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Nest site selection and nesting success of five species of passerines in a South American open *Prosopis* woodland

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Abstract I analyzed nest site preferences and whether these preferences were linked to nest success of five bird species breeding in an arid area of southern South America. Most nests (90%) were located in three plant species (*Geoffroea decorticans*, *Capparis atamisquea*, and *Atriplex lampa*). *Serpophaga griseiceps*, *Poospiza ornata*, and *P. torquata* nested in plants with size significantly different from randomly selected plants. At the mesohabitat scale (i.e., habitat patch surrounding the nest), four species showed clear differences from random patches within the general habitat, and the remaining species (*Saltatricula multicolor*) showed a non-significant trend. The daily survival rate of *S. griseiceps* nests placed in the preferred plant species (i.e., *G. decorticans*) was lower than those in the other nest-plants. In the other four bird species, nest survival did not differ between preferred and other plants used for nesting. At the scale of microhabitat (i.e., plant size and location of the nest inside the plant), no significant differences were detected between unsuccessful and successful nests. Similarly, unsuccessful nest patches did not differ significantly in habitat features from those that were successful. High nest predation rates found in this habitat (around 85% for the total assemblage) and a relatively high diversity of predators (and of predation tactics) appear to impede the presence of “safe” sites for nesting (i.e., there are trade-offs between avoidance strategies).

Keywords Argentina · Arid areas · Habitat selection · Monte Desert · Nest predation

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Introduction

Birds are not distributed at random among habitats (Hildén 1965). Within habitats, ecologically important substrates used by birds (e.g., vegetation) usually exist as patches. Bird species presumably perceive differences between patches and preferentially use some habitat localities (Martin 1998; Rotenberry and Wiens 1998). Regarding nest site selection, many studies have found differences between the habitat used for nesting and the available nesting habitat (Holway 1991; Nolte and Fulbright 1996; Braden 1999; Misenhelter and Rotenberry 2000). Currently, it is assumed that these patterns of habitat use are the result of the process of natural selection acting on a long-term scale (Martin 1998; Clark and Shutler 1999), because nest site selection may have a direct influence on individual fitness.

Most studies of nest site selection have assessed whether there are differences between the general habitat and the portion of the habitat used for nesting, and whether habitat characteristics of successful and unsuccessful nest sites differ (Kelly 1993; Norment 1993; Kilgo et al. 1996; Hoover and Brittingham 1998). This approach may show that some patterns might have emerged over evolutionary time due to the process of natural selection and that this process may be acting on the short-term scale (Clark and Shutler 1999). Nevertheless, to strengthen the evidence supporting the action of the process of natural selection in shaping nest site preferences it is also necessary to show that some measure of fitness is higher in preferred nest sites (i.e., that there is an adaptive response) (Martin 1998; Clark and Shutler 1999; Rotenberry and Knick 1999). However, this prediction is seldom tested in studies of nest site selection (reviewed in Clark and Shutler 1999).

Nest predation is usually the main cause of egg and chick mortality (Ricklefs 1969; Martin 1993a; Morton et al. 1993; Mezquida and Marone 2001). It has been found in some species that the probability of nest predation varies with the species of plant that supports the

nest and the location of the nest inside the plant (Murphy 1983; Alonso et al. 1991) or with the features of the immediate area around the nest (Martin and Roper 1988; Kelly 1993; Martin 1993b, 1998). Thus, it is widely believed that nest site selection in birds may have evolved mainly as an adaptive response against nest predators (Martin 1993b). However, other studies have reported no relationship between nest success probability and nest location (Barnard and Markus 1990; Morton et al. 1993; Filliater et al. 1994; Farnsworth and Simons 1999).

In this paper, I analyze whether there are nest site preferences in five bird species that nest in an arid area of southern South America and, if so, whether such preferences are positively associated with reproductive success. First, I examine the differences in vegetation characteristics between nests and the available habitat at two spatial scales (nest site and nest patch). Secondly, I analyze the fitness consequences of selection patterns at both nest scales.

Methods

Field work was carried out in the Reserve of Ñacuñán (34°03'S, 67°54'W; 12,282 ha) during the 1995-1996, 1996-1997, 1997-1998, and 1998-1999 breeding seasons (September through February). The Reserve of Ñacuñán is located in the province of Mendoza, Argentina, at an intermediate latitude of the Monte Desert biome (Morello 1958). The reserve is situated in the Mendoza plains at 540 m elevation and has been excluded from grazing and logging for more than 30 years. The dominant habitat is an open algarrobo (*Prosopis flexuosa*) woodland with scattered chañar trees (*Geoffroea decorticans*). The shrub stratum is made up of tall shrubs such as jarilla (*Larrea divaricata*), atamisque (*Capparis atamisquea*), zampa (*Atriplex lampa*), and piquillin (*Condalia microphylla*), and low shrubs of the genera *Lycium*, *Verbena*, *Bougainvillea*, *Acantholippia*, and *Ephedra*. Perennial grasses of the genera *Trichloris*, *Pappophorum*, *Digitaria*, *Setaria*, *Sporobolus*, and *Aristida*, and several annual forbs prevail among the herbaceous stratum. Ñacuñán's climate is dry and temperate with cold winters. Mean annual rainfall is 331 mm, although it is highly variable from year to year, with most precipitation (78%) occurring in spring and summer (October to March) (Marone et al. 2000).

Bird species studied include *Rhinocrypta lanceolata* (Crested Gallito) (Rhinocryptidae), *Serpophaga griseiceps* (Gray-crowned Tyrannulet) (Tyrannidae), *Poospiza ornata* (Cinnamon Warbling-Finch), *P. torquata* (Ringed Warbling-Finch), and *Saltatricula multicolor* (Many-colored Chaco-Finch) (Emberizidae). The relatively high number of nests found of each of these species led to their selection. *R. lanceolata* is a relatively large bird with a bushy crest, predominantly terrestrial, with secretive habits, and is resident in Ñacuñán (Ridgely and Tudor 1994). The nests are globular with a side entrance (Mezquida 2001). The name *S. griseiceps* that I use in the present study seems to correspond to an undescribed cryptic species of tyrant flycatcher that Straneck (1993) considered referable to *S. griseiceps*. However, Straneck's revalidation of the taxon appears to be unsubstantiated and the assignment of the name to the taxon invalid (Herzog 2001, and personal communication). *S. griseiceps* is a small foliage-gleaning tyrant flycatcher with gray plumage, a semi-concealed white coronal patch and dark tail. It is a spring and summer dweller in the study area and builds small open-cup nests (Mezquida and Marone 2000). *P. ornata* and *P. torquata* are mid-size finches, boldly patterned and colorful in a subdued way, with rufous, gray and white predominating (Ridgely and Tudor 1994). *P. ornata* is a spring and summer dweller in the

reserve while *P. torquata* is a resident species (Marone et al. 1997). Both species build similar open-cup nests. *S. multicolor* is a bigger finch, also colorful and boldly patterned (Ridgely and Tudor 1994). It is a resident species in Ñacuñán and builds open-cup grassy nests (Marone et al. 1997).

I located nests by systematic searches in the vegetation and by following the adult birds (Martin and Geupel 1993) to avoid finding only the most conspicuous nests. Nests were visited every 1–3 days until failing or the young fledged. Nests that fledged at least one young were considered successful. Daily survival rate of nests was estimated using the Mayfield method (Mayfield 1975), as modified by Johnson (1979) and Hensler and Nichols (1981). Total exposure days were calculated as the interval from first egg laying date or, when egg laying was already initiated, from the day when the nest was found until the day when the young fledged, or halfway between the two subsequent visits between which a nest failed (see Mezquida and Marone 2001).

I measured nest habitat features on two scales. One included the plant that supported the nest and nest placement inside the plant (microhabitat), and the other the vegetation patch surrounding the nest (mesohabitat). At the microhabitat scale, the following set of variables was measured for all nests: plant species, height and canopy diameter (average of the maximum diameter and the perpendicular one), height of the nest's rim (open nests) or the nest's entrance (closed nests) above the ground, distance from the nest's upper limit to the top of the plant directly above the nest, a nest position index (visually calculated as the ratio of trunk to nest distance divided by the canopy radius at nest height; Lazo and Anabalón 1991), and a measure of vegetation density. Vegetation density was measured by passing a thin aluminum rod with five marks (at 10-cm intervals) horizontally from the nest through the vegetation in the four cardinal directions and also vertically over and under the nest, and counting the number of contacts ("hits") by vegetation. I calculated the vegetation density as the number of 10-cm intervals with hits divided by all intervals (i.e., 30).

I characterized the mesohabitat of each nest along 10-m transects extending outward from a distance of 1 m from the nest, following the four cardinal directions (Norment 1993). Twenty random points, with a distance ≥ 10 cm between consecutive points, were selected along each transect. Thus, the total number of points measured per patch was 80. At each sampling point, I recorded the height and species of plant that contacted a thin, vertically held, aluminum pole (graduated at 25-cm intervals). Several variables of the nest patch were estimated: horizontal cover of algarrobo, chañar, jarilla (*Larrea* spp.), atamisque, piquillin, zampa, low shrubs (*Lycium* spp., *Verbena aspera* and *Bougainvillea spinosa*) and grasses. In all cases, the horizontal cover was calculated as the number of sample points in which each plant or group of plants touched the pole divided by 80.

Following the same approach described above, the height and canopy diameter of 755 randomly selected plants were also measured, including the six plant species more commonly used by birds for nesting in this area (algarrobo, chañar, jarilla, atamisque, piquillin, and zampa). For that purpose, I selected several widely separated random transects within the study area, choosing the closest plant at 25-m intervals. Additionally, vegetation characteristics were measured in 60 random patches using the same protocol as for nest patches.

I calculated an index of nest plant preference (Li and Martin 1991) as a measure of selectivity by the five bird species. I compared the frequency of nest placement among available plants using chi-square analyses to determine if nest plants were used in proportion to their availability. To estimate the density of each plant species, the area covered by each species on the 60 random circular patches was calculated and divided by the mean crown area of each plant species. The mean crown area of the plant species used by birds for nesting was calculated from the sample of plants selected at random. For each plant, the area of the ellipse formed by the maximum diameter of the crown and its perpendicular was calculated.

To compare the characteristics of random plants with those used by birds for nesting, I used *t* tests or *t'* tests (when variances were not homogeneous). To summarize the patterns of covariation

present in the eight mesohabitat variables (i.e., horizontal cover of algarrobo, chañar, jarilla, atamisque, piquillín, zampa, low shrubs and grasses) measured on nest and random patches, a principal component analysis (PCA) was performed. The comparisons of principal component scores between nest mesohabitats of each bird species with mesohabitats randomly chosen were made using *t* tests or *t'* tests for each extracted factor.

I calculated daily survival rates for nests placed in the plant species most frequently used and for nests in all other plant species. Comparisons of daily survival rate were made using the Hensler and Nichols (1981) test. To examine the relationship between nest sites and reproductive success, I contrasted nest site variables between unsuccessful and successful nests for each bird species by using *t* tests. Some microhabitat variables (e.g., nest position index, vegetation density) could not be measured in all nests because the nest was displaced by predators or inclement weather. For this reason, I analyzed nest site variables using univariate tests instead of a multivariate analysis. Principal component scores of unsuccessful and successful nest patches were also compared using *t* tests to determine if nest patch variables could discriminate between both groups. For all analyses I included all the nests from all the years. Although this study took place over 4 years, most habitat data were collected in the last three breeding seasons, and nest survival did not differ among years for any of the bird species included in this study (Sauer and Williams test: $\chi_2^2 < 1.9$, $P > 0.05$, for all species).

Results

Each bird species preferentially used one or two plant species to build the nest (Table 1). Out of the nine plant species used by these birds as nest support (Table 1), chañar, atamisque, and zampa were more frequently used than expected by their availability in random patches ($\chi_1^2 = 66.9$, $P < 0.0001$, $\chi_1^2 = 277.0$, $P < 0.0001$, and $\chi_1^2 = 8.3$, $P < 0.01$, respectively). Jarilla was underused in relation to its availability ($\chi_1^2 = 166.2$, $P < 0.0001$), and algarrobo and piquillín were used in proportion to their abundance ($\chi_1^2 = 0.6$, $P > 0.05$, and $\chi_1^2 = 0.3$, $P > 0.05$, respectively).

The atamisque plants used by *R. lanceolata* and *S. multicolor* were, on average, of similar size to random plants (Table 2). *S. griseiceps* nested in bigger chañar trees than the average, *P. ornata* in smaller chañar trees, and *P. torquata* in chañars of similar height, but with a

somewhat smaller canopy diameter (Table 2). When *P. ornata* and *S. multicolor* nested in zampa, they used plants similar in size to average plants, whereas *P. torquata* nested in plants of zampa significantly bigger than those randomly measured (Table 2).

The PCA of eight mesohabitat variables measured on nest and random patches yielded three factors that collectively accounted for 52.8% of the total variation in the original data (Table 3). The first factor contrasted patches with low cover of algarrobo and atamisque, and high cover of grasses, with patches principally composed of algarrobo and atamisque, and few grasses. The second factor sorted the patches in a gradient from those with low cover of jarilla and abundant zampa to patches dominated by jarilla and low cover of zampa. The third factor contrasted patches with abundant chañar trees and low shrubs with those with little cover of these plants. Thus, these factors defined three new variables that synthetically described the principal dimensions of variation, independent of each other, in the composition of patches.

Habitat patches surrounding the nests of four out of the five bird species analyzed were significantly different from random patches (Table 4). *R. lanceolata* nested in patches with high cover of algarrobo and atamisque, and low cover of grasses, and *S. griseiceps* selected patches with abundant chañar and low shrubs compared to those randomly available (Table 4). *P. ornata* and *P. torquata* placed their nests in patches dominated by grasses and zampa, and little algarrobo, atamisque and jarilla compared to those available in the habitat (Table 4). Finally, habitat patches around *S. multicolor* nests did not differ from those randomly available, probably because of the low and heterogeneous sample size, although this species tended to nest in patches with abundant grasses and little algarrobo and atamisque (Factor I: $P = 0.051$).

The daily survival rate of nests placed in the preferred plant species was similar to that in the other plants used for *R. lanceolata*, *P. ornata*, *P. torquata* and *S. multicolor* (Hensler and Nichols test, $Z < 0.71$, $P > 0.05$, in all cases;

Table 1 Percentage of nests built in various plant species of the open *Prosopis* woodland in the Reserve of Ñacuñán. Algarrobo: *P. flexuosa*, chañar: *G. decorticans*, jarilla: *Larrea* spp., atamisque: *C. atamisquea*, piquillín: *C. microphylla*, zampa: *A. lampa*

Bird species	Plant species							n
	Algarrobo	Chañar	Jarilla	Atamisque	Piquillín	Zampa	Other ^d	
<i>Rhinocrypta lanceolata</i>	6.7	13.3	0.0	75.0	1.7	1.7	1.7	60
<i>Serpophaga griseiceps</i>	0.0	94.4	1.6	0.0	0.8	1.6	1.6	125
<i>Poospiza ornata</i>	0.0	56.7	10.0	1.7	3.3	25.0	3.3	60
<i>Poospiza torquata</i>	0.0	46.8	0.9	4.6	0.9	45.0	1.8	109
<i>Saltatriculamulticolor</i>	0.0	10.0	10.0	45.0	5.0	30.0	0.0	20
Average use (U) ^a	1.3	44.2	4.5	25.3	2.3	20.7	1.7	
Availability (A) ^b	2.5	15.0	65.7	2.0	3.3	11.5	—	
Preference index ^c : (U-A)/100	-0.01	0.29	-0.61	0.23	-0.01	0.09		

^aAverage percentage that a plant species was used for nesting by all species

^bEstimated percentage of all of these plants that each plant species represented in 60 random plots

^cLi and Martin (1991)

^dIncluding *Bulnesia retama*, *Lycium* spp. and *Verbena aspera*

Table 2 Height (m) and mean canopy diameter (m) of the three plant species preferably used for nesting by five bird species in Nacuñán and randomly selected plants. Entries are mean \pm SE (*n*)

	<i>Rhinocrypta lanceolata</i>	<i>Serpophaga griseiceps</i>	<i>Poospiza ornata</i>	<i>Poospiza torquata</i>	<i>Saltatricula multicolor</i>	Random plants
Atamisque						
Height	2.3 \pm 0.1(42)				2.1 \pm 0.1(9)	2.2 \pm 0.1(114)
Canopy diameter	n.s. 3.4 \pm 0.1(37)				n.s. 3.0 \pm 0.4(9)	3.4 \pm 0.1(114)
Chañar						
Height		2.8 \pm 0.1(107)	1.8 \pm 0.1(31)	2.0 \pm 0.1(50)		2.0 \pm 0.1(122)
Canopy diameter		1.6 \pm 0.1 (92)	1.0 \pm 0.1 (31)	1.0 \pm 0.0 (50)		1.2 \pm 0.1 (122)
Zampa						
Height			1.3 \pm 0.1(15)	1.5 \pm 0.0(43)	1.2 \pm 0.1(6)	1.2 \pm 0.0(116)
Canopy diameter			n.s. 1.7 \pm 0.1(15)	n.s. 2.1 \pm 0.1(40)	n.s. 1.6 \pm 0.2(6)	1.6 \pm 0.1(116)

n.s. $P > 0.05$
* $P < 0.05$

** $P < 0.01$
*** $P < 0.0001$

Table 3 Principal components analysis of 60 random and 260 nest patches (mesohabitat). Entries indicate factor loadings of each variable (those $> |0.40|$ are presented in bold type)

Variables	Factor		
	I	II	III
Cover of algarrobo	-0.68	0.19	-0.13
Cover of chañar	0.12	-0.18	0.83
Cover of jarilla	0.15	-0.78	-0.11
Cover of atamisque	-0.63	-0.01	0.11
Cover of piquillín	-0.18	0.06	0.11
Cover of zampa	0.22	0.75	-0.26
Cover of low shrubs	-0.27	0.24	0.63
Cover of grasses	0.71	0.15	0.00
Eigen values	1.68	1.40	1.15
Percent total variance	21.0	17.5	14.4
Cumulative variance	21.0	38.5	52.8

Fig. 1). The only exception was *S. griseiceps* whose nests in the plant species most frequently used (i.e., chañar) showed lower survival rate than those in the other plants

($Z = 2.95$, $P < 0.01$; Fig. 1). The rate of nest failure was high in the five bird species studied (see also Mezquida and Marone 2001), so the sample of successful nests was relatively low, especially for some species, compared to that of unsuccessful nests (Table 5). At the scale of microhabitat, no significant differences were detected in the univariate analyses of unsuccessful and successful nest sites (Table 5; *R. lanceolata*: $t < 0.41$, $P > 0.69$, for all variables; *S. griseiceps*: $t < 1.69$, $P > 0.09$; *P. ornata*: $t < 1.80$, $P > 0.08$; *P. torquata*: $t < 0.41$, $P > 0.69$; *S. multicolor*: $t < 1.53$, $P > 0.15$). Thus, the size of the selected plant and the location of the nest in the plant did not appear to have had any influence on nest survival. At the mesohabitat scale, nest patch characteristics as determined by PCA did not show significant differences between unsuccessful and successful nests (Fig. 2; *R. lanceolata*: $t < 0.68$, $P > 0.50$, for the three factors; *S. griseiceps*: $t < 0.87$, $P > 0.39$; *P. ornata*: $t < 1.16$, $P > 0.25$; *P. torquata*: $t < 1.96$, $P > 0.05$; *S. multicolor*: $t < 1.12$, $P > 0.28$).

Table 4 Principal components scores (means \pm 1 SE) of random and nest patches of five bird species. Below, the results of univariate analyses (t test or t' test) that compare principal components scores of nest patches with random patches are shown

	<i>n</i>	Factors		
		F-I	F-II	F-III
Random patches	60	-0.225 \pm 0.141	-0.205 \pm 0.118	-0.338 \pm 0.104
<i>R. lanceolata</i>	30	-0.916 \pm 0.217	-0.405 \pm 0.169	-0.034 \pm 0.236
		**	n.s.	n.s.
<i>S. griseiceps</i>	87	-0.106 \pm 0.089	-0.288 \pm 0.084	0.406 \pm 0.113
		n.s.	n.s.	***
<i>P. ornata</i>	47	0.621 \pm 0.104	0.334 \pm 0.168	-0.029 \pm 0.130
		***	**	n.s.
<i>P. torquata</i>	80	0.189 \pm 0.099	0.394 \pm 0.117	-0.155 \pm 0.093
		*	***	n.s.
<i>S. multicolor</i>	17	0.346 \pm 0.207	0.137 \pm 0.223	-0.018 \pm 0.288
		n.s.	n.s.	n.s.

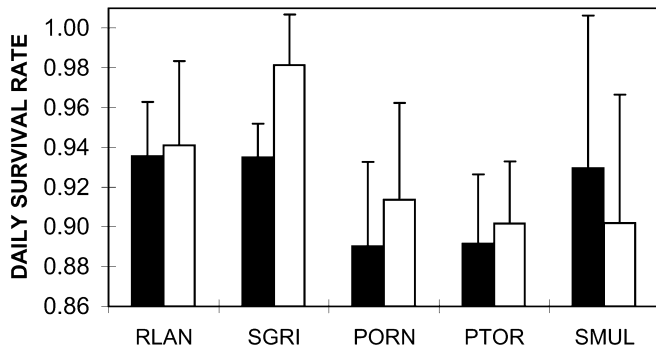


Fig. 1 Daily survival rate for nests placed in the plant species most frequently used (*filled bars*), and all other plant species (*open bars*) (see Table 1). Confidence range indicated at 95% according to Hensler and Nichols (1981). *RLAN* *R. lanceolata*, *SGRI* *S. griseiceps*, *PORN* *P. ornata*, *PTOR* *P. torquata*, *SMUL* *S. multicolor*

Discussion

The results of this study suggest that patterns of nest site selection are common among some bird species of the Monte Desert. For example, each bird species preferred only one or two plants to support their nests, and at least some of them also actively selected them by their size. Likewise, all but one species showed clear patterns of selection at the patch scale. Undoubtedly, these patterns could be interpreted as the result of a long-term process of selection (Clark and Shutler 1999).

The comparisons of nest survival rates in different plant species did not show clear patterns. *S. griseiceps* was the only species out of five that showed higher nest survival rate in the non-preferred plants. This suggests that nests placed in uncommonly used plant species will be more successful than those placed in commonly used plants, as the rare site hypothesis proposes (Filliater et al. 1994). This implies that predators should concentrate their search on the more frequently used sites and avoid those used infrequently. In accordance with that hypothesis, bird species of the study area (mainly Emberizidae) that nested in jarilla, a widely available tall shrub but rarely used as a nest site, showed higher nest survival (Mezquida and Marone 2001). However, these

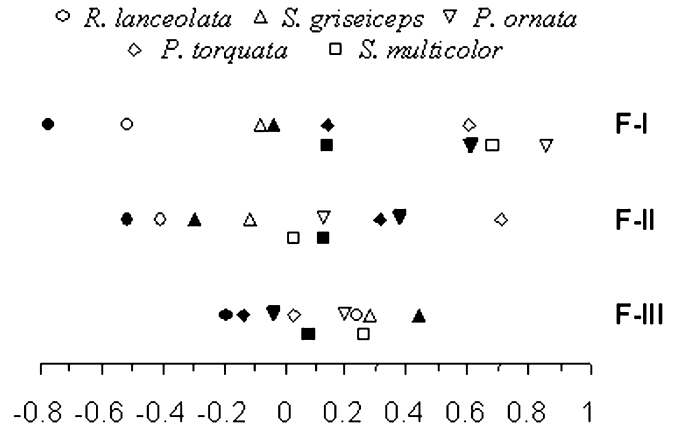


Fig. 2 Average scores of unsuccessful (*filled*) and successful (*open*) nest patches on three principal components (see Table 3) for five bird species from Nacuñán

results should be interpreted cautiously due to the low number of nests in the rarely used plant species for estimating daily survival rates, and the pooling of data from several plant species. For instance, zampa was the second most frequent nesting plant used by both *Poospiza* and *S. multicolor*, but the data on nest survival in this plant was pooled with those in other plant species uncommonly used.

Plant size and nest location inside the plant did not affect the fate of nests in any bird species. Murphy (1983) and Alonso et al. (1991) found that nests located at intermediate heights in the canopy of trees, and far from the main trunk, but not on the canopy periphery, showed greatest survival, and Collias (1997) suggested that such nest placement reduces predation. However, other studies have failed to find differences in nest success related to nest position inside the supporting plant (Filliater et al. 1994; Howlett and Stutchbury 1996; Meilvang et al. 1997). On the other hand, although each species actively selected a particular type of habitat patch around the nest-plant, there were no differences in patch characteristics according to reproductive success. Overall, this does not appear to be surprising since studies reporting evidence for the adaptive basis of nest site selection are very scarce (Clark and Shutler 1999).

Table 5 Variables (mean \pm 1 SE) measured at unsuccessful (U) and successful (S) nest sites (microhabitat) of each bird species. All variables are in metres except the last two indexes

Species	U/S (n)	Plant height	Canopy diameter	Nest height	Nest to canopy	Nest position index	Vegetation density
<i>R. lanceolata</i>	U(27)	2.7 \pm 0.2	3.3 \pm 0.2	1.5 \pm 0.1	0.7 \pm 0.1	0.50 \pm 0.05	0.42 \pm 0.03
	S(6)	2.6 \pm 0.3	3.2 \pm 0.5	1.5 \pm 0.2	0.7 \pm 0.1	0.53 \pm 0.12	0.41 \pm 0.02
<i>S. griseiceps</i>	U(67)	2.7 \pm 0.1	1.6 \pm 0.1	1.8 \pm 0.0	0.6 \pm 0.0	0.36 \pm 0.02	0.31 \pm 0.01
	S(18)	2.9 \pm 0.2	1.8 \pm 0.2	1.6 \pm 0.1	0.6 \pm 0.1	0.39 \pm 0.05	0.33 \pm 0.02
<i>P. ornata</i>	U(35)	1.6 \pm 0.1	1.3 \pm 0.1	0.8 \pm 0.1	0.6 \pm 0.1	0.28 \pm 0.03	0.38 \pm 0.02
	S(14)	1.5 \pm 0.1	1.3 \pm 0.2	0.7 \pm 0.1	0.5 \pm 0.1	0.32 \pm 0.06	0.41 \pm 0.04
<i>P. torquata</i>	U(73)	1.8 \pm 0.1	1.6 \pm 0.1	1.0 \pm 0.0	0.5 \pm 0.0	0.38 \pm 0.03	0.42 \pm 0.01
	S(18)	1.6 \pm 0.1	1.5 \pm 0.1	0.9 \pm 0.1	0.4 \pm 0.1	0.46 \pm 0.06	0.36 \pm 0.02
<i>S. multicolor</i>	U(13)	1.6 \pm 0.2	2.2 \pm 0.4	0.7 \pm 0.1	0.6 \pm 0.1	0.43 \pm 0.06	0.51 \pm 0.04
	S(4)	2.0 \pm 0.2	2.5 \pm 0.3	0.6 \pm 0.2	1.1 \pm 0.4	0.40 \pm 0.11	0.41 \pm 0.09

Nesting success of the bird species included in this study appear to be very low in Ñacuñán, where the main cause of nest mortality was predation (Mezquida and Marone 2001), as has been commonly recorded in passeriforms (Ricklefs 1969; Martin 1993a, 1995). High nest predation rate may be expected to be a strong selection pressure guiding the choice of nest sites less vulnerable to predators (Murphy 1983; Martin and Roper 1988; Li and Martin 1991). Nevertheless, in this study I did not find differences in the type of nest microhabitat nor in the habitat patch surrounding the nest according to variations in nest success.

One reason for these unexpected results might be the high nest mortality found for these birds (>85%; Mezquida and Marone 2001) during the study period, making it difficult to discern hypothetical habitat differences between unsuccessful and successful nests. Moreover, Filliater et al. (1994) proposed that a high incidence of nest predation and, especially, the presence of different predators with distinct predation tactics should preclude the existence of safe nest sites. This may be the case at Ñacuñán, where the main nest predators seem to be birds, although small mammals could also have an impact (Mezquida and Marone 2002). Furthermore, several species of mammals and reptiles present in the area (Contreras 1979) are usually considered as potential nest predators, although their incidence has not been confirmed at Ñacuñán (Mezquida and Marone 2002), but there is some evidence pointing to a higher impact of terrestrial predators (Quse 2001). Thus, when multiple predator species occur there are trade-offs between avoidance strategies (Schmidt and Whelan 1999). For example, both *Poospiza* usually nested in two structurally very different plant species (chañar and zampa). Nests in chañar were placed higher (*P. ornata*: 1.04 m, *P. torquata*: 1.17 m) and less concealed (vegetation density: 0.34 and 0.38) than those in zampa (nest height: 0.65 and 0.77 m; vegetation density: 0.43 and 0.44). So nests placed in chañar trees were supposedly more vulnerable to avian predation whereas those in zampa were vulnerable to terrestrial predators, but nests in both plant types showed similar low survival rates (Mezquida and Marone 2001). Other authors have also found results consistent with this hypothesis (Braden 1999; Farnsworth and Simons 1999; Dion et al. 2000).

The observed patterns of habitat patch selection for nesting could also be a response to food availability or protection against abiotic factors. However, the availability or abundance of suitable foraging sites seems to be an important feature for territory selection (i.e., for spatial scales larger than the nest patch) (Braden 1999; Misenhelter and Rotenberry 2000), and nest mortality due to abiotic factors was infrequent in Ñacuñán (Mezquida and Marone 2001).

The high nest predation pressure suffered by the assemblage of passerines at Ñacuñán suggested that adaptive responses should be found. However, these responses were not evident, at least in the studied

patterns. Nest site selection strategies are complex because many factors can influence them (e.g., Rauter et al. 2002; Weidinger 2002). For example, differences in parental defense behavior may be more important in determining a nest's fate than nest placement (Cresswell 1997; Murphy et al. 1997), although the effect of this behavior varies depending on the type of predator. Changes in climate conditions can also influence the selection of microsites for nesting, but these shifts in habitat use can increase risk of nest predation due to microhabitat overlap among coexisting species (Martin 1996, 2001). Finally, birds seem to exhibit some behavioral plasticity in nest site choice as a function of previous success (Martin 1998). Thus, more information about local predators, their foraging strategy and relative impact on nests of the different bird species would be important to better understand nest site selection strategies, and ultimately integrate this knowledge as part of a model of predator-prey interactions (Schmidt 1999).

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