Spatial analysis of sap consumption by birds in the Chaco dry forests from Argentina

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Abstract. Sap is a resource of high energy content that is usually inaccessible to birds, although woodpeckers have the ability to drill into living trees to obtain sap. Because spatial patterns of resource availability influence avian abundance, we explored how spatial patterns of sap availability determine the spatial distribution of two sap-feeding species in the semiarid Chaco of Argentina. We studied the White-fronted Woodpecker (*Melanerpes cactorum*), which obtains sap by drilling holes into tree trunks, and the Glittering-bellied Emerald (*Chlorostilbon aureoventris*), which can obtain sap only from active woodpecker holes; 12 other bird species also exploited the sap flows from holes drilled by White-fronted Woodpeckers. The abundance of tree species used for sap feeding did not explain the spatial patterns of territorial groups of White-fronted Woodpeckers. However, within each territory, the abundance of Woodpeckers was centred on a single tree from which sap was obtained. The abundance of the Emeralds was strongly associated with the availability of trees with active sap-holes. During the dry season, sap is a major component in the diet of White-fronted Woodpeckers and Glittering-bellied Emeralds. However, the spatial distribution of these two consumers in relation to the availability of sap was species-specific. This species-specific response was closely related to the ecology and life history of each species. The abundance of woodpeckers could be determined by local mechanisms, such as location of a single sap tree in their small territories, whereas non-territorial hummingbirds would be able to track sap wells at a larger scale than the territory of a single territorial group of Woodpeckers. Our results show the importance of spatial analysis in identifying the ecological determinant of habitat selection and niche differentiation within species.

Additional keywords: *Chlorostilbon aureoventris*, facilitation, foraging behaviour, Glittering-bellied Emerald, hummingbirds, *Melanerpes cactorum*, resource tracking, White-fronted Woodpecker.

Introduction

Among American woodpeckers, a number of species are known to drill holes in living trees to consume phloem sap, including species of *Melanerpes* (Genise *et al*. 1993), *Sphyrapicus* (Tate 1973), *Picoides* (Kozma 2010) and *Campephilus* (Schlatter and Vergara 2005). Sap-consuming woodpeckers select among and within tree species (Kattan 1988; Blendinger 1999; Eberhardt 2000) so the availability of sap trees might be a determining factor in the spatial distribution of these species of woodpecker. Similarly, the spatial distribution of sap trees and the sap holes created by woodpeckers might also determine the spatial patterns and abundance of other sap-feeding species that exploit woodpeckers' sap holes. Because sap and nectar provide similar food resources, nectarivorous birds are particularly likely to feed on sap from sap holes created by woodpeckers. Hummingbirds in North America include high volumes of sap in their diets (Miller and Nero 1983), for example sap in holes drilled by the Yellow-bellied Sapsucker (*Sphyrapicus varius*) can be the main resource for the Ruby-throated Hummingbird (*Archilochus colubris*) especially during the nesting season when the hummingbirds rarely take flower nectar (Southwick and Southwick 1980).

Some honeyeater species (Meliphagidae) in Australia also regularly use sap flows, though the extent of such sap foraging is not well known and apparently under-reported (Chapman *et al*. 1999).

Our study focussed on the responses of sap-feeding species to spatial patterns of sap availability in the Chaco dry forests of South America. There the White-fronted Woodpecker (*Melanerpes cactorum*) drills holes in branches and trunks of trees to feed on sap flows (Genise *et al*. 1993), providing an energy-rich food resource for other birds to exploit during the cold dry season, when insects, fruits and flowers are scarce (Codesido and Bilenca 2004). At least 15 species of birds are known to eat sap from active holes drilled by woodpeckers in the dry woodlands of southern South America (Genise *et al*. 1993; Blendinger 1999). The ability of birds to track the spatial variability of food availability depends on factors such as the scale at which each consumer species perceives resources and the relative importance of the resource in the diet (Nekola and White 1999; Shochat *et al*. 2002; Seppänen *et al*. 2007). Spatial structure is an important component of natural systems that needs to be included in the analysis of ecological processes (Wagner and Fortin 2005; García

et al. 2009). A spatially explicit analysis of the resource–consumer relationship may contribute valuable information on the gradient of scales at which these factors operate and on the spatial structure of ecological responses by species to spatial resource heterogeneity (Fortin and Dale 2005; Wagner and Fortin 2005).

The first aim of this study was to evaluate if the spatial distribution of tree species used for sap consumption determined the pattern of use of territories by White-fronted Woodpeckers and to explore the spatial scale at which individuals responded to the resource. If sap resource availability determines the distribution of Woodpeckers, we expected a spatial relationship between the abundance of Woodpeckers and the abundance of trees used for sap extraction. The second aim of the work was to evaluate if active holes drilled by White-fronted Woodpeckers determined the use of space by the Glittering-bellied Emerald (*Chlorostilbon aureoventris*), the most abundant hummingbird species in the Chaco dry forest. If hummingbirds track sap holes, we expect that the spatial patterns of abundance of this consumer should be structured in response to the distribution of White-fronted Woodpeckers.

Methods

Study area and study species

We conducted the study in Rivadavia Banda Sur (24°11′S, 62°53′W), Salta Province, in north-western Argentina. The climate is seasonal monsoonal, with dry winters and rainy summers and an average annual of 650 mm. The dry season normally extends from May to October. The area is located in the semiarid Chaco, in the Chaco phytogeographic province (Morello and Adámoli 1968; Cabrera and Willink 1980), characterised by semi-deciduous xerophilous forest. The White-fronted Woodpecker forms resident groups throughout the year (M. G. Núñez Montellano, P. G. Blendinger and L. Macchi, unpubl. data). They spend most of the day near trees with active sap holes (M. G. Núñez Montellano *et al.*, unpubl. data) and show strong territorial behaviour and aggressive interactions, mainly with conspecifics as well as other species that approached the sap holes (Blendinger 1999). Our previous field observations suggested that forest structure and abundance of birds differed with distance from water in the semiarid Chaco. Thus, to select the study site we explored, at the landscape scale, the differences in abundance of sap consumers between areas located near and far from ponds. In 10 different ponds spaced 500 m or more apart, we established a pair of transects, each 200 m long and 700 m apart. The abundance of sap-feeding birds was four times greater near ponds than in forests far from waterbodies (Wilcoxon matched-pairs test, $Z = 2.66$, $n = 10$, $P < 0.01$); thus, sampling was conducted in a site adjacent to a small permanent pond.

Sampling of birds and trees

The size of our study plot was large enough to include several territorial groups of White-fronted Woodpeckers and the structural heterogeneity representative of forests located near ponds. We established a 450×300-m plot along the edge of the pond (450 m) and extending into the forest (300 m), split into a grid of 108 cells 50×25 m. We were interested in the spatial distribution of the activity of sap-feeding birds. In each cell we quantified

the relative abundance of White-fronted Woodpeckers and Glittering-bellied Emeralds, as a spatially explicit measure of the use of forest sites by these species, and determined the abundance of trees used for sap consumption.

To measure avian activity, three observers surveyed birds on three dates in June 2007. On each date, each observer surveyed one transect, comprising a block of 12 cells block perpendicular to the pond; we sampled each cell for 10 min, for a total of 30 min per cell and 2 h per transect. Each block of 12 cells was covered at three different times and on alternate days to ensure uniform sampling effort among cells. We recorded the exact location of all individuals seen or heard within each cell, whether they were eating sap or other food, and the plant species used. For each cell we estimated the abundance of all adult plants of the species from which sap was obtained. We counted every tree >10 cm diameter at breast height and all shrubs >1 m tall. To determine the number of groups and the area of their territories, Woodpeckers were mist-netted and colour-marked. Individual birds and groups were observed throughout the study site and their position was recorded with a geographical positioning system (GPS; Garmin eTrex Legend).

In addition to the transect surveys, we spent total of 31 h following individual Woodpeckers in the plot, recording the amount of time they spent in trees with active sap holes.

Statistical analyses

We first explored the spatial relationship between the abundance of tree species from which sap obtained and the abundance of White-fronted Woodpeckers. We selected the consumer–resource relationships that were significant at $P < 0.05$ using a simple regression analysis, and we used these relationships in spatial models.

We explored the pattern of White-fronted Woodpecker (consumer) abundance and its covariance with resources (abundance of tree species from which sap obtained) at different scales using spatially explicit analyses. We used Moran's I correlograms (Legendre and Legendre 1998) to explore spatial autocorrelation among consumers, with distance classes of variable length but with similar number of compared point pairs and with a significance level of $P < 0.05$. We used correlograms to evaluate autocorrelation intensity, size of the area of influence, and type of spatial pattern of the study variable. For the first objective, we used principal coordinates of neighbour matrices (PCNM) to generate spatially explicit models that decompose spatial variation of the response variable (abundance of White-fronted Woodpeckers) and relate it to predictor variables (abundance of trees used for sap consumption). First, a series of vectors of principal coordinates is generated from an ordination analysis (principal coordinate analysis). These vectors represent all the periodical spatial structures that can be established from a spatially explicit group of sampling points (Borcard and Legendre 2002). We then used multiple regression analysis to contrast all the spatial vectors with the response variable (abundance of White-fronted Woodpeckers). Multiple regression analysis selects spatial templates (vectors) that can explain spatial variation in the response variable (those vectors with a partial regression coefficient significant at $P < 0.05$). It also provides the percentage of spatial variance accounted for by these templates

and generates expected values of the response variables. We explored the association between these expected values of consumer abundance and values of sap abundance by simple regressions (Borcard *et al*. 2004; García *et al*. 2009). We also used spatial analysis by distance indices (SADIE) (Perry and Dixon 2002), to explore the spatial association between the abundance of White-fronted Woodpeckers and that of trees used for sap consumption during the study period (with values 1 and 0 per 50×50-m sample unit). SADIE assesses local spatial association using the index X, which represents the correlation coefficient between the clustering indices of the two populations sampled. The significance of X was tested with a randomisation test after adjustment for spatial autocorrelation.

For the second objective, we evaluated the spatial relationship between the abundance of Glittering-bellied Emeralds and White-fronted Woodpeckers. We consider the spatial abundance of Woodpeckers to be a good indicator of the distribution of sap available to the hummingbirds, given that the hummingbirds could only consume sap from trees used by the Woodpeckers, and because the Woodpeckers ate sap from only a few individual trees, in which they spent >75% of their time. We applied the PCNM analysis using the abundance of Glittering-bellied Emeralds as the response variable and the abundance of White-fronted Woodpeckers as the predictor variable. We performed spatial analyses with the software SAM v2.0 (Rangel *et al*. 2006).

Results

Five family groups of Woodpeckers, a total of 28 individuals ($n = 5, 5, 5, 9$ and 4 individuals, mean $\pm$ s.d. $= 5.6 \pm 1.95$), held territories wholly or partly in the 13.5-ha study plot. Mean size of territories was 1.39 ± 0.17 ha and included at least one individual of *Stetsonia coryne*, a columnar cactus in which Woodpeckers drill holes that are used as roosting sites by the entire family group. Each group mainly used one tree from which to obtain sap, although more than one tree per territory was used per group (M. G. Núñez Montellano *et al*., unpubl. data). We recorded a total

of 13 bird species consuming sap at holes excavated by the Woodpeckers, the most frequent being Glittering-bellied Emeralds, Monk Parakeets (*Miopsitta monachus*), Greater Wagtail-Tyrants (*Stigmatura budytoides*), and Black-capped Warbling-Finch (*Poospiza melanoleuca*) (Table 1). The abundance of four species that fed on sap was correlated with the abundance of White-fronted Woodpeckers (Table 1). However, only the Glittering-bellied Emerald was abundant enough to allow a reliable spatial test.

Sap consumption by White-fronted Woodpeckers

Woodpeckers obtained sap from seven species of tree (Table 2), but mainly from *Prosopis ruscifolia* (87% of records). Of all the species from sap was obtained, *P. ruscifolia* was the only one whose abundance was significantly and positively associated with the abundance of White-fronted Woodpeckers (simple regression, $R^2 = 0.05$, $n = 108$, $P = 0.022$) (Table 2).

The abundance of White-fronted Woodpeckers showed a significant positive autocorrelation among very close sites (mean distance of 54.3 m) and among those at a mean intermediate distance of 151.5 m (Fig. 1*a*), showing aggregated patterns that correspond to territories and the spacing among them respectively. Abundance of *P. ruscifolia* did not show significant autocorrelation for any of the distance classes. PCNM generated 52 spatial vectors for the 108-cell grid. Four of the vectors were significantly associated with abundance of White-fronted Woodpeckers; these vectors represent the structure of the spatial variation in the abundance of Woodpeckers. Overall, all spatial vectors accounted for 21% of variability in the abundance of White-fronted Woodpeckers (multiple regression, $R^2 = 0.22$, $P < 0.001$). Expected spatial values of Woodpecker abundance were not correlated with the abundance of *P. ruscifolia* ($R^2 = 0.10$, $P = 0.36$). However, the abundance of Woodpeckers was spatially associated with the location of trees from which sap was obtained (spatial association index $X = 0.42$, $P = 0.005$).

**Table 1. Records of sap-feeding by birds in the study area**

n, relative abundance (numbers of each species recorded in transects); Foraging records, the total number of observations of foraging; Sap-feeding, the total number of individuals observed feeding on sap at holes drilled by White-fronted Woodpecker; *R* and *P* values for the regression analysis between the abundance of each species and the abundance of White-fronted Woodpeckers (only species with *n* > 5 were analysed)

	n	Foraging records	Individuals feeding on sap	*R*	*P*
Greater Wagtail-Tyrant (*Stigmatura budytoides*)	102	81	5	0.23	0.018
Masked Gnatcatcher (*Polioptila dumicola*)	68	58	2	0.16	0.10
Glittering-bellied Emerald (*Chlorostilbon aureoventris*)	62	54	46	0.68	<0.001
House Wren (*Troglodytes aedon*)	18	18	1	0.28	0.004
Black-capped Warbling-Finch (*Poospiza melanoleuca*)	18	14	5	0.25	0.010
Monk Parakeet (*Myiopsitta monachus*)	14	6	6	0.43	<0.001
Blue-and-yellow Tanager (*Thraupis bonariensis*)	8	5	1	0.18	0.07
White-tipped Plantcutter (*Phytotoma rutila*)	4	2	2	–	–
Pearly-vented Tody-Tyrant (*Hemitriccus margaritaceiventer*)	3	3	1	–	–
Cream-backed Woodpecker (*Campephilus leucopogon*)	2	2	1	–	–
Epaulet Oriole (*Icterus cayanensis*)	2	2	2	–	–
Red-crested Cardinal (*Paroaria capitata*)	1	1	1	–	–
Many-coloured Chaco-Finch (*Saltatricula multicolor*)	1	1	1		

Table 2. Number of sap consumption events and simple regression analysis of abundance of White-fronted Woodpeckers and abundance of tree species from which sap obtained

Species with which abundance of Woodpeckers significantly associated indicated in bold

	n	R^2	P
Aspidosperma quebracho-blanco (Apocynaceae)	2	0.03	0.08
Bulnesia sarmientoi (Zygophyllaceae)	5	<0.01	0.62
Ruprechtia apetala (Polygoneacea)	6	<0.01	0.70
Prosopis ruscifolia (Fabaceae)	104	**0.05**	**0.022**
Ruprechtia triflora (Polygonaceae)	2	<0.01	0.43
Schinus sp. (Anacardiaceae)	2	<0.01	0.70
Ziziphus mistol (Rhamnaceae)	2	<0.01	0.87
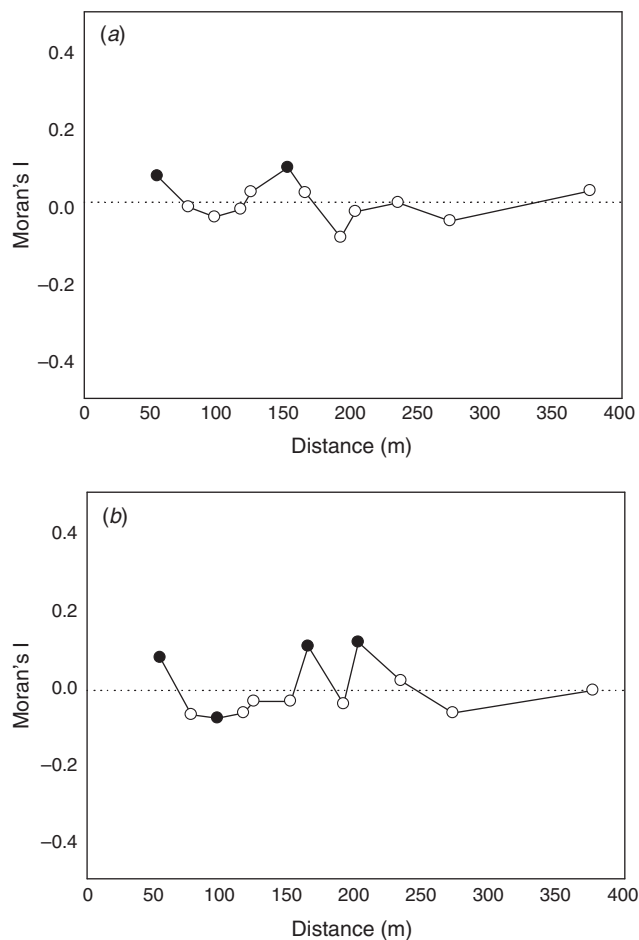
Fig. 1. Moran's I correlograms for (*a*) White-fronted Woodpecker (*Melanerpes cactorum*) and (*b*) Glittering-bellied Emerald (*Chlorostilbon aureoventris*). Black circles show distance classes statistically significant at $P < 0.05$.

Sap consumption by Glittering-bellied Emeralds

The Glittering-bellied Emeralds foraged mostly on sap (83% of 54 observations), with; the remaining observations being consumption of nectar (14%) and insects (3%). The abundance of the Emeralds was positively associated with the abundance of White-fronted Woodpeckers ($R^2 = 0.46$, $P < 0.001$).

The abundance of Glittering-bellied Emeralds showed three positive autocorrelations: one at short distances (mean distance of 54.3 m) and two at intermediate distances (mean distances of 164.5 m and 201.8 m); and one negative autocorrelation (mean distance of 97.0 m) (Fig. 1*b*), indicating a patchy or aggregated distribution. PCNM showed that 7 of the 52 spatial vectors were significantly associated with abundance of Glittering-bellied Emeralds, together accounting for 35% of variability in abundance (multiple regression, $R^2 = 0.35$, $P < 0.001$). The correlation of the abundance values expected for the Glittering-bellied Emerald with the abundance of White-fronted Woodpecker accounted for 11% of the distribution ($R^2 = 0.11$, $P = 0.01$).

Discussion

Sap is an important component in the diet of White-fronted Woodpeckers and Glittering-bellied Emeralds during the dry season in the semiarid woodlands of Argentina. However, the spatial match between the abundance of the consumers and sap availability was species-specific. Our study suggests that processes related to sap consumption differ strongly between these two sap-eating species. The abundance of White-fronted Woodpeckers was not spatially correlated with the abundance of tree species used for sap consumption. For Woodpeckers, sap is an abundant resource and its availability and exploitation are more related to the social behaviour of territorial groups than to resource abundance. In contrast, the abundance of Glittering-bellied Emeralds was spatially structured in response to sap availability. This consumer–resource spatial relationship may be a result of spatial structuring of sap availability itself, in turn generated by regular spacing of the territories of White-fronted Woodpeckers.

At the local scale, neither abundance of tree species from which sap was obtained nor abundance of the most consumed species (*P. ruscifolia*) determined the pattern of use of territories by White-fronted Woodpeckers. This absence of spatial adjustment between the Woodpeckers and their sap trees at the local scale highlights other important aspects of the ecology of the species. On the one hand, the absence of resource tracking might result from a concentration of territorial groups, along with dense territorial packing in the area, which poses serious limitations on the movements of Woodpeckers in search of resources. On the other hand, a group territory might not be the appropriate scale to estimate availability of sap. Most sap consumption by each territorial group was concentrated at a single tree where the Woodpeckers actively maintained sap flows in the holes and drilled new ones. Thus, the availability of sap could be related more to single trees more than to all exploitable trees in a group territory.

We have shown that the hummingbirds are able to track sap resources successfully within the territories of the Woodpeckers. Tracking is a suitable foraging strategy for food resources that undergo predictable changes in spatial abundance over time. Glittering-bellied Emeralds are likely to be using sap as a replacement for nectar during periods of acute shortage of flowers, as they are equivalent resource in terms of energy and nutritional characteristics. Food scarcity is typical during the cold

dry season (May–September) in the semiarid Chaco (Codesido and Bilenca 2004). During the study period, only two species of flower (*Capparis salicifolia*, *Tillandsia* sp.) were available to hummingbirds, which consumed their nectar. However, the Glittering-bellied Emerald does not consume sap during the flowering period of most plant species, in late spring.

Our findings raise interesting questions for further research on foraging and spatial distribution, which may be deeply influenced by the use of social information (Galef and Giraldeau 2001; Seppänen *et al.* 2007). Resource tracking may be facilitated by the activity of other species consuming the same resource, through tracking cues or signals (Saracco *et al.* 2004). The activity of sap consumption by White-fronted Woodpeckers is likely to provide a signal to Glittering-bellied Emeralds, facilitating both the resource and its spatial location in the forest.

In conclusion, the analysis of spatial patterns was a useful approach to explore the mechanisms that determine avian decisions related to sap consumption and how these processes interact between different species affecting their use of space. We found a strong difference between two species of sap-feeder in the scale of their spatial coupling with sap availability. This species-specific response is closely related to the ecology and life history of the two species. Future research should explore the spatial patterns of sap exploitation by facultative nectar consumers, such as orioles (Icteridae), which are the main nectar consumers of several plant species in the Neotropical region (Toledo and Hernández 1979; Ragusa-Netto 2002).

Acknowledgements

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