second-growth), but also include open habitats such as prairies, bushlands, exotic beaver ponds, and bogs (Soto et al. 2012, 2017; Ojeda and Chazarreta 2014). Woodpeckers may respond to such habitat heterogeneity by being reluctant to cross-open habitats or intensifying their searching for prey in forest stands with more senescent trees. Here, we aim at examining the adoption of an ARS strategy across a heterogeneous forested landscape using the FPT approach, which allows for the identification of areas where woodpeckers behave as ARS foragers. We hypothesized that woodpeckers remain longer (i.e., higher FPT) not only in areas where individual trees are more senescent but also in areas dominated by old-growth forest with low representation of open habitats.

**Methods**

**Study landscape**

We conducted our study in a ca. 64 km² landscape located on Navarino Island in the southernmost region of Chile (54°56′S, 67°36′W; Fig. 1). The study landscape was covered by Magellanic subpolar forest, which is dominated by southern beech forest of *Nothofagus betuloides*, *N. pumilio*, and *N. antarctica* (Fig. 1). The climate of Magellanic subpolar forest region is characterized by a long winter period during which a large amount of snow is accumulated. Depending on altitude and distance from the coast, the understory of subpolar forest is absent or sparse. Open habitats also were present in this landscape and included patches of shrublands, wetlands, peat bogs, meadows, and ponds, with the latter two being produced by the introduced beaver (*Castor*...
canadensis) (Fig. 1) (Soto et al. 2012). The cover of N. pumilio, N. betuloides, and N. antarctica forest in the study landscape was 29.2, 29.5 and 6.4%, respectively (Table 1). Although forest stands in old-growth stage of succession covered 45.3% of the land, forest disturbances (e.g., logging and fires) have resulted in some second-growth stands (20.2%). Shrublands and meadows (upland open areas) covered 10.2% of the study area and peat bogs and ponds (lowland open areas) represented 6.5% of the landscape (Table 1).

**Movement data**

We acquired GPS locations from 24 tagged male Magellanic Woodpeckers (Soto et al. 2017; Vergara et al. 2019) using ATS G10 UltraLITE GPS Logger (Advanced Telemetry Systems, Inc.) devices, each attached to a very high-frequency transmitter (ATS model A2440, 2.3 g) for later recovery. GPS devices were attached to the back feathers by applying a small amount of epoxy glue, remaining they attached between one and seven days. We chose adult males, because males guide family groups by eliciting a dominant social behavior while moving across forest habitat (Ojeda 2004; Duron et al. 2018). The locations of woodpeckers were recorded every 5 min between 08:00 and 16:00 and during the 2014–2015 post-reproductive period (Jan–Mar). Such a short time interval for data acquisition is consistent with the residence time of woodpeckers on individual trees (Vergara et al. 2016).

We estimated the accuracy (measurement error) of GPS locations as 12.9 ± 2.9 m (mean ± SE), which was obtained by quantifying the Euclidean distances (m) between 12 different GPS measurements and the actual position of a reference point identified on an imagery-based map layer (Vergara et al. 2019). We calculated the overall speed for each woodpecker by dividing the total traveled distance (i.e., the sum of the distance between GPS relocations) by the total time of a given burst of continuous relocations.

**First-passage time**

We examined the role of habitat heterogeneity on the movement of woodpeckers by estimating the first-passage time (FPT) from GPS location data. FPT can be used as an indicator of foraging behavior along animal’s tracks, with longer FPT areas being interpreted as evidence of Area-Restricted Search (ARS) behavior at ecologically proper spatial scales (Fauchald and Tveraa 2003, 2006; Kappes et al. 2010). The first-passage time is defined as the time spent by an individual in circles of radius r centered on subsequent GPS positions along each trajectory (i.e., a movement path consisting of a sequence of GPS locations within the home range; Fig. 2a) (Frair et al. 2005). As r increases, longer trajectory sections will be included in the circle (Fauchald and Tveraa 2003). We established the proper spatial scale of FPT analysis by searching the value of r that maximizes the relative variance [S(r)] of the FPT, because the ability of the FPT to detect area-restricted search (ARS) increases as the variance takes maximum values (Fauchald and Tveraa 2003). The ARS is a behavior characterized by slow and tortuous movements typically displayed by woodpeckers when selecting trees for foraging (Vergara et al. 2015).

To estimate the FPT, we used the fpt function of the R package adehabitatLT. The last six woodpecker’s data were excluded from further analysis, because it was not possible to define a regular trajectory due to the different time lag between relocations (Fig. S1). The first-passage time method is designed for trajectories with three or more relocations, so the trajectory data with less than three observations were eliminated. Because observations of six woodpeckers were discarded from the analysis, we estimated the first-passage time (FPT) from the trajectories of 18 woodpeckers, totaling 62 trajectories. We maximized S(r) for each trajectory and individual by estimating FPT over 50 different radii (r) in a range from 12 to 250 m (Table S1) corresponding, respectively, to the GPS accuracy and a quarter of the calculated net displacement (i.e., the sum of Euclidean distances between successive locations) of woodpeckers (Barraquand and Benhamou 2008). We determined the proper FPT scale, r value at which S(r) reached its maximum value, by examining plots of S(r) against r. From S(r) plot examination, a set of 36 trajectories were selected out of 62 trajectories (Table S1), including a total of 1441 GPS locations (Fig. S2). When we did not observe a maximum value of S(r), we assumed that the path traced by a woodpecker was random and did not represent a movement pattern including different behavioral modes, as shown by the eighth trajectory of woodpecker 3 (Fig. S2). However, we considered proper FPT scales for trajectories where a local maximum was

| Habitat type       | Total cover (%) |
|--------------------|-----------------|
| N. antarctica      | 6.38            |
| N. betuloides      | 29.23           |
| N. pumilio         | 29.52           |
| Open upland habitats | 10.21         |
| Open lowland habitats | 6.49          |
| PSRIa              | − 0.73 (0.31)   |
| Old-growth forest  | 45.34           |
| Second-growth forest | 20.22        |

For the Plant Senescence Reflectance Index (PSRI), the mean and SE value are shown

aMean (SD)
observed, for example, the first trajectory of woodpecker 4 (Fig. S2). Thus, the radii of the FTP circles changed between trajectories (Table S1). Based on the proper FPT scales, we defined two spatial scales to quantify properties of the habitat used by woodpeckers (see below), including site (habitat-patch) scale, defined by the area of each FPT circle (Fig. 2a), and home-range scale, defined by the area comprising the union of all the FPT circles along the trajectory (Fig. 2b).

**Habitat variables**

We quantified habitat variables at the site and home-range scales using a high-resolution (0.50 m) multispectral image from the WorldView-2 sensor (2014). We created geographic information system (GIS) layers of the main categories of habitat types and tree species in the study site as well as the Plant Senescence Reflectance Index (PSRI), a remote-sensing index of tree senescence (Table 1). We used digital supervised classification and a Bayesian maximum likelihood algorithm carried out by (Soto et al. 2017) to classify habitat types based on age and composition of forest stands as well as the cover of different habitat types. We categorized habitats as old-growth forest, second-growth forest, open upland (shrub and meadows), and open lowland (peatlands and beaver ponds). We also determined the composition of dominant tree species by quantifying the cover of *N. antarctica*, *N. betuloides*, and *N. pumilio*. Tree senescence was estimated with the remote-sensing-based Plant Senescence Reflectance Index (PSRI), which distinguishes between tree decay states based on the spectral carotenoid/chlorophyll ratio with increasing values for increasing tree decay (Soto et al. 2017). We used an image segmentation algorithm to identify individual trees, estimate their PSRI and classify them by species of tree (Vergara et al. 2016; Soto et al. 2017). The PSRI values of the subpolar forest range from −2.7 to 0.4 (Table 1) (Soto et al. 2017).

We used the GIS maps of habitat type, tree composition and PSRI to derive the habitat variables used in statistical analysis. First, for each FPT circle, we estimated the percentage of old-growth forest, second-growth forest, open upland habitats and open lowland habitats. Second, we estimated the percentage cover of the dominant *Nothofagus* species. Third, we averaged PSRI values over all cells in each FPT circle and considered those values as estimates of tree senescence at the site level (Fig. 2). Fourth, PSRI values were averaged at the individual level over all FPT circles, considering those values as estimates of tree senescence at the home-range level (Fig. 2). Tree senescence estimated at the site and home-range scales were not collinear (see below; Table S1), hence those variables were included in the same statistical models. All tree species located at the site and home-range levels (i.e. all trees across the trajectories) were interpreted as the foraging habitat quality at the home-range scale (Vergara et al. 2016).

**Statistical modelling**

We used a methodological framework based on Linear Mixed Effect models (LMM) to determine the effects of habitat variables on FPT (Fig. 3). This approach was intended to reduce spatial autocorrelation arising from consecutive circles whose areas tend to be overlapped along trajectories (Fauchald and Tveraa 2003; Fig. 3a). To analyze independent FPT data, we performed a randomization procedure by randomly selecting subsets of not-overlapping circles for each trajectory (Fig. 3). This procedure was repeated 1000 times, which resulted in 1000 sets of trajectories, each contained independent data later used in LME analyses (Fig. 3). LME were fitted to different datasets, which precluded comparing models with a criterion derived from likelihood functions, such as the Akaike Information Criteria (AIC) (Korner-Nievergelt et al. 2015). Thus, for each of the 1000 sampled
datasets, we used the RMark R package to compute model-averaged coefficients based on the AIC weights (Burnham and Anderson 2002). The AIC weight quantifies the probability that a given model is the best among a set of candidate models (Burnham and Anderson 2002; Grueber et al. 2011). The distributions of model-averaged coefficients were assumed to represent the effects of predictors. The mean and 95% confidence intervals of those distributions were used to interpret the significance of the coefficients. Model averaging was carried out on a set of 93 models including all possible combination of variables derived from a global model. The global model was built to assess the independent effects of habitat variables. Thus, we checked collinearity with the variance inflation factor (VIF; Table S1), where a VIF > 10 indicates lack of orthogonality between variables (Craney and Surles 2002). From this analysis, we detected that the percent cover of Nothofagus species and that of old-growth forest were collinear, so we discarded the latter from
analyses (Table S1). Therefore, the global model included as predictors the cover percentage of dominant *Notofagus* species, second-growth forest, open upland habitats and open lowland habitats, in addition to the PSRI values quantified at site and home range levels. The dependent variable (FPT) was divided by the area of each circle to obtain the time woodpeckers spent in an area of similar size (s/m²), and thus to allow the comparison between trajectories with circles of different radii. The trajectory and individual were included as random effects in LMM, with analysis being performed using the lme4 R package (Bates et al. 2014).

**Results**

The overall speed and radius of FPT circles differed among individuals and trajectories, with speed ranging from 0.1 to 36.89 m/s (mean ± SE 12.8 ± 1.1 m/s; Table S2) and radius ranging from 21.7 to 225.7 m (98.3 ± 4.6 m; Table S3). Significant effects of tree senescence (PSRI), tree composition, and open habitats on the FPT of woodpeckers were estimated from the 95% Confidence Intervals of the distributions of model-averaged coefficients (Table 2). Specifically, FPT was lower when woodpeckers moved in stands dominated by *N. antarctica*, open upland habitats, and open lowland habitats (Table 2; Fig. 4). Conversely, FPT was higher in stands and home ranges where tree senescence (PSRI) was higher at the site and home-range levels (Table 2; Fig. 4).

**Discussion**

Our results suggest that adoption of an area-restricted search (ARS) strategy by Magellanic Woodpeckers is influenced by the quality of foraging habitat (i.e., tree senescence as estimated by PSRI) at different scales, in addition to the cover of open habitats and tree stand composition. Furthermore, the positive effect of tree senescence at the home-range scale on FPT suggests that woodpeckers adjust their movements based on the foraging quality of home ranges. Earlier studies have revealed Magellanic Woodpeckers switch to the transient mode (exploratory movement) when the trees located in the proximity of the individual are either, on average, poor in quality or highly variable in quality (Vergara et al. 2019). Moreover, the residence time of Magellanic Woodpeckers on individual trees is positively associated with the home range foraging quality (Vergara et al. 2016), suggesting that individuals with more suitable territories adopt a more intensive prey searching, consistent with an ARS behavior. The combined use of spatial memory and random exploration is suggested to be a proximate mechanism underlying the movement behavior of animals within their home ranges (Gautestad and Mysterud 2010). Considering the stock of prey in a tree may be depleted after intensive feeding, the use of both long-term memorized information and short-term gathered information about senescent trees should contribute woodpeckers to make more efficient their ARS behavior.

Woodpecker preferences for more senescent trees, as found in Magellanic Woodpeckers, have also been reported in other species of woodpeckers (Nappi et al. 2015). For instance, Red-cockaded Woodpeckers (*Leuconotopicus borealis*) intensify foraging activity when surrounded by a habitat of better quality (McKellar et al. 2015) whereas Black-backed Woodpeckers (*Picoides arcticus*) have smaller home ranges in higher quality habitat (i.e., habitats with more recently killed trees) (Tingley et al. 2014). However, habitat preferences of woodpeckers also can be influenced by factors other than foraging habitat quality. For example, fledgling Northern Flickers (*Colaptes auratus*) occupied habitats with greater densities of trees, presumably for protection against predators (Gow and Wiebe 2014). Some large woodpeckers, such as Pileated Woodpeckers (*Dryocopus pileatus*), spend much of their time defending their roosting and nesting sites (Tomasvic and Marzluff 2018a). Our study, however, was carried out during the warmer, post-reproductive season (late summer), when central place foraging is not required, and the availability of feeding items is relatively high. Thus, the movement and foraging behavior observed in Magellanic woodpeckers may reflect the seasonal patterns of life cycle and resource distribution in subpolar forest. First, woodpeckers may remain longer in sites offering them with better habitat conditions when it is not needed to return to nests. Second, under more favorable seasonal conditions, the levels of intraspecific competition become reduced, making suitable microhabitats available for more individuals (Duron et al. 2018).

**Table 2** Summary statistics of the distributions of model-averaged coefficients associated with habitat variables affecting the First-Passage Time (FPT) of Magellanic Woodpecker

| Variable                              | Mean   | SE    | Lower CI | Upper CI |
|---------------------------------------|--------|-------|----------|----------|
| PSRI (site level)                     | 0.10   | 0.00  | 0.01     | 0.21     |
| PSRI (home-range level)               | 0.61   | 0.02  | 0.00     | 1.62     |
| *N. antarctica* (%)                  | −0.21  | 0.00  | −0.41    | −0.01    |
| *N. betuloides* (%)                   | 0.01   | 0.00  | −0.22    | 0.33     |
| *N. pumilio* (%)                      | 0.01   | 0.01  | −0.23    | 0.43     |
| Open Upland habitats (%)             | −0.37  | 0.01  | −0.94    | −0.14    |
| Second-growth forest (%)             | 0.05   | 0.01  | −0.42    | 0.71     |
| Open Lowland habitats (%)            | −0.27  | 0.00  | −0.54    | −0.10    |

The mean, standard error (SE) and 95% confidence intervals (CI) are shown. Significant effects (bolded) are interpreted from CI values (see text)

Value × 100
The cover of non-forest habitats was important in influencing woodpecker movements. Magellanic Woodpeckers spent less time in open habitats, suggesting that woodpeckers tended to adopt a transient (exploratory) movement when moving across, or near to, meadows, shrub, and peatlands. Woodpeckers have been observed responding to open habitats on different spatial scales, including within their home-range, among home ranges and regional (Rolstad et al. 2000; Pierson et al. 2010; Tomasevic and Marzluff 2018b). For instance, open habitats act as barriers for dispersal of Black-backed Woodpeckers over broad spatial scales, thus reducing migration and gene flow (Pierson et al. 2010). Similarly, the spatial genetic structure of Magellanic woodpecker populations seems to be related to the deforestation pattern in southern Chile (Poblete et al. 2020), as also suggested for some European woodpeckers (Pasinelli 2006). However, the avoidance of open habitats by woodpeckers may also result from the spatial distribution of feeding resources rather than from the reluctance of individuals to cross unsuitable habitats (Rolstad et al. 2000). That fact that Magellanic woodpeckers remained less time in areas with more cover of open habitat may be interpreted as resulting from either the spatial patterns of resource distribution or habitats that act as barriers. First, the quality of forest sites may decrease as closer to an open habitat, causing woodpeckers to intensify foraging activity far away from the forest edge. However, this explanation seems not very likely as previous studies suggest forest sites close to beaver-modified open habitats offer Magellanic woodpeckers with trees that decompose more rapidly due to wetter soil conditions (Soto et al. 2012). Second, woodpeckers can avoid crossing or approaching open habitats by being perceived as inhospitable habitats, where they face a high predation risk or stressful microclimatic conditions. Such a behavioral response has been described in red-cockaded woodpeckers, whose exploratory movement is hampered by the presence of open habitats (Trainor et al. 2013) as well as red-bellied woodpeckers (Melanerpes carolinus), which are dispersal limited in fragmented landscapes. Unpublished field observations suggest that Magellanic Woodpeckers flying through open areas are more susceptible to aggressive encounters with raptor species, such as Southern Caracaras (Caracara plancus) and Chilean Hawk (Accipiter chilensis). Independent from the mechanisms involved, the possibility that open habitats act as barriers poses concerns for the conservation of local populations of Magellanic Woodpeckers. Landscape connectivity for this species may be reduced as the forest habitat is fragmented and substituted by human-created open habitats.

Our results provide insights into woodpecker’s preferences for Nothofagaceae tree species composing old-growth forest ecosystems. The negative effect of _N. antarctica_ cover on the residence time of woodpeckers can

Fig. 4 Relationships between habitat variables (Table 1) and First-Passage Time (FPT) values of Magellanic Woodpeckers predicted from the distribution of model-averaged coefficients shown in the inserted density histograms. Grey areas are confidence intervals of the prediction.
be interpreted as no preference for stands of \textit{N. antarctica} when compared to those dominated by the other \textit{Nothofagus} tree species. The phenology of \textit{N. pumilio} contrasts with that of \textit{N. betuloides} (deciduous and evergreen, respectively). However, \textit{N. antarctica} trees have distinctive biological characteristics that may be responsible for this negative effect, as suggested by their distinctive remote-sensing characteristics (Soto et al. 2017). First, the scaly bark of \textit{N. antarctica} trees could be difficult to be excavated for foraging woodpeckers. Second, the low height and, in some cases, the bush-like shape of \textit{N. antarctica} trees may make them substrates of low attractiveness for woodpeckers. Third, the high soil moisture conditions where \textit{N. antarctica} trees grow may impose limitations for the colonization of some wood-boring insects that are important prey for Magellanic Woodpeckers (Vergara et al. 2017). Although the biological characteristics of \textit{N. antarctica} may explain the movement decisions of woodpeckers (as addressed above), the response of woodpecker populations to the cover of \textit{N. antarctica} forest in the landscape requires further exploration.

Conclusions

The adoption of the ARS behavior in Magellanic Woodpecker is accounted for forest composition, avoidance of open habitats and tree senescence. These findings provide not only novel information on the ecology of Magellanic Woodpeckers, but also insights into their conservation in subpolar forest. We recommend that conservation efforts should focus on protecting the remaining old-growth native forest, restoring open areas and reducing edge habitat, especially in protected areas surrounded by anthropogenic landscapes. Taking actions to preserve the Magellanic Woodpeckers would also help to preserve other forest-dwelling species due to their ecological importance as primary cavity excavator of south Patagonian forest and even other possible important ecological roles.

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