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Patterns of habitat selection by wintering and breeding granivorous birds in the central Monte desert, Argentina

Patrones de selección del hábitat por aves granívoras en invierno y primavera en el Monte central, Argentina

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ABSTRACT

We report on 6-yr patterns of habitat occupancy by wintering- and breeding-granivorous birds over two habitats in the central Monte desert, Argentina: an open forest and a shrubland, both with abundant grass cover. We examine the hypothesis that the pattern of habitat occupancy changes seasonally in a way that is consistent with the distinct habitat requirements of wintering (i.e., mostly food) and breeding birds (i.e., food but also nesting sites). The seasonal change was widely corroborated for the whole guild, which did not distinguish between habitats in winter but was significantly more abundant in the open forest in spring. Similar changes were apparent for several individual species as well. Seed availability during 1993 and 1994, measured over two mesohabitats, usually did not differ between open forest and shrubland; whereas nest-site availability (i.e., trees and tall thorny shrubs) was quite greater in the open forest. This evidence suggests that the seasonal modification of habitat occupancy here reported may reflect changes in the *template* of what constitutes a suitable habitat for wintering- and breeding-granivorous birds inhabiting the Monte desert.

Key words: granivorous-bird abundance, habitat requisite, seed bank, nesting-site.

RESUMEN

Discutimos el patrón de ocupación del hábitat por aves granívoras en invierno y primavera en dos tipos de hábitat del desierto del Monte central, Argentina: bosque abierto y arbustal, ambos con importante cobertura de pastos. Examinamos la hipótesis que la selección del hábitat cambia estacionalmente, y que ese cambio es consistente con los diferentes requerimientos de hábitat de las aves en invierno (i.e., principalmente alimento) y primavera (i.e., alimento pero también sitios para nidificar). Corroboramos el cambio estacional a nivel gremial y, aparentemente, también a nivel de varias especies individuales. El gremio granívoro no distinguió entre hábitats en invierno, pero en primavera fue significativamente más abundante en el bosque abierto. La disponibilidad de semillas para las aves en 1993 y 1994, medida sobre dos mesohábitats distintos, fue generalmente similar en el bosque abierto y arbustal; pero la disponibilidad de sitios para nidificar (i.e., árboles y arbustos altos espinosos) fue muy superior en el bosque abierto. Esos datos sugieren que la modificación estacional de la ocupación del hábitat puede reflejar cambios en el template de lo que constituye un hábitat apropiado en invierno y en temporada de cría para las aves granívoras que habitan el desierto del Monte.

Palabras clave: abundancia de aves granívoras, requisito de hábitat, banco de semillas, sitio de nidificación.

INTRODUCTION

Patterns of avian habitat selection have generated numerous interesting questions in behavioral and community ecology (Cody 1985, Block & Brennan 1993), and the assessment of avian habitat relationships has become an important part of wildlife and resource management (Verner et al. 1986). Birds may be viewed as possessing an internal image or template of what constitutes a suitable habitat, based on such environmental variables as food, foraging or nesting sites, and presence of other species

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(Wiens 1989). Determining the relative importance of such requisites to habitat selection is crucial to the goal of increasing the predictive capacity of ecological theory.

Hutto (1985) suggested that food acquisition must figure prominently in decisions on the use of space by wintering birds, since getting food to store fat or merely survive is likely to be the single most important factor affecting habitat selection of nonbreeding birds. In desert landscapes, the abundance of wintering granivorous birds may be limited by seed availability (Schluter & Repasky 1991); consequently, those birds may be strongly influenced by the distribution of seed-producing plants (Block & Brennan 1993). Nevertheless, when other habitat requirements are incorporated into the template, birds must "trade off" food against other services of the habitat, and food alone may be insufficient for predicting bird distributions. For example, breeding birds must select habitats having appropriate sites for nesting; if the availability of such sites does not covary positively with food distribution, breeding birds may not track food availability in a clear-cut fashion.

The pattern of habitat use by granivorous birds in the Monte desert of Argentina has seldom been examined. Moreover, at present we do not know whether this pattern changes for wintering and breeding assemblages. Marone (1990a) reported species-specific responses of granivorous birds to habitat modifications during the early post-fire succession of a *Larrea* shrubland. In a regional analysis, however, such birds did not respond markedly to any of the several environmental gradients examined, not even to variation in the cover of grasses whose seeds the birds presumably consume (Marone 1990b, 1991). This pattern, however, may have resulted from the unbalanced sampling design and the inconsistency with which the granivorous guild occupied undisturbed habitats (Marone 1991). Therefore the assessment of the pattern of habitat selection by those birds deserves more thorough study.

Here we assess granivorous-bird abundance in winter and spring during a 6-yr period over two contrasting habitats: an open forest of *Prosopis flexuosa* De Candolle 1822, and a shrubland of *Larrea cuneifolia* Cavanilles 1801, which notably differ in the total supply of appropriate nesting sites (i.e, the cover of trees and tall thorny shrubs, see Marone 1990b). We examine the hypothesis that the pattern of habitat selection changes seasonally probably as a consequence of the distinct habitat requirements of wintering- (i.e., mostly seeds) and breeding-bird assemblages (seeds but also nesting sites). In so doing, we measure seed availability to birds in the patchy landscape of the central Monte desert, Argentina.

METHODS

Study sites and bird sampling

The open forest of *Prosopis flexuosa*, and the shrubland of *Larrea cuneifolia*, both with extensive grass cover (see Table 1), are located in the Biosphere Reserve of Ñacuñán (Mendoza, Argentina). Descriptions of the flora and general habitat of the reserve may be found in Roig (1981) and Marone (1991).

TABLE 1

Average cover of several plant strata and of bare ground in the open forest and shrubland, expressed as the percentage of soil occupied by each stratum. Total sum surpasses 100% because different strata partially overlapped. Percentages were recalculated from Table 1 of Marone (1991), and were obtained by using a modification of the point quadrat method (n=4,000 points in each habitat).

Cobertura promedio de varios estratos de vegetación y de suelo desnudo en el bosque abierto y arbustal, expresada como el porcentaje de suelo ocupado por cada estrato. Las sumas exceden 100% porque los estratos se superponen entre sí. Estos porcentajes fueron recalculados a partir de la Tabla 1 en Marone (1991), y obtenidos mediante una modificación del método de "point quadrat" (n=4000 puntos en cada hábitat).

Stratum	Open forest	Shrubland
Trees and tall thorny shrubs	17.9	4.8
Nonthorny tall shrubs	27.1	42.1
Low shrubs	21.4	9.3
Grasses	54.9	57.9
Bare ground	20.2	9.4

We counted birds on several-belt transects (Bibby et al. 1993) in the winter (July or August) and spring (October or November) of 1985-1988 and 1993-1994. Four (1985-1988) or three (1993-1994) 200-m long transects were established in both habitat types. Each transect was run several times in each winter or spring during successive days, after sunrise for no more than 4 h. All runs on every transect were averaged to obtain the mean-bird density per transect on each sampling occasion. Such mean was used as a replication (i.e., a datum) for statistical purposes. Bird counts for 1985-1988 were recalculated from Marone (1990b).

Granivorous bird species recorded in our transects were: *Phrygilus carbonarius* (D'orbigny & Lafresnaye 1837), *Zonotrichia capensis* (Latham 1790), *Diuca diuca* (Molina 1782), *Saltatricula multicolor* (Burmeister 1860), *Poospiza torquata* (Todd 1922) (a notably granivorous species only in autumn-winter), and *Poospiza ornata* (Leybold 1863) (a spring-summer dweller in the central Monte desert). All these species were assigned to a granivorous guild in an a posteriori fashion (Jaksic 1981), according to the results of detailed quantitative analyses of stomach contents and foraging behavior made simultaneously with this study (J. Lopez de Casenave, L. Marone & V.R. Cueto, unpublished data).

Differences in the abundance of the entire granivorous guild between the open forest and the shrubland were analyzed through two-factor (habitat x year) ANOVA with proportional replication, separately for wintering and breeding assemblages (Zar 1984; violation of ANOVA assumptions were severe when a three-factor trial was applied). Raw data were log-transformed. After the ANOVAs, statistical comparisons of bird densities at the species level between habitats would lead to the problem of simultaneous inference (Rice 1989, Beal & Khamis 1991). Given the small sample size, adjusting alpha levels (see Rice 1989) weakened the statistical power so much that it was virtually impossible to reject any null hypothesis for single-species comparisons. Thus, we present only mean values and their standard errors.

Estimating seed abundance

We surveyed soil seed banks in the winter and spring of 1993 and 1994 over three 2-ha plots (200 x 100 m) in both the open forest and the shrubland. Roughly one third of the sampling effort was allocated to each plot, using a stratified random design (Marone & Horno in press). The sampling encompassed two different mesohabitats: under the canopy of trees and shrubs (hereafter: UC mesohabitat), and in exposed areas between them (hereafter: EX mesohabitat).

We used a cylindrical sampler, 3.2 cm in diameter and 2 cm deep. The cylinder was pushed into the soil, and then a metal scoop was pushed carefully just under the bottom edge of the cylinder to isolate the soil within. Sampler contents were placed in 250-ml plastic vials, air-dried for at least 7 d in the laboratory, and then sifted through a sieve (0.27 mm mesh). The finer fraction was discarded (trial inspections showed that none of the discards contained seeds), and the coarser fraction was washed on the same sieve under water pressure for 8-12 min. The residue on the mesh was dried, and then searched for seeds under a stereoscopic microscope. Seed scans under the microscope were repeated twice by different observers. Numbers of apparently viable seeds (those that did not crumble when probed with forceps) were recorded and identified using a reference collection. The residue was treated with gibberelic acid (20 mg/l), then placed in a growth chamber (14 h light at 30°C; 10 h darkness at 15°C), and seedlings were recorded during the next 15 d. We estimated total seed mass by multiplying each species' abundance by its mean per-seed mass, obtained from husked seeds (i.e., without any investing structures).

More than 80% of the seed mass consumed by birds in 1993 and 1994 was from grasses (almost 90 stomach contents analyzed, J. Lopez de Casenave, L. Marone & V.R. Cueto unpublished data). Some bird species like *D. diuca* or *P. torquata* appeared to forage almost exclusively on grass seeds, whereas such seeds represented 70% to 90% of the diet of *S. multicolor*, *P. carbonarius*, and *P. ornata*. Only one species

(*Z. capensis*) seemed to forage systematically on forb seeds, though it also consumed a great proportion of grass seeds. Therefore, to identify differences in food availability from the birds' point of view, we analyzed changes in grass-seed mass between habitats using the nonparametric Mann-Whitney Rank Sum Test (Zar 1984).

RESULTS

Total density of the wintering granivorous guild did not differ significantly between open forest and shrubland (Table 2). Furthermore, except for *P. torquata* and *Z. capensis* that seemed to prefer the open forest in 1988 and 1994 respectively, wintering granivorous species did not appear to show any preference between both habitats (Fig. 1). In the breeding season, instead, the open forest supported higher guild density than the shrubland (Table 2). Moreover, out of five breeding species *D. diuca, S. multicolor,* and *P. ornata* appeared to concentrate on the open forest in several of the springs analyzed (Fig. 2). On the other hand, *Z. capensis* might have prevailed in the shrubland in 1993; and *P. carbonarius* would not have shown habitat preferences at all (Fig. 2).

In winter as well as spring, grass seed mass in the UC mesohabitat was quite similar in the open forest and shrubland during 1993 and 1994 (Fig. 3, left side). In the EX mesohabitat, on the other hand, grass seed mass was also similar in both habitats in 1993, but it was higher in the shrubland during 1994 (Fig. 3, right side). In sum, grass seed mass was similar in the open forest and shrubland (or prevailed in the shrubland) during the study period.

DISCUSSION

Our analyses of habitat use suggest that the spatial pattern of granivorous birds changes between winter and spring in the central Monte desert. While wintering birds see-

TABLE 2

(a) Mean abundance (±SE) of the wintering and breeding bird-granivorous guild in two habitats of the central Monte desert during a 6-yr study. The number of replicates (the same for all habitat-season combinations within a given year) is shown in parentheses. (b) Two-way analyses of variance (habitat x year) made separately for wintering and breeding birds.

(a) Densidad media (±EE) del gremio de aves granívoras en invierno y primavera, en dos hábitats del Monte central durante 6 años. El número de réplicas, que permaneció constante cada año en todos los hábitats y estaciones, se indica entre paréntesis. (b) Análisis bifactoriales de la varianza (hábitat x año), realizados separadamente para invierno y primavera.

(a)

	Granivorous-bird abundance (individuals/ha)			
	Winter		Spring	
year	Open Forest	Shrubland	Open Forest	Shrubland
1985	0.97±0.56 (4)	3.75±3.48	2.46±0.43	2.27±0.60
1986	3.93±1.46 (4)	2.52±1.47	3.66±0.65	2.10±0.51
1987	3.94±1.97 (4)	2.67±1.34	1.46±0.20	1.46±0.70
1988	2.65±0.91 (4)	0.78±0.22	1.18±0.34	0.75±0.17
1993	1.64±1.18 (3)	0.58±0.22	3.09±0.78	1.10±0.24
1994	1.81±1.01 (3)	2.12±2.12	0.39±0.11	0.32±0.16
total	2.49±1.24 (6)	2.07±1.21	2.04±1.24	1.33±0.76

(b)

	Winter				Spring			
Effects	df	Mean square	F	P	df	Mean square	F	P
Habitat	1	0.978	1.59	0.22	1	0.766	8.51	0.006
Year	5	0.540	0.88	0.51	5	0.898	9.97	0.000
Interaction	5	0.239	0.39	0.85	5	0.093	1.04	0.410
Error	32	0.620			32	0.090		

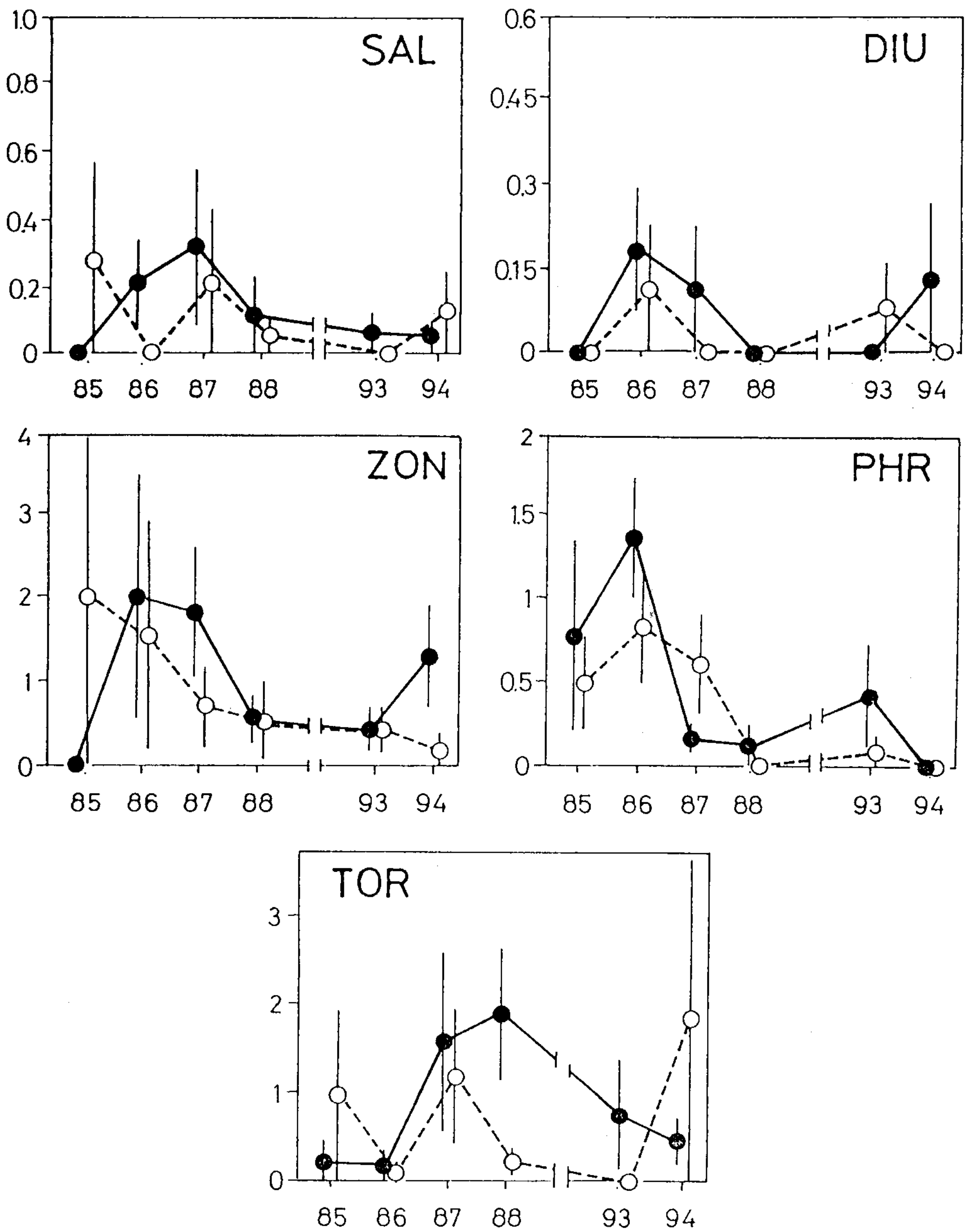

Fig. 1: Winter abundance (ind/ha) of five granivorous bird species in the open forest (closed circles) and shrubland (open circles) during a 6-yr study in the central Monte desert. Means (±1SE) are indicated. Sample sizes as in Table 2. Bird-species acronyms, SAL: *Saltatricula multicolor*, PHR: *Phrygilus carbonarius*, ZON: *Zonotrichia capensis*, DIU: *Diuca diuca*, TOR: *Poospiza torquata*.

Abundancia invernal (ind/ha) de cinco especies de aves granívoras en el bosque abierto (círculos negros) y el arbustal (círculos blancos) durante 6 años en la porción central del desierto del Monte. Se muestra la media (±1EE). Los tamaños muestrales son los indicados en la Tabla 2. Los códigos de las especies son, SAL: *Saltatricula multicolor*, PHR: *Phrygilus carbonarius*, ZON: *Zonotrichia capensis*, DIU: *Diuca diuca*, TOR: *Poospiza torquata*.

med not to discriminate between open forest and shrubland, the entire guild and three of five individual species appeared to prefer the open forest while breeding (Table 2). We conjecture that such change may be brought about by the modification of the *template* of wintering and breeding birds (Hutto 1985).

For assessing the probable cause of the seasonal shift in bird habitat occupancy we

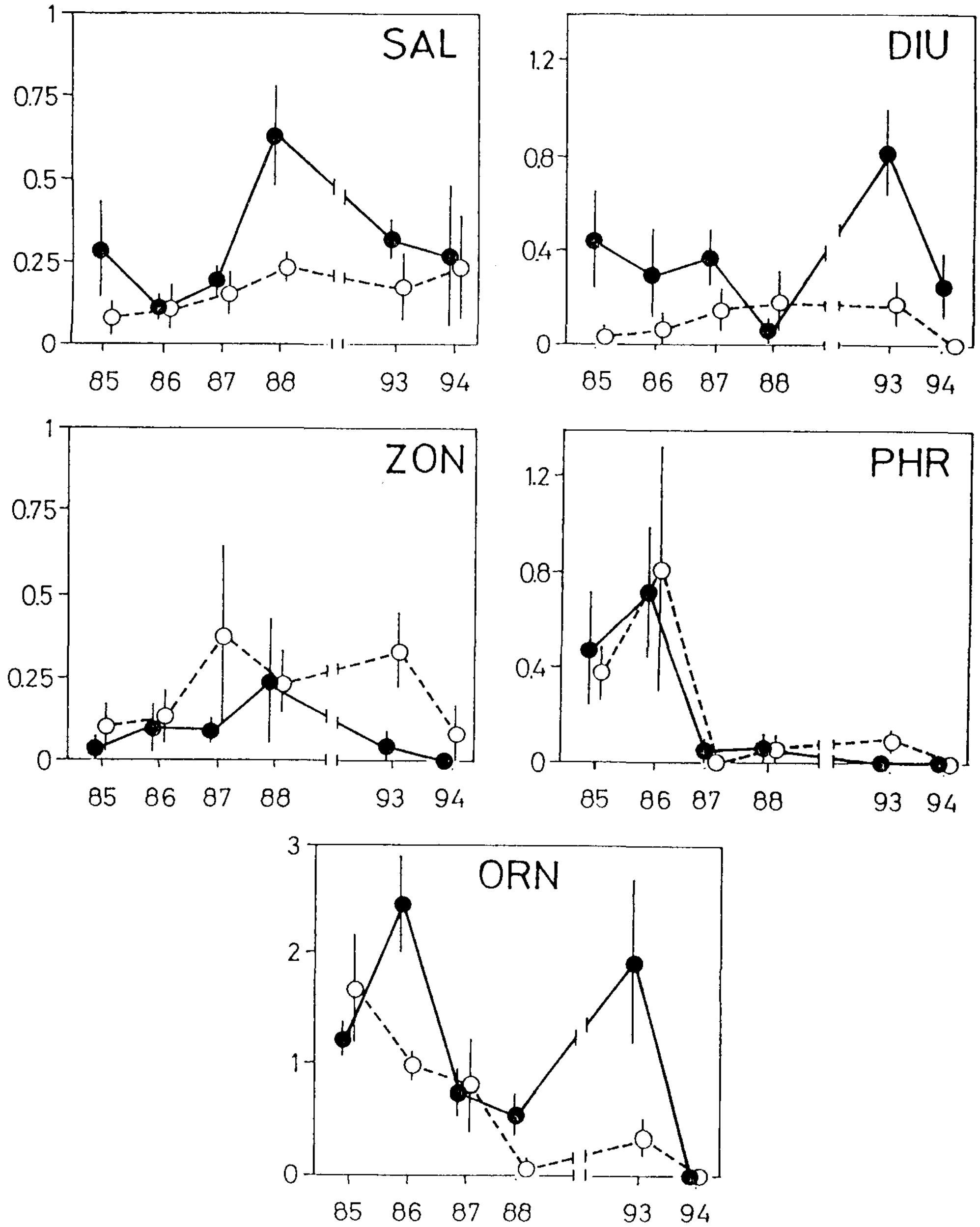

Fig. 2: Spring abundance (ind/ha) of five granivorous bird species in the open forest (closed circles) and shrubland (open circles) during a 6-yr study. Means (±1SE) are indicated (sample sizes as in Table 2). Bird-species acronyms as in Fig. 1, except for ORN: *Poospiza ornata*.

Abundancia primaveral (ind/ha) de cinco especies de aves granívoras en el bosque abierto (círculos negros) y el arbustal (círculos blancos) durante los 6 años analizados. Se muestra la media (±1EE). Los tamaños muestrales son los indicados en la Tabla 2. Los códigos de las especies son los mismos de la Fig. 1, excepto ORN: *Poospiza ornata*.

compared seed availability in the open forest and shrubland in 1993 and 1994. In so doing, we assume that the pattern of grass-seed distribution in such years is representative of the entire study period. We think this is a parsimonious assumption because grass cover remained the same in the open forest as in the shrubland, or changed following a similar trend during the study (L. Marone, personal observations).

The distribution of wintering granivorous birds in the open forest and shrubland was mostly consistent with the hypothesis that habitat selection in the winter is prima-

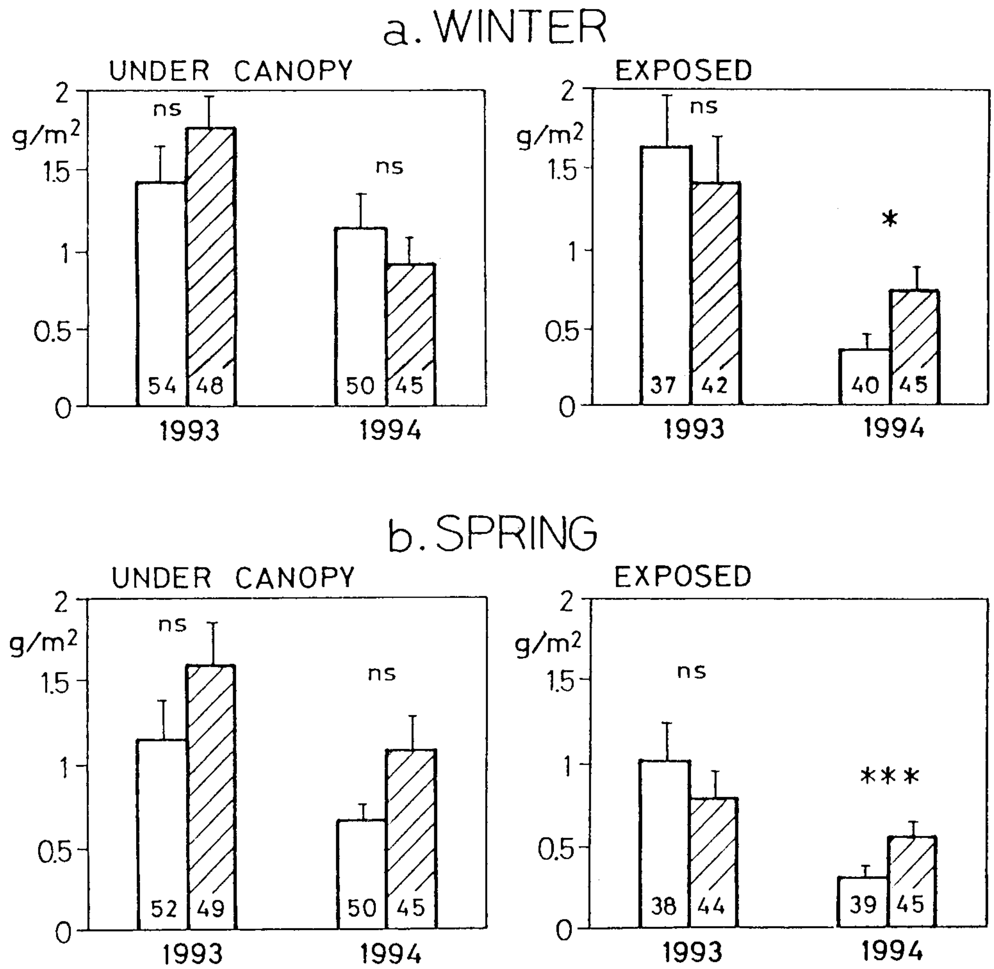

Fig. 3: Mean grass seed mass (±1SE) in winter (a) and spring samplings (b), in the open forest (open bars) and shrubland (hatched bars). Data for 1993 and 1994 over two mesohabitats: under the canopy of trees and shrubs and in exposed areas. Sample sizes are indicated for each bar. ns: not significant, * P<0.05, *** P<0.001.

Masa promedio de semillas de gramíneas (±1EE) en muestreos de invierno (a) y primavera (b), en el bosque abierto (barras blancas) y el arbustal (barras achuradas). Se indican los valores para 1993 y 1994 en 2 mesohábitats: bajo el canopeo de árboles y arbustos, y en zonas expuestas. Los tamaños muestrales se indican en cada barra. ns: no significativo, * P<0.05, *** P<0.001.

rily influenced by food, i.e. both habitats supported similar seed availability (Fig.3) and wintering bird densities (Table 2 and Fig. 1) in spite of their differences in plant structure (Table 1). On the contrary, the spatial pattern of breeding granivorous birds is not in agreement with the hypothesis: these birds usually preferred the open forest (Table 2 and Fig. 2) in spite of the similar seed availability in both habitats, or even the higher grass seed mass in the shrubland (Fig. 3).

This last pattern may be associated with habitat differences related to reproductive resources (e.g., nesting sites). At present, some evidence supports this idea. Over an 8-ha area of open forest and shrubland, Marone (1990b) found 84 nests of many bird species, including some sparrows. All nests occurred on thorny trees and tall-thorny shrubs, whose cover is more than 3 times greater in open forest than in shrubland (Table 1). Likewise, in central Chile Lazo & Anabalón (1991) found nests of *D. diuca* on trees with high leaf density and no thorns or, alternatively, on shrubs with thorns and low leaf density. These authors suggested that such nest placement lowers predation risk: either crypsis or thorns are likely to decrease predators' efficiency (cf. Lima 1990). In the central Monte desert there are no trees with high leaf density and, as in other American deserts, birds avoid nesting on the nonthorny *Larrea* shrubs (Anderson & Anderson 1946, Austin 1970). The slender upright branches of *Larrea* provide few suitable forks to support nests, and the lack of thorns that might discourage predators seems to make these shrubs undesirable for nesting. As *Larrea* shrubs prevailed over other shrubs in the shrubland (Table 1), we may also infer that this habitat is avoided by some breeding sparrow species looking for suitable nest sites.

Our results also suggest that *Z. capensis* and *P. carbonarius*, which often did not discriminate between habitats in spring (Fig. 2) may differ from the other granivorous bird species in their habitat requirements for breeding. *Zonotrichia capensis* often nests on the ground, or next to it, in zones with high herbaceous cover (Mason 1985, Canevari et al. 1991, Lazo & Anabalón 1992), whereas *P. carbonarius* also builds nests near the ground, in grassy areas (Pereyra 1937). Actually, such microhabitats are readily available both in the open forest and shrubland. On the other hand, we cannot discard the possibility that the spatial pattern of all these birds arises from interspecific interactions, since both interference or exploitation competition could account for contrasting patterns of habitat selection (Repasky & Schluter 1994).

Marone (1992) suggested that breeding, but not wintering granivorous-bird densities may be limited by seed availability during exceptionally dry periods in the central Monte desert. The springs of 1988 and 1994 appeared to be periods of seed shortage (L. Marone, J. Lopez de Casenave & V.R. Cueto, unpublished data). Therefore, it is difficult to account for the relative independence of habitat selection from seed availability during the breeding season: birds appear to neglect the spatial tracking of seeds when the likelihood of seed limitation is maximum. This fact strengthens the hypothesis that the fulfillment of reproductive requisites such as nesting site influence the pattern of habitat selection of granivorous birds.

In conclusion, we suggest that the patterns of habitat occupancy by wintering and breeding granivorous birds in the open forest and shrubland suffer major changes in the central Monte desert, and that the alteration of the *template* of what constitutes a suitable habitat for wintering (i.e., mainly food) and breeding birds (i.e., food and nesting sites) might account for such changes. A last but important point is that bird species did not respond as a whole to habitat differences. Instead, some of them showed species-specific habitat affinities, mainly while breeding (see for example the contrasting patterns of *Z. capensis* and *D.diuca*). Therefore, any monitoring program involving granivorous birds should include as many species as possible (George et al. 1992) because one or a few "indicator" species are not likely to provide reliable information on the status of the whole bird guild.

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