

Habitat features affecting bird spatial distribution in the Monte Desert, Argentina

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Resumen. Se estudió la relación de diversas características del hábitat con la abundancia de gremios y la diversidad de especies de aves, con el objeto de identificar factores próximos de selección del hábitat. En la estación de cría, los gremios arborícolas (herbívoros e insectívoros) siguieron el primer eje de la complejidad ambiental, generado por la cobertura de los árboles y arbustos que les brindan alimento y sustrato de forrajeo. La distribución de los cazadores de insectos en vuelos largos sobre ese eje fue bi-modal, a consecuencia de las diferentes tácticas de caza de sus especies. Los granívoros terrícolas no rastrearon ningún gradiente ambiental, incluido el generado por las plantas que les proveen semillas y brotes. Este resultado estuvo afectado por el diseño de muestreo, pero surgiría principalmente de la inestabilidad con que el gremio ocupó los ambientes no perturbados. La distribución espacial del ensamble invernal de aves (mayoritariamente constituido por granívoros) también fue independiente de los gradientes ambientales. La diversidad de especies de aves se correlacionó positiva y significativamente con la complejidad vertical, horizontal y florística del hábitat en temporada de cría; mientras que en invierno dicha correlación no fue significativa. El modelo correlacional basado en la diversidad de aves fue menos efectivo que el enfoque gremial para detectar factores próximos de selección del hábitat, debido a que los índices simples de complejidad ambiental que utiliza dicho modelo covariaron, y a que el significado biológico de la relación entre la diversidad de aves y la complejidad ambiental es confuso.

Abstract. The association of several habitat features with bird guild abundance and bird species diversity was studied, aiming at identifying proximate factors of bird habitat selection. In the breeding season, tree-guilds (herbivores and insectivores) always tracked the first axis of environmental complexity, generated by the cover of those trees and shrubs that would supply them with food and foraging surfaces. The distribution of long-flight insect-hunters over the same axis was bi-modal due to the different hunting modes of their constituent species. Terrestrial-granivores did not follow any environmental gradient, including the ones generated by the cover of those plant species which supply them with seeds and buds. This result was affected by the sampling design used, but it would mainly arise from the instability with which this guild occupied undisturbed sites. The winter bird assemblage (mainly made up of granivores) did not track any environmental gradient either. During the breeding season, there was a positive and significant correlation between bird species diversity and habitat vertical, horizontal and floristic complexity. In winter, no significant correlation was found between these variables. The correlational model based on bird diversity was less efficient to detect proximate factors of habitat selection than the bird guild approach because habitat complexity indices co-varied and the biological meaning of the correlation between bird diversity and habitat complexity was misleading.

Introduction

The use of experiments to determine the effect of habitat complexity on the abundance and distribution of bird species has increased over the past two decades. Some studies involved direct habitat manipulation (Wiens et al. 1986), whereas others took advantage of fortuitous habitat alterations as those caused by fires (Marone 1990a), or herbicides (Beaver 1976). Nevertheless, the detection of patterns of bird habitat occupancy has often been approached by correlational studies (MacArthur 1972, Rotenberry and Wiens 1980, Cody 1981, Wiens and Rotenberry 1981).

Correlational studies are based on two general models. One of them uses habitat structure complexity indices as independent variables and bird species diversity indices as dependent ones. The justification of this model is that habitat structure complexity promotes niche diversification. On this account, niche theory predicts a positive correlation between habitat complexity and species diversity. This approach was apparent from the work of MacArthur and his colleagues (MacArthur and MacArthur 1961, MacArthur et al. 1962), and presents several advantages. It is a simple and intuitive approach, because the independent variables used synthesize a great number of habitat features such as food items, nesting sites, or cover from predators. However, there exists increasing evidence that falsifies the positive correlation between habitat structure complexity and bird species diversity (Roth 1981, Wiens and Rotenberry 1981, Jaksic and Braker 1983, Ralph 1985). Another disadvantage of this approach is that, even when the predicted positive correlation is shown, its biological meaning remains unclear because the model does not identify what habitat feature is selected by each bird species (Cody 1985, Wiens 1983).

An alternative correlational model uses multivariate axes that synthesize the variance of habitat floristic and physiognomic features as independent variables, and bird species or guild densities as dependent ones. The justification of the guild approach is that food and foraging modes are important factors in bird habitat selection. On this account, the species of the same guild would select the same habitat features and, therefore, their habitats would overlap. This model does not assume *a priori* implications about the existence of species interactions (Jaksic 1981, Wiens 1983), and advances in the identification of proximate factors of bird habitat selection. With the ready availability of multivariate statistical packages on computers, the number of studies based on this model has increased (Rotenberry and Wiens 1980, Rice et al. 1983). Nevertheless, comparisons of the results of the two correlational approaches to the same study case have been seldom shown.

The objectives of this paper are (1) to study the influence of several habitat features on the abundance and distribution of bird guilds and on bird species diversity; (2) to compare the suitability of the correlational approaches mentioned above for identifying proximate factors of bird habitat selection.

Materials and Methods

Study Area

The Biosphere Reserve of Ñacuñán (12,282 ha) is located in the province of Mendoza, Argentina (34° 02' S, 67° 58' W), in the Monte Desert (Morello 1958). All economic activities, previously connected with wood cutting and cattle raising, ceased in this area about 20 years ago. The reserve is located in an alluvial plain and comprises an open forest of mesquite (*Prosopis flexuosa*) with high shrub (specially *Larrea* spp.) and grass cover. Its climate is markedly seasonal: winters are cold (mean < 10°C) and dry (mean = 53.9, SD = 32.0 mm), and summers are warm (mean > 20°C) and rainy (mean = 279.0, SD = 77.0 mm). Wide year-to-year precipitation variations are an outstanding feature of Ñacuñán's climate.

Bird counts were made in six sampling sites during winter, spring and summer. Four undisturbed 4-ha sites (80 x 500 m) were established at random inside the reserve (Und1, Und2, Und3, Und4) where bird counts were made from 1985 through 1988. Since the spring of 1986, two 4-ha spatial replicates were established in a zone (naturally?) burnt in February 1986 (Burned site). Finally, during

Table 1. Vegetation features of the six 4-ha sites where bird samplings were carried out. Plant species cover is expressed as the percentage of the total sampling points where the species was present. The habitat vertical, horizontal, and floristic complexity indices are defined in the text.

Tabla 1. Principales características de la vegetación en los seis sitios de 4 ha en los que se llevaron a cabo muestreos de aves. La cobertura de especies vegetales se expresa como el porcentaje del total de puntos de muestreo en los que la especie estuvo presente. Los índices de complejidad vertical, horizontal y florística del hábitat son definidos en el texto.

Vegetation	Und1	Und2	Und3	Und4	Burned	Grazed
Thorny trees and tall thorny shrubs	20.30	15.50	6.60	3.10	0.40	10.90
<i>Prosopis flexuosa</i>	12.10	5.20	4.30	1.00	0.20	6.30
<i>Geoffroea decorticans</i>	6.30	7.20	1.30	1.20	0.10	2.20
<i>Atamisquica emarginata</i>	2.30	3.20	0.70	0.50	0.10	2.10
<i>Condalia microphylla</i>	1.80	1.50	0.90	0.70	0.00	1.50
Non-thorny tall shrubs	26.00	28.20	41.20	43.00	9.90	25.50
<i>Larrea divaricata</i>	25.90	11.20	9.10	4.50	3.50	8.90
<i>Larrea cuneifolia</i>	0.10	16.50	30.80	38.20	6.20	17.90
<i>Atriplex lampa</i>	0.80	0.90	1.70	0.60	0.20	1.50
Low shrubs (< 75 cm)	27.20	15.50	11.40	7.20	1.40	15.10
<i>Lycium spp</i>	12.70	13.00	10.80	7.20	--	--
<i>Verbena aspera</i>	10.30	2.70	1.10	0.50	--	--
<i>Acantholippia seriphoides</i>	7.10	1.50	0.80	0.20	--	--
Grasses	56.80	53.00	61.40	54.50	4.10	25.40
Forbs						
October 1986	5.50	2.10	1.90	3.10	33.00	--
December 1986	3.70	2.70	2.10	1.50	40.70	--
October 1987	2.50	3.40	3.10	2.20	24.40	--
December 1988	1.70	2.20	1.50	2.10	8.80	3.70
Vertical habitat complexity	2.30	2.27	2.13	1.97	1.04	2.34
Horizontal habitat complexity	1.42	1.34	1.17	1.08	0.83	1.50
Floristic habitat complexity	1.56	0.71	-0.23	-0.83	-1.40	0.21

the winter, spring and summer of 1988, bird counts were made in a 4-ha site outside the reserve, which had been grazed during the two previous years (Grazed site). Table 1 shows the cover of plant species and habitat structure indices for all six sites.

Vegetation samplings

Vegetation features were recorded by using a modification of the point quadrat method (Daget and Poissonet 1969). This method consisted in erecting a "stiff wire", marked at intervals 0.25 m high, in a number of randomly selected sampling points, and then counting the leaves it touched (MacArthur and MacArthur 1961). The basic records for each sampling point were the number of contacts of each plant species on the wire, and the height at which contacts occurred. This basic data allowed determination of the cover of plant species as well as the foliage proportion in vertical and horizontal layers.

Table 2. Factor loading of vegetation principal components (direct gradient analysis). Only those values that were significantly correlated ($n = 6$, $P < 0.05$) with any of the first three components are shown.

Tabla 2. Carga de los componentes principales de vegetación (análisis directo de gradiente). Se indican aquellos valores que se correlacionaron significativamente ($n = 6$, $P < 0.05$) con alguno de los tres primeros componentes del análisis.

Factor Vegetation variable	I 63.2%	II 20.2%	III 8.2%
<i>Prosopis flexuosa</i>	0.40	--	--
<i>Geoffroea decorticans</i>	0.37	--	--
<i>Atamisquea marginata</i>	0.36	--	--
<i>Condalia microphylla</i>	0.40	--	--
<i>Larrea divaricata</i>	0.38	--	--
<i>Larrea cuneifolia</i>	--	0.64	--
<i>Atriplex lampa</i>	--	--	0.66
Total cover of low shrubs (<0.75 m)	0.41	--	--
Grasses	--	--	--

In each of the 4-ha sites, 2,000 sampling points were established. They were taken at random over 100 lines 80 m long, located across the strip transect, 10 meters apart from each other (in the Grazed site only 200 points were established). Plant cover was estimated as the proportion of the total sampled points where the species was recorded.

In order to estimate horizontal habitat complexity (HHC), maximum vegetation heights were determined in 400 squares of 10 x 10 m (except for the Grazed site where only 40 squares of identical size were used). This approach rendered a grid that encompassed every 4-ha site completely. Each square was then classified into one of seven height categories: 0 to 0.5 m, 0.5 to 1.0 m, 1.0 to 2.0 m, ..., 5.0 to 6.0 m. The proportions of squares in every category were the p_i in Shannon's diversity formula: $HHC = -\sum p_i \ln p_i$. The same formula was used as an index of vertical habitat complexity (VHC). To this purpose, the foliage proportions in every 0.25 m vertical layer were taken as the p_i in Shannon's formula. This approach discards all possible *a priori* assumptions about the number of vegetation layers present in Ñacuñán (Wiens 1983). Habitat floristic complexity is expressed by the values of the first axis of the vegetation principal component or direct gradient analysis (see below, Statistical Methods). This axis synthesizes 63.2% of the variance of the cover of plants or groups of plants (Table 2).

Bird samplings

Bird samplings were made by using the strip transect method (Burnham et al. 1980). Every transect was run several times on each sampling occasion (average = 8) after dawn for no more than four hours, and during the last three hours of daylight. All individuals observed within the transects were recorded, except for those that flew across them at great height.

The species recorded were assigned to five guilds (Capurro and Bucher 1986, Marone 1990b): (1) terrestrial-granivores; (2) tree-herbivores; (3) insectivores that feed on surfaces (ground, bark or leaves) by gleaning, digging or pecking; (4) insect-hunters using short flights among the foliage; and (5) insect-hunters using long flights (their prey remaining in the air or on the ground) (see Appendix).

Bird species diversity in each sampling site was estimated after Hill (1973): $N2 = (\sum p_i^2)^{-1}$, where p_i is the proportion of the i^{th} species in the sample. Aiming at eliminating year-to-year differences, the diversity values of each year were normalized (divided by the annual mean, calculated for all the sites involved in the analyses).

Statistical Methods

Multivariate statistics is an appropriate tool for quantifying the multidimensional Hutchinsonian niche (Rotenberry and Wiens 1980). Principal component analysis (PCA) reduces the great number of environmental variables the niche is made up of to a smaller, more manageable set of orthogonal variables (components or axes), that still accounts for a large part of the total variation in the environmental data set. Here, PCA was used to synthesize the spatial variation of both vegetation (direct gradient analysis) and bird guilds (indirect gradient analysis).

The direct analysis was based on the cover of seven plant species (*Prosopis flexuosa*, *Geoffroea decorticans*, *Atamisquea emarginata*, *Condalia microphyla*, *Larrea divaricata*, *L. cuneifolia*, and *Atriplex lampa*) and two groups of plant species (low shrubs and grasses). Forbs were discarded on account of the intense year-to-year dynamics they showed in the burned site (Table 1). The indirect gradient analysis, based on bird-guild density changes, involved matrices having the five guilds as rows. In order to eliminate year-to-year differences, density data corresponding to each year were normalized. Throughout the study, the association between variables was analyzed through simple linear correlation (Pearson's Product-moment model).

Results

Bird guild distribution and environmental gradients

The first axis of the vegetation PCA was determined by the cover of thorny trees and tall thorny shrubs, low shrubs and *Larrea divaricata*, and accounted for 63.2% of the environmental variance (Table 2). In spring ($r = 0.89$, 18 d.f., $P < 0.001$) and summer ($r = 0.90$, 18 d.f., $P < 0.001$), this axis was significantly and positively correlated with the first component of bird guilds, generated by the abundance of the three tree-guilds and (negatively) by the abundance of long-flight insect-hunter species (Tables 3 and 4).

The second axis of the vegetation PCA was determined by the cover of *Larrea cuneifolia* (Table 2). During the breeding season, the second component of the analysis of bird guilds was largely determined by long-flight insect-hunters (Table 4). In spring ($r = -0.77$, 18 d.f., $P < 0.001$) and summer ($r = -0.71$, 18 d.f., $P < 0.001$) both axes were significantly but negatively correlated with each other, which made it evident that these birds did not occupy sites with high cover of *Larrea cuneifolia*.

Finally, the density of terrestrial-granivores generated the third component of the indirect gradient analysis in spring and summer (Table 4). This third component was correlated neither with the three main environmental gradients, nor with grass cover (spring: $r = 0.04$, 18 d.f.; summer: $r = 0.18$, 18 d.f.), nor with grass + forb cover (spring: $r = 0.16$, 18 d.f.; summer: $r = 0.24$, 18 d.f.). Although granivores were fewer in the grazed site (Table 3), where grass cover was lower (Table 1), this site had little impact on the overall analysis (1/16 samplings).

In winter, the first axis of the indirect analysis accounted for 99.2% of the variance of guilds, and it was generated by the abundance of terrestrial granivorous species. This axis was not correlated with any of the three principal axes of the vegetation analysis, with grass cover ($r = 0.15$, 17 d.f.), or with grass + forb cover ($r = 0.23$, 17 d.f.).

Bird species diversity and habitat complexity

Table 5 includes the results of the simple correlation analyses between bird species diversity and habitat vertical, horizontal and floristic complexity. The results indicate that variations in bird species diversity are independent of the habitat features in winter, but closely associated with them in spring and summer.

Table 3. Bird guild density (individuals per ha) in the six sampling sites located in the Biosphere Reserve of Ñacuñán (Und1, Und2, Und3, Und4, Burn), and in their surroundings (Gra), in winter, spring and summer from 1985 through 1988. The species consuming plant material from among the foliage (tree-herbivores) during the breeding season feed on seeds on the ground, or next to it, in winter. These data were the basic matrices for the indirect gradient analyses, carried out through PCA. T.G.: terrestrial granivores, S.I.: surface insectivores, S.F.I.H.: short-flight insect-hunters, L.F.I.H.: long-flight insect-hunters, T.H.: tree herbivores.

Tabla 3. Densidad de gremios de aves (individuos por ha) en los seis sitios de muestreo ubicados en la Reserva de la Biosfera de Ñacuñán (Und1, Und2, Und3, Und4, Burn), y en sus proximidades (Gra), en invierno, primavera y verano, desde 1985 a 1988. Las especies que se alimentan del follaje de árboles (tree herbivores) durante la estación reproductiva se alimentan de semillas del suelo durante el invierno. Estos datos formaron las matrices básicas de los análisis indirectos de gradiente calculados mediante PCA. T.G.: granívoros terrestres, S.I.: insectívoros de superficie, S.F.I.H.: cazadores de insectos de vuelo corto, L.F.I.H.: cazadores de insectos de vuelo largo, T.H.: herbívoros arborícolas.

plots	Und1				Und2				Und3				Und4				Burn			Gra
year	85	86	87	88	85	86	87	88	85	86	87	88	85	86	87	88	86	87	88	88
WINTER																				
T.G.	1.2	2.7	3.3	1.4	1.6	2.5	0.9	2.1	5.8	1.7	1.3	1.2	0.7	0.6	0.7	0.1	--	3.8	0.1	0.1
S.I.	0.1	0.1	0.3	0.0	0.1	0.1	0.1	0.1	0.2	0.1	0.2	0.2	0.1	0.0	0.1	0.2	--	0.1	0.0	0.1
S.F.I.H.	0.1	0.1	0.2	0.0	0.0	0.0	0.3	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	--	0.0	0.0	0.1
L.F.I.H.	0.0	0.0	0.1	0.0	0.0	0.0	0.1	0.0	0.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0	--	0.0	0.0	0.0
SPRING																				
T.G.	1.7	1.4	0.7	0.6	1.6	2.9	1.5	1.2	1.7	0.6	1.5	0.4	1.1	1.6	0.4	1.1	2.0	1.8	0.3	0.1
T.H.	2.0	1.5	2.2	2.2	1.4	0.8	1.5	2.2	0.8	0.6	1.1	0.9	0.5	0.3	1.0	1.1	0.1	0.1	0.0	1.5
S.I.	2.1	1.4	1.9	1.4	1.5	1.9	1.2	1.4	0.7	0.6	0.6	0.6	0.1	0.3	0.4	0.4	0.2	0.2	0.6	1.0
S.F.I.H.	1.1	1.2	1.0	1.4	1.7	0.7	1.1	1.1	0.3	0.4	0.5	0.6	0.1	0.0	0.3	0.2	0.0	0.0	0.0	1.2
L.F.I.H.	0.1	0.1	0.0	0.1	0.1	0.1	0.1	0.1	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.1	0.1	0.1	0.7	0.4
SUMMER																				
T.G.	2.3	2.0	2.7	0.2	3.6	2.9	2.8	0.3	1.0	0.5	2.2	0.8	3.5	3.0	2.4	0.6	3.2	0.5	0.5	0.5
T.H.	1.7	1.6	2.2	2.1	0.9	1.7	1.6	0.8	1.3	0.7	1.1	0.6	0.4	0.7	1.0	0.5	0.0	0.0	0.0	0.8
S.I.	1.5	2.0	2.8	1.9	2.6	1.8	2.0	1.9	1.2	0.8	0.8	1.4	0.5	0.8	0.5	0.5	0.5	0.2	0.1	1.2
S.F.I.H.	1.2	1.2	1.5	1.3	0.6	0.6	0.7	0.6	0.9	0.5	0.4	0.7	0.1	0.1	0.1	0.1	0.0	0.0	0.0	1.3
L.F.I.H.	0.6	0.1	0.1	0.6	0.3	0.1	0.2	0.4	0.1	0.1	0.0	0.4	0.1	0.2	0.0	0.1	0.7	0.9	0.9	0.6

Discussion

Bird guild distribution and environmental gradients

During the breeding season tree-herbivores, surface-insectivores, and short-flight insect-hunters (i.e., tree-guilds) tracked the cover of trees and shrubs such as *Prosopis*, *Geoffroea*, *Atamisquea*, *Condalia* and *Lycium*. More than 80% of birds belonging to these guilds were recorded on those plant species, where they look for food (Marone *pers. obs.*). On the other hand, the positive correlation found between density of these guilds and the cover of *Larrea divaricata* would be a misleading result. Orians et al. (1977) hold that the diet of a great variety of herbivorous arthropods, and of their predatory birds, depends on shrubs of *Larrea* in Andalgalá. In Ñacuñán these shrubs were observed to be scarcely used by birds for foraging, perching or nesting activities, which is in accordance with the findings of Anderson and Anderson (1946), Rait and Maze (1968), Austin (1970), and Rait and Pimm (1976), who indicated a very low use of *Larrea divaricata* by birds in North American deserts. The different role of *Larrea* in Andalgalá and Ñacuñán may be a consequence of the greater structural and floristic complexity of Ñacuñán.

Long-flight insect-hunters preferred zones which, for different reasons, showed low cover of *Larrea cuneifolia* (Tables 1 and 3). This guild was more abundant in structurally complex sites (e.g., Und1) and in disturbed sites (Burned and Grazed). This peculiar environmental distribution of the guild responded to the fact that its species did not show the same habitat requirements, probably due to their different hunting modes. *Xolmis coronata*, *Tyrannus savanna* and *Myiarchus tyrannulus* usually hunt for arthropods on the ground or next to it. They preferred open habitats and were more

Table 4. Factor loading of the principal component analysis of bird guilds (indirect gradient analysis). Only those values that were significantly correlated ($n = 20$ in spring and summer and $n = 19$ in winter; $P < 0.05$) with any of the first three components of the analysis are shown.

Tabla 4. Carga del análisis de componentes principales de gremios de aves (análisis indirecto de gradiente). Sólo se muestran los valores que se correlacionaron significativamente ($n = 20$ en primavera y verano, $n = 19$ en invierno; $P < 0.05$) con alguno de los tres primeros componentes del análisis.

Factor	I			II			III		
	win	spr	sum	win	spr	sum	win	spr	sum
Percent	99.2	54.0	56.5	--	32.6	29.7	--	9.5	8.5
Bird guilds									
terrestrial granivores	1.00	--	--	--	--	-0.23	--	0.99	0.83
tree herbivores	--	0.48	0.52	--	--	--	--	--	--
surface insectivores	--	0.42	0.45	--	0.34	--	--	--	--
short-flight insectivores	--	0.54	0.61	--	0.38	--	--	--	--
long-flight insectivores	--	-0.54	-0.39	--	0.83	0.87	--	--	--

Table 5. Correlation analyses between bird species diversity and habitat vertical (VHC), horizontal (HHC) and floristic (EI) complexity in winter ($n = 19$), spring ($n = 20$) and summer ($n = 20$). The correlation coefficient is indicated only when $P < 0.05$.

Tabla 5. Análisis de correlación entre la diversidad de especies de aves y la complejidad vertical (VHC), horizontal (HHC) y florística (EI) del hábitat en invierno ($n = 19$), primavera ($n = 20$) y verano ($n = 20$). Se indica el coeficiente de correlación sólo cuando $P < 0.05$.

	VHC	HHC	EI
Winter	--	--	--
Spring	0.54 *	0.66 **	0.79 ***
Summer	0.48 *	0.64 **	0.59 **

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

abundant in the Burned site. *Tyrannus melancholicus* dominated in the Grazed site, and *Epidonotus aurantioatrocristatus* showed a more even distribution throughout the environment (Marone 1990b). The last two species hunt insects mainly in the air, sallying from tall trees, as those present in the Grazed and undisturbed sites.

The spatial distribution of terrestrial-granivores did not appear to be influenced by the environmental gradients derived from PCA or by grass and forb cover. Nevertheless, the samplings made in the Grazed site indicated that granivorous birds abandoned areas where they were subjected to stress caused by food reduction (Table 3). Besides, it has been proposed that the decrease in forb cover from September 1987 in the Burned site provoked the dive of granivore density in 1988 in this area (Marone 1990a, see Tables 1 and 3). The lower impact of the Grazed site on the overall study would obscure the correlation between granivore density and grass and forb cover. Nevertheless, the most important fact that obscured that correlation was the instability with which granivorous birds occupied the undisturbed sites. Those sites which one year were clearly preferred by granivores may not be as attractive the following year and viceversa (Table 3, contrast with the relative greater stability that tree-guilds showed in site occupation). The four undisturbed sites have a compact and homogeneous grass cover (Table 1), therefore they may be assumed as equally preferred by

granivores. Year-to-year modifications in granivore occupation of these sites would then be due to intra-habitat migrations within an unsaturated environment (Marone *in press*). Preferences for some site, if any, would be the consequence of behavioral (e.g., site tenacity) or random factors.

These results concur with what happened in winter. Only terrestrial-granivores were abundant in this season, and they broadly determined the first component of the indirect gradient analysis (Table 4). This axis did not follow any environmental gradient, as the third indirect axis did in spring and summer, confirming the independence of granivore distribution from any vegetational gradient.

Bird species diversity and habitat complexity

The breeding season data confirmed the positive association between habitat complexity and bird species diversity predicted by niche theory. However, nothing definite can be said about the differential predictive value of every vegetational variable used as niche axis, because their estimates co-varied over the habitat as they would usually do in nature (Roth 1976, but see Rotenberry and Wiens 1980) (Table 5). For this reason, observational approaches would be inefficient to identify the kind of habitat complexity that affects bird species diversity. Furthermore, even though the identification of the precise kind of habitat complexity was possible, the biological meaning of its correlation with bird species diversity would not be immediately apparent (e.g., the spatial co-variation of two or more bird species may arise when every species selects different habitat features which, in turn, co-vary over the environment) (Cody 1985, Wiens 1983).

In winter, bird species diversity did not correlate significantly with any measure of habitat complexity. As indicated above, the winter bird assemblage is mainly made up of terrestrial-granivores, which spread over the habitat without tracking the environmental gradients. As a result, correlating the diversity of this assemblage with environmental gradients will be most unlikely.

Conclusions

Both correlational models concurred in pointing out that the spatial distribution of wintering birds was independent of the various habitat features considered. I suggest that this pattern arose from the fact that terrestrial-granivores, which never tracked environmental gradients in Nacuñán, highly prevailed in winter samplings.

In the breeding season, the two approaches suggested that both bird species diversity and bird guilds (except for terrestrial-granivores) tracked environmental gradients. The analyses based on multivariate axes that synthesize habitat complexity seem to be more efficient for identifying proximate factors of habitat selection than those based on bird species diversity, because of the co-variation of environmental indices and the difficulties in interpreting the biological meaning of the relationship between these indices and bird diversity.

The guild approach may be a useful tool for studying bird-habitat relationships. In Nacuñán, several guilds responded as a whole to various habitat features: tree-herbivores, surface-insectivores and short-flight insect-hunters tracked the cover of trees and shrubs. On the other hand, long-flight insect-hunters did not track the cover of trees and shrubs because the guild involved several species that hunt in open habitats. Terrestrial-granivores did not track any environmental gradient, casting doubt upon the capability of correlational approaches for identifying bird-habitat relationships when birds do not saturate the habitat (i.e., when the available patches are not totally occupied by the birds that select them).

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Appendix. Specific composition of each bird guild. Species cited have been observed at least on one occasion in one of the sampling sites. Scientific names are after Olrog (1978).

Apéndice. Composición específica de cada gremio de aves. Las especies citadas han sido observadas por lo menos en una ocasión en alguno de los sitios de muestreo. La nomenclatura científica usada sigue a Olrog (1978).

Terrestrial-granivores: *Eudromia elegans*, *Columba livia*, *Columba maculosa*, *Zenaida auriculata*, *Sicalis luteola*, *Diuca diuca*, *Phrygilus carbonarius*, *Junco capensis*, *Poospiza ornata*, *Carduelis magellanica*.

Tree-herbivores: *Cyanoliseus patagonus*, *Myiopsitta monacha*, *Phytotoma rutila*, *Saltator aurantirostris*, *Poospiza torquata*, *Saltatricula multicolor*.

Surface-insectivores: *Rhinocrypta lanceolata*, *Mimus triurus*, *Sturnella supercilialis*, *Pseudoseisura lophotes*, *Coccyzus cinereus*, *Colaptes melanolaemus*, *Drymornis bridgesii*, *Lepidocolaptes angustirostris*, *Upucerthia certhioides*, *Leptasthenura aegithaloides*, *Synallaxis albescens*, *Certhiax pyrrhophia*, *Tripophaga* spp., *Troglodytes aedon*.

Short-flight insect-hunters: *Anairetes flavirostris*, *Stigmatura budytoides*, *Serpophaga munda*, *Elaenia albiceps*

Long-flight insect-hunters: *Epidonomus aurantioatrocristatus*, *Pyrocephalus rubinus*, *Myarchus tyrannulus*, *Tyrannus melanocephalicus*, *Tyrannus savana*, *Xolmis coronata*.

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