

Habitat selection by the Pale-breasted Spinetail (*Synallaxis albescens*) at multiple spatial scales in the central Monte Desert, Argentina

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Abstract. Habitat selection by birds is the result of hierarchical decisions that may be based on different cues at different spatial scales. However, studies rarely assess patterns of selection at multiple scales simultaneously in order to understand the processes leading to the observed selection patterns. In the central Monte Desert, at the habitat scale, the density of Pale-breasted Spinetails (*Synallaxis albescens*) during the breeding season is higher in mesquite (*Prosopis flexuosa*) open woodlands than in creosote (*Larrea cuneifolia*) shrublands. Causes of this pattern may be revealed by exploring how Pale-breasted Spinetails use space at different scales. At the microhabitat scale, birds selected the highest mesquite trees and avoided creosotes for territorial displays. However, they did not establish territories in patches where mesquite trees were taller than expected. Moreover, at the mesohabitat scale, the cover of mesquite trees within territories was greater than expected only in the plot with a lower cover of mesquite trees. Therefore, the pattern of vegetation selection at the habitat scale matched that at the microhabitat scale, but not completely at the mesohabitat scale. Our study provides insight about the mechanisms driving patterns of habitat selection by Pale-breasted Spinetails in the central Monte Desert. It also highlights the significance of considering vegetation structure and composition at multiple spatial scales when evaluating how birds select where to establish their territories.

Additional keywords: mesquite trees, song posts, spatial scale, territory.

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Introduction

Habitat selection by birds is related to features of vegetation structure and floristic composition, because vegetation may determine the distribution and abundance of food, availability of singing perches, shelter from predators, and availability of nesting locations (Cody 1985). Within habitats, birds may also select certain structural characteristics to establish their territories (e.g. Jones and Robertson 2001). Furthermore, within a territory, birds may choose certain microsites for different activities. There are many studies on microhabitat selection for foraging (e.g. Whelan 2001) and nest-sites (e.g. Mezquida 2004) but other patterns of use of microhabitats within territories, such as selection of song posts, have received less attention (but see Beck and George 2000).

If habitat selection in birds is the result of hierarchical decisions based on different environmental cues (Jones 2001), then the best way to understand the processes leading to the observed selection patterns is to evaluate those patterns at multiple scales simultaneously (Wiens 1989b). These cues are commonly associated with food availability, nesting sites or predation risk (Wiens 1989a), and may or may not change from one scale to

another (e.g. Sedgwick and Knopf 1992; Robichaud and Villard 1999).

Most studies in the ornithological literature are of insectivorous birds in temperate forests, whereas studies in desert environments are scarce (Wiens 1991). In the central Monte Desert of Argentina, insectivores constitute 52% of all the bird species recorded (Marone 1992). The Pale-breasted Spinetail (*Synallaxis albescens*) is an insectivore that gleans prey items mainly from the foliage (Remsen 2003) and arrives in the central Monte Desert during spring (Marone 1992) as a short-distance migratory bird (Chesser 1994). In this desert, at the habitat scale, the density of Pale-breasted Spinetails is higher in mesquite (*Prosopis flexuosa*) open woodlands than in creosote (*Larrea cuneifolia*) shrublands (Cueto *et al.* 2008). However, the reason why this species mainly uses this habitat type has not been studied in detail.

The aim of this study was to assess how features of vegetation structure and floristic composition are correlated with selection of territories by Pale-breasted Spinetails, that is, at the mesohabitat scale, and with the selection of sites to perform territorial displays, that is at the microhabitat scale.

Methods

Study area

Our study was conducted in the Man and Biosphere Reserve of Ñacuñán (34°03'S, 67°54'W), in the central Monte Desert, Argentina. The landscape is mainly open mesquite woodland intersected by tracts of creosote shrublands. In the open woodland, the mesquites (*Prosopis flexuosa*) are scattered within a matrix of tall shrubs (mainly *Larrea divaricata*). Other woody species present are *Geoffroea decorticans* trees, and tall shrubs (*Capparis atamisquea* and *Condalia microphylla*). Creosote shrublands are dominated by *Larrea cuneifolia*, and the cover of trees and other tall shrubs is low. The climate of the study area is temperate; the average annual rainfall is 333.6 mm, and is highly seasonal and varies between years (Lopez de Casenave 2001).

Sampling and analysis of vegetation

Two plots (P1 and P2), each of 10 ha and 800 m apart, were established in the open mesquite woodland. Each plot was divided into squares 25 × 25 m. We mapped all mesquite trees taller than 3 m (i.e. exceeding the height of the shrub stratum, Milesi 2006); measured the height of each tree; and estimated the diameter of the crowns. The maps of each plot were geo-referenced and exported to ArcView 3.3 (ESRI 2002). Horizontal and vertical vegetation cover was characterised using 189 locations at a random orientation and distance from the corners of each square within each plot. At each of the 189 locations, we recorded trees and shrubs touching a pole at 25-cm intervals up to 4 m, and a unique interval ≥ 4 m.

Sampling and analysis of territories: the mesohabitat scale

During November and December 2008, plots were systematically searched on alternate days during the first 4 h after dawn and the last 3 h before sunset. We recorded locations of birds performing territorial vocalisations or aggressive interactions. We made the analysis at the mesohabitat scale considering this scale as the area used by birds to set their territories in each 10-ha plot.

We estimated the size of territories by determining minimum convex polygons, and used the Animal Movement Analysis extension (Hooge and Eichenlaub 1997) and Spatial Analyst (ESRI 2000) in ArcView 3.3 (ESRI 2002) to calculate the areas and boundaries of the territories. We determined the average area of territories in both plots and compared them using a *t*-test.

We converted the maps of the mesquite trees >3 m tall into a grid format of squares 4 × 4 m generated by ArcView 3.3. Squares were classified as with or without mesquite cover to obtain the percentage of mesquite cover within territories. This procedure was performed in each plot for the observed territories and for 30 randomly arranged territories. Random territories were circular and equivalent to the average area of the observed territories from each plot. We resampled the 30 randomly arranged territories in 1000 samples of size *n*, with *n* being the number of observed territories in each plot. We then calculated the average mesquite cover in each of the samples, obtaining a distribution of random expected values for the average mesquite cover in *n* territories. We tested the following null hypothesis: the

average mesquite cover in *n* observed territories is less than or equal to the average cover expected in *N* randomly selected territories. We also set 0.5-m intervals of height and compared cumulative frequency distributions using a Kolmogorov–Smirnov goodness-of-fit test to compare the frequency of mesquite heights in the plot with the observed frequency of mesquite heights inside the territories.

Sampling and analysis of song posts: the microhabitat scale

During the breeding seasons of 2007 and 2008 we recorded plant species, plant height and height of perches used by singing birds in each plot. In addition, each singing bird was assigned to an exposure category (high, medium, low) corresponding to the outer, intermediate and inner parts of the plant. This analysis represented the microhabitat scale because this scale recorded the sites where birds performed territorial displays within their territories. Consecutive observations of the same individual were included because they can provide a more complete description of the behavioural repertoire of the species (e.g. Morse 1990). However, sequential observations are not independent (Hejl *et al.* 1990). To reduce the bias, we treated the sequence of data of an individual as a single observation (Airola and Barrett 1985) and the observations from different days were treated as independent samples.

We used a Chi-square goodness-of-fit test to determine if the observed frequency distributions of four different traits (plant species used for singing, height of the singing perch, height of mesquites used for singing, and exposure during singing) were equal to the expected frequency distributions. We estimated expected frequencies of use of woody plants from the relative cover of each woody species. We segregated data on the height of singing perches into 1-m height-categories and estimated expected frequencies of use of different heights from the profile of foliage cover. Additionally, each mesquite tree was assigned to one of five height categories (at 1-m intervals) in each of the plots, yielding the expected use frequency of tree-heights. Finally, to determine the expected singing exposure we assigned the same probability to the three possible categories.

Results

Characterisation of territories

There were four non-overlapping territories in each plot and their average size (\pm s.d.) was higher in Plot 1 (P1: 1.09 \pm 0.15 ha) than in Plot 2 (P2: 0.67 \pm 0.21 ha) ($t=3.28$, $P=0.017$). The average mesquite cover inside the territories was 23.3 \pm 0.61% in P1 and 43.0 \pm 1.0% in P2. The average mesquite cover of territories in P1 was significantly higher than in randomly selected territories (resampling test, critical value = 23.0%, $P=0.046$), whereas these were not significantly different in P2 (resampling test, critical value = 46.5%, $P=0.182$).

There were no differences in the observed cumulative frequency distribution of heights of mesquites >3 m tall inside the territories in relation to their expected cumulative frequency in each plot (Kolmogorov–Smirnov test: P1, $D_{\max}=0.066$, $P>0.05$, $n=186$; P2, $D_{\max}=0.05$, $P>0.05$, $n=276$).

Characterisation of song posts

From the number of territories found, we estimate that our study population consisted of ~8 Pale-breasted Spinetails in each of the 2 years of the study. Pale-breasted Spinetails did not use woody species in proportion to their availability in either plot (Fig. 1; P1: $\chi^2_5 = 216$, $n = 58$, $P < 0.001$; P2: $\chi^2_5 = 46$, $n = 25$, $P < 0.001$). Mesquites were used more by singing Spinetails than would be expected based on their availability; *Larrea divaricata* was avoided; and the other woody species with low cover were rarely used by singing Spinetails. Birds selected the highest perches of the vegetation from which to sing in both plots, and used the lower heights less than expected (Fig. 2; P1: $\chi^2_4 = 1138$, $n = 59$, $P < 0.001$; P2: $\chi^2_4 = 185.4$, $n = 25$, $P < 0.001$).

The height pattern of available mesquite trees differed between plots (Fig. 3). In P1, trees 5–6 m tall dominated, whereas in P2 trees 3–4 m tall were more abundant. However, in both plots Pale-breasted Spinetails selected mesquite trees >5 m tall from which to make territorial displays, and lower trees were used less than expected relative to their abundance (Fig. 3; P1: $\chi^2_4 = 48.7$, $n = 59$, $P < 0.001$; P2: $\chi^2_4 = 31.9$, $n = 33$, $P < 0.001$). Also, Pale-breasted Spinetails selected the most exposed locations to perform territorial displays in both plots, whereas the other two exposure categories were used less than expected (Table 1).

Discussion

In this study, we evaluated how vegetation structure and floristic composition are associated with the use of space by Pale-breasted Spinetails at two different spatial scales in the central Monte Desert. At the mesohabitat scale, the response depended upon characteristics of the study plot. Neither in P1 nor P2 was there evidence of selection of areas with the tallest trees. However, in P1 there was a selection for areas with a higher cover of mesquites in which to establish territories. These results indicate that there may be a threshold of mesquite cover during territorial selection by Pale-breasted Spinetails. In P1, mesquite tree cover is lower than in P2 (P1 = 12.2%, P2 = 23.8%), so birds may not find suitable sites in which to establish territories in some areas of P1, and therefore tend to select sites with greater cover of mesquites in this plot. On the other hand, mesquite cover in P2 may be sufficiently high, and any site in the plot may be suitable for establishment of a territory. Furthermore, territories in P1 were larger on average than in P2, suggesting that differences in the size of territories between plots could reflect the scarcity of important features or resources. Pale-breasted Spinetails are less abundant in creosote shrubland than in mesquite woodland (Cueto *et al.* 2008), and a potential prediction is that territories might be even larger in creosote shrubland.

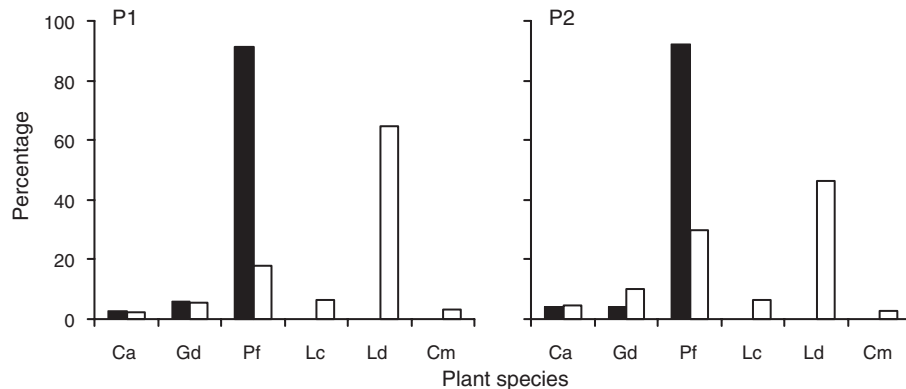


Fig. 1. Observed (filled bars) and expected (open bars) use of woody plants for territorial displays by Pale-breasted Spinetails in Plot 1 (P1) and Plot 2 (P2). Plant species: Ca, *Capparis atamisquea*; Gd, *Geoffroea decorticans*; Pf, *Prosopis flexuosa* (mesquite); Lc, *Larrea cuneifolia* (creosote); Ld, *Larrea divaricata*; Cm, *Condalia microphylla*.

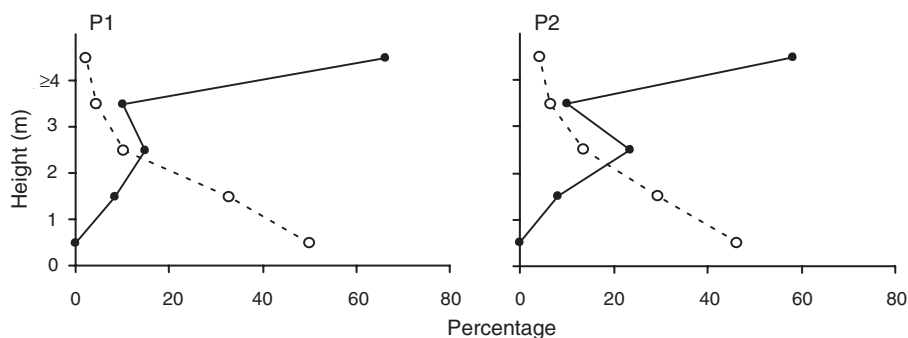


Fig. 2. Observed (filled circles) and expected (open circles) use of heights of song posts for territorial displays by Pale-breasted Spinetails in Plot 1 (P1) and Plot 2 (P2).

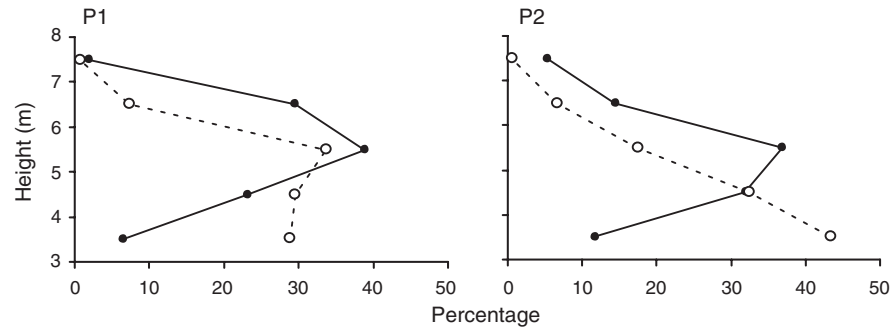


Fig. 3. Observed (filled circles) and expected (open circles) use of mesquite trees of different heights for territorial displays by Pale-breasted Spinetails in Plot 1 (P1) and Plot 2 (P2).

Table 1. Comparison of observed and expected singing exposure of birds in each plot performed by Chi-square goodness-of-fit test. The three exposure categories were considered as equally probable

Exposure	Observed frequencies	
	Plot 1	Plot 2
Low	8.50	3.83
Medium	11.34	6.33
High	37.16	14.84
<i>n</i>	57	25
χ^2_2	26.26	7.97
<i>P</i>	<0.0001	0.018

At the microhabitat scale, Pale-breasted Spinetails selected mesquites for territorial displays. Furthermore, Spinetails selected the tallest mesquite trees and the most exposed places for territorial displays. Birds that sing in high and exposed locations increase their risk of predation (Krams 2001) but may improve the acoustic transmission of their songs (Marten and Marler 1977). Pale-breasted Spinetails have modest plumage coloration and often vocalise very close to the branch on which they are perched, which makes birds difficult to see (Canevari *et al.* 1991). The coloration and behaviour of Pale-breasted Spinetails may therefore reduce predation risk and be an important factor in the process of selecting song perches for territorial displays. On the other hand, the song of this bird is characterised by short notes and repetitive vocalisations (Remsen 2003), which could have strong acoustic degradation in closed environments owing to the effect of echoes (Tubaro and Lijtmaer 2006). Consequently, acoustic transmission of Pale-breasted Spinetail songs from high and exposed locations may avoid the degradation potentially produced by the dense shrub stratum in the study site.

Habitat selection at mesohabitat and microhabitat scales may be related to the fact that Pale-breasted Spinetails are more abundant in mesquite open woodlands than in creosote shrublands (Cueto *et al.* 2008). Our results suggest that mesquite trees are important for the location of territories and for the territorial displays of Pale-breasted Spinetails. However, it is still not known whether Pale-breasted Spinetails actually select tree-height *per se* or the mesquite trees, which happen to be tall. The vegetation-height profile in open mesquite woodland is higher than in creosote shrubland (Marone 1991). Consequently, the observed pattern of habitat use may be a result of differences in the height of

vegetation between habitats and not only a result of differences in cover of mesquite. Moreover, Pale-breasted Spinetails forage mainly on mesquites but also in other woody species (Blendinger 2005) and it nests largely in *Geoffroea decorticans* trees (Mezquida 2001), a species that has greater cover in the mesquite open woodland than in creosote shrublands (Marone 1991). Therefore, it is possible that it is not only the presence of mesquite trees that is important in explaining the difference in abundance among habitats but that other woody species, such as *Geoffroea decorticans*, are also important.

Evaluating use of space at the mesohabitat scale partially explains the observed pattern at the habitat scale, that is that birds depend upon the mesquite cover in each plot. In contrast, the pattern was better explained when analysed at the microhabitat scale. In this study, we assessed selection patterns at multiple scales simultaneously in order to try to understand the processes leading to the observed selection patterns.

It is of note that our results at the mesohabitat scale show that it is not only important to consider the scale at which we are studying patterns but also differences within those scales. In this case, one of the plots had almost double the tree-cover of the other. Consequently, our conclusions about the importance of mesquite trees in the patterns of habitat and territorial selection of Pale-breasted Spinetails would be different if only one plot was examined, at least at the mesohabitat scale.

This study improves our understanding of the selection of territories and use of habitat by Pale-breasted Spinetails in the central Monte Desert. Our research also shows the significance of considering multiple scales and context within the same scale in ecological studies, specifically, the importance of vegetation structure and composition across scales relative to territorial selection and defence.

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