

## Foraging behaviour of birds in an arid sand-dune scrubland in Argentina

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**Abstract.** Studies of the foraging behaviour of birds allow exploration of the mechanisms that structure species assemblages. The major objective of this study was to describe relationships among various components of foraging behaviour and whether changes in those relationships reflected seasonal changes in assemblage structure of birds from an arid scrubland of the Monte Desert, Argentina. Foraging behaviour was described in terms of attack manoeuvres, food substrate (i.e. substrate from which food was taken), foraging site (i.e. the substrate and height from where birds launched the attack), and plant species used. Between-species differences in attack manoeuvres, food substrate and foraging site were interrelated, the association being strongest between foraging sites and food substrates. During the non-breeding season, foraging sites and food substrates differentiated species. The most important changes between seasons were related to the arrival in summer of aerial-foraging tyrant flycatchers, a functional group absent during the non-breeding season. Foraging sites explained most of the differences among species groups, suggesting that habitat heterogeneity and structural complexity of vegetation are important environmental variables that determine the avian assemblage structure. Moreover, temporal changes in food availability, mediated by strong seasonality in climate, were important factors that were correlated with compositional and structural variability in functional groups of birds (i.e. granivores-insectivores, surface insectivores and aerial insectivores).

### Introduction

Foraging behaviour has played an important role in empirical studies of avian foraging ecology. A thorough understanding of how species respond behaviourally to availability of food can highlight the proximate mechanisms that structure bird species assemblages. Foraging behaviour has been used to describe the trophic ecology of bird assemblages and has been used to cluster bird species into functional groups based on how and where birds obtain their food. In such studies, attention has focused on identification of groups of species that have similar foraging ecologies (Holmes *et al.* 1979; Ford *et al.* 1986; Holmes and Recher 1986; Osborne and Green 1992; Recher and Davis 1997, 1998), or on description of differences among species within a specific group (e.g. Petit *et al.* 1990; Sillett 1994; Keast and Recher 1997).

To understand differences in foraging behaviour among species in an assemblage, that behaviour needs to be broken down to components such as manoeuvres used to capture food, the attributes of the substrates from where the birds forage, and the substrate from which the food is taken (Remsen and Robinson 1990). Foraging behaviour can vary with different life-history traits of bird species and thus amongst birds exhibiting different traits. Also, foraging behaviour can change within a species in response to

temporal and spatial variation in availability of resources and interspecific interactions. Seasonal variation in foraging behaviour is common in many species of terrestrial birds, and has been reported from various temperate habitats (e.g. Miles 1990a; Cale 1994; Wilson and Recher 2001). Thus, analyses of foraging ecology without consideration of seasonal variation among species could obscure relevant information about temporal changes in bird assemblage structure. Here, I examine the foraging behaviour of an assemblage of birds in the Monte Desert of Argentina. I investigated foraging behaviour in terms of attack methods and foraging sites, and I investigated how species changed aspects of their foraging behaviour in a spatial context. Finally, seasonal changes in the assemblage structure are described based on the foraging behaviours displayed.

### Methods

The study was conducted in the Flora and Fauna Reserve of Telteca (32°21'S, 68°03'W), Mendoza, Argentina. The reserve is in the central Monte Desert (Blendinger, in press), in arid scrubland vegetation growing largely in sand-dunes. The shrub cover is dominated by *Larrea divaricata* (jarilla), *Tricomaria usillo* (usillo), *Bulnesia retama* (retamo) and *Bouganvillea spinosa* (monte negro), with a herbaceous layer rich in grasses such as *Panicum urvilleanum*, *Aristida mendocina* and *Bouteloua aristidooides*. In the lower areas between dunes grows open woodland of *Prosopis flexuosa* (algarrobo dulce) less than 10 m tall, with scattered shrubs of *Capparis atamisquea* (atamisqui), *B. retama*

and *Lycium tenuispinosum* (llaullín). The climate is temperate and arid, with warm and rainy summers and cold and dry winters (Morello 1984). The mean annual rainfall at Encón, 30 km north of the study area, is 163 mm (data from Meteorological Program of the Regional Center for Scientific and Technological Investigations, Mendoza).

I studied the foraging behaviour of birds from November 1996 to February 1999. At different hours of the day, I walked randomly throughout an area of 5 km<sup>2</sup> observing bird activity. After a bird was detected, I recorded a single attack manoeuvre of the bird, the height and the substrate from which the bird launched its attack, and the food substrate (from where food was taken) (Table 1). The plant species was recorded when the food was taken from a plant. I took only one forag-

ing sample per individual, and only one individual per species when flocks were involved, to assure independence between samples (Morrison 1984; Recher and Gebski 1990). To avoid over-estimation of conspicuous behaviours, I started to record foraging activities 10 s after a bird was detected (Hejl *et al.* 1990).

Nesting in the Monte Desert is strongly seasonal, with all species breeding during spring and summer (Blendinger, in press). Thus, to study seasonal changes in assemblage structure, I grouped samples from October to January as the breeding season and samples from April to September as the non-breeding season.

Uncommon and occasional species were not considered in this study; the number of birds captured with mist-nets (36-mm mesh,

**Table 1. Categories of foraging behaviour used in this study; equivalent categories in the classification of attack manoeuvres proposed by Remsen and Robinson (1990) are shown in brackets**

Some behaviours used only occasionally were not considered, such as scratching the leaf-litter with both feet to expose food (recorded for *Zonotrichia capensis*) or flushing prey from the foliage and then chasing it (recorded for *Saltatricula multicolor*)

Attack method		In the analysis, I combined for each attack method category a foraging manoeuvre (aerial or from a perch) with the substrate from which food was obtained.
(a <sub>1</sub> ) Manoeuvres from a perch		The food item was obtained from the substrate on which bird was perched.
Perching	(glean, reach, probe, peck)	I grouped the manoeuvres of picking food directly from the surface of the substrate (including the ground), probing into the substrate (e.g. probing bark by <i>Lepidocolaptes angustirostris</i> ) or removing substrate with the beak to expose food (e.g. when <i>Melanerpes formicivorus</i> peck in a previous hole to allow sap exudation).
Hanging	(hang)	The bird hangs, with the body below its feet.
Hammering	(hammer)	The bird makes a rapid series of pecks, typical of woodpeckers. If the bird was hanging while hammering, I treated it as hammering, following Remsen and Robinson (1990) who considered that in this case hanging is a posture rather than a foraging manoeuvre.
(a <sub>2</sub> ) Aerial manoeuvres	The food item obtained in flight.	
Hovering	(sally-stall, sally-hover)	The bird flew from a perch and stayed a moment in the same place in the air to capture the prey from a solid substrate (usually foliage). Most cases involved flights of <1 m.
Sallying	(sally-strike, sally-glide)	The bird flew from a perch to attack a prey item in the air, then landing on the same or different perch.
(b) Substrate		The substrate from which the bird obtained the food item.
Ground		The food item was on the ground or just under the surface.
Grass		The food item, usually seeds, was taken from grasses.
Foliage		The food was taken from leaves and thin stems of shrubs and trees, usually <0.5 cm in diameter.
Branch		The food item was taken from branches 1–3 cm in diameter.
Trunk		The food item was taken from branches and trunks >3 cm in diameter.
Between the foliage		Prey was captured when it was flying among the foliage of a shrub or tree.
Open space		Prey item was in the air in an open space between plants or over the vegetation.
Foraging site		From where the bird launched the attack; each category combines the substrate and the height where the bird was.
(a) Ground or vegetation		
Ground		Perched on the ground.
Herb or grass		The bird was perched on the herbaceous layer; always < 1 m above ground.
Short shrub		The bird was foraging on shrubs <1 m tall; most of the observations were on <i>Lycium tenuispinosum</i> , with many also on <i>Atriplex lampa</i> , <i>Plectocarpa</i> species or saplings of other shrub species.
Tree or shrub		Foraging on shrubs taller than 1 m or on trees, broken into height intervals of: <1 m, between 1 and 2 m, between 2 and 3 m, between 3 and 5 m, >5 m.
(b) Air		For the analysis, each of the following categories was subdivided according to the distance of the bird to the ground when prey was captured: <1 m, between 1 and 2 m, between 2 and 3 m, between 3 and 5 m, and > 5 m.
Lower air		Flying lower than the highest cover of the surrounding shrubs, usually ≤3m.
Medium air		Flying through the space between the canopy of the shrubs and the canopy of the trees.
Higher air		Flying over the vegetation, in most cases >5 m above the ground.

12.4 m long, 2 m tall) was used as a rough measure of relative abundance of species. Despite different biases using mist-nets for estimation of abundance (Remsen and Good 1996), species analysed in this paper include all the more abundant small bird species (<90 g body mass) recorded with point counts in Telteca (Blendinger 2000) except *Anairetes flavirostris* (Yellow-billed Tit-Tyrant) and *Phrygilus carbonarius* (Carbonated Sierra-Finch). Given that low vegetation (<3 m tall) covered most of the study area, I assumed that mist-net captures at ground-level would be an adequate measure of relative abundance of species in the Monte Desert. Mist-nets were opened during each visit to the study area (see details in Blendinger, in press), until the total capture effort exceeded 350 net-hours. Mist-nets were opened at dawn, for ~4 h, and before sunset for ~3 h.

I obtained foraging data for 43 bird species in summer and for 36 in winter, and a total of 773 and 665 independent samples respectively. Only species that represented more than 1% of mist-net captures were included. However, some species were less likely to be captured than others and I included two species (*Empidonomus aurantioatrocristatus*, Crowned Slaty-Flycatcher, and *Rhinocrypta lanceolata*, Crested Gallito) whose abundance were underestimated by captures in mist-nets. Thus, I report on the structure of the bird assemblage of Telteca based on 22 species (652 foraging samples) in the breeding season and 16 species (600 samples) in the non-breeding season. For species classification and taxonomic arrangement I followed Remsen *et al.* (2004).

#### Statistical analysis

I used correspondence analysis (CA) to investigate the relationships between bird species in their foraging behaviours. Analysing the ordination of the species in the multidimensional space generated by their foraging behaviour allows exploration of the structure of bird assemblages (Miles 1990b; Moser *et al.* 1990). Correspondence analysis gives information on the importance of every foraging category for the species ordination, allowing interpretation of the causes that determine their dispersion in the ecological space. To eliminate the arch effect detected in a preliminary analysis, I used a detrending-by-polynomials variant of CA (Jongman *et al.* 1995). To explore if the use of CA was adequate for the matrices of foraging behaviour from Telteca, I analysed the length of the first ordination axis using CA with detrending by segments. With this technique, the length of the first ordination axis is expressed in multiples of standard deviation (see Jongman *et al.* 1995 for a detailed explanation). The length of the first axis was higher than 3.2 s.d. in all cases except for the matrix of foraging sites from the non-breeding season, which was 2.2 s.d. higher. The lengths of these gradients allow most species to have unimodal response curves on the axis of foraging behaviours, thus justifying the use of CA. I performed CA with the computer programme CANOCO 3.12 (ter Braak 1991).

Congruence between matrices of attack manoeuvres, food substrates, and foraging sites was compared with a Mantel procedure (McCune and Grace 2002). I performed a Monte Carlo test with 9999 randomised runs; Euclidean distance was used to calculate the

similarity matrices. Test *G* of heterogeneity was used to analyse frequencies of foraging categories between species in the breeding and non-breeding seasons. Related behaviours with low frequencies were put together in the same category. As a coarse measure of foraging specialisation, I calculated for each species its mean Euclidean distance in the multidimensional space determined by foraging sites and attack behaviours. I assumed that more specialised species should have a larger mean Euclidean distance, whereas species with more generalized foraging behaviour should be closer to the assemblage centroid.

## Results

### *Non-breeding season (April to September): attack behaviour*

Ordination axes 1 and 2 explained 53% of between-species variation in attack behaviour (Table 2). On the first axis a gradient of food substrates was expanded, with ground and vegetation at opposite extremes, while aerial prey did not contribute significantly (Fig. 1a). Attack manoeuvres were also spread on the first axis, with perching and hammering on different extremes.

Thus, a group of species that obtained their food on trunks and branches, using various attack manoeuvres, could be differentiated (Fig. 1a). These species descended to the ground only occasionally. To this group belong both species of woodpeckers, especially *Picoides mixtus* (Checkered Woodpecker), that hammered branches and trunks looking for insects, and *Lepidocolaptes angustirostris* (Narrow-billed Woodcreeper), *Leptasthenura platensis* (Tufted Tit-Spintail) and *Cranioleuca pyrrhophia* (Stripe-crowned Spintail) that captured most of their prey (≥85%) while perching on shrubs and trees. On the other side of axis 1 was located a group of species that directed 60–100% of their attack manoeuvres to food items on the ground (Table 3). This group was composed of granivorous species, such as *Columbina picui* (Picui Ground-Dove) and *Diuca diuca* (Common Diuca-Finch), and some insectivores such as *Rhinocrypta lanceolata*, *Upucerthia certhioides* (Chaco Earthcreeper) and *Asthenes baeri* (Short-billed Canastero).

A species could be located close to the diagram centre for three reasons: (1) it could have a bimodal distribution on the axis; (2) it could show a unimodal response curve, with the optimal part of its distribution near the centre of the diagram; or (3) a species could be unrelated with the gradient of

**Table 2. Matrix trace and variation explained by the first two axes in a detrended correspondence analysis of the foraging behaviour of bird species in a Monte Desert assemblage**

	Total inertia	Eigenvalue			
	$\lambda$	$\lambda_1$	% <sub>1</sub>	$\lambda_2$	% <sub>2</sub>
Non-breeding season					
Attack methods	1.83	0.71	38.8	0.25	13.8
Foraging site	1.11	0.68	60.8	0.16	14.2
Breeding season					
Attack methods	2.88	0.80	27.7	0.43	14.9
Foraging site	1.99	0.79	39.4	0.45	22.5

variation in foraging behaviours explained by this axis (Jongman *et al.* 1995). Thus, to further understand how species were related along the main axis of attack behaviours displayed by the ordination diagrams, I explored the distribution of attack behaviours of each species on the first ordination axis. Occurrence frequency of every foraging category for each species close to the diagram centre (Fig. 1a) was plotted against its score on axis 1. *Pseudoseisura lophotes* (Brown Cacholote) had a bimodal distribution; it captured prey on the vegetation, as well as on the ground. *Saltator aurantirostris* (Golden-billed Saltator) showed a unimodal response with its optima close to the centre, although its dispersal over the first axis was broad. *Poospiza torquata* (Ringed Warbling-Finch) and *Stigmatura budytoides* (Greater Wagtail-Tyrant) are also close to the centre of the diagram but they did not have a clear relationship with the first ordination axis. These last two species were split on the second axis.

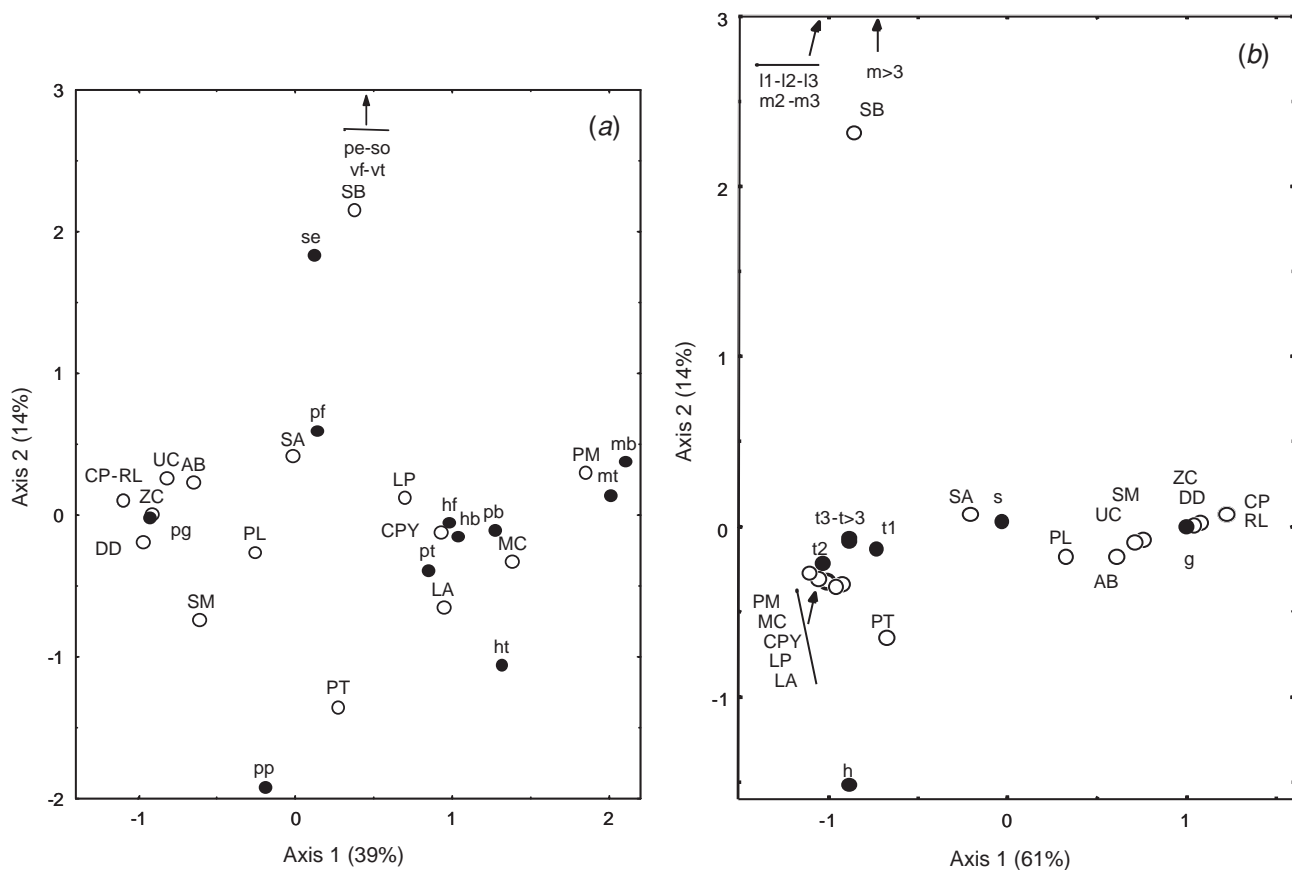
Species were clearly separated on the second ordination axis by the substrates from which food was obtained. *Stigmatura budytoides* is alone on one extreme of the

diagram (Fig. 1a), because it was the only wintering species that used multiple attack manoeuvres to capture flying prey (Table 3). *Poospiza torquata* was segregated on the opposite extreme because it foraged on grasses, where it feeds on grains from spikes. *Saltatricula multicolor* (Many-coloured Chaco-Finch) also took seeds from grass spikes, but it reached them from the ground and rarely perched on grasses, as does *Poospiza torquata*.

The third axis (not shown) gave information on attack manoeuvres that were related to the ability to forage by hanging on different sizes of branches. *Lepidocolaptes angustirostris* hung from trunks to probe interstices of the bark, and thus differed from *Cranioleuca pyrrhophia* and *Leptasthenura platensis*, which hung from thinner branches to pick prey from the foliage (Table 3).

#### Non-breeding season: foraging sites

The first two axes of ordination explained 75% of the inter-specific variation in use of foraging site (Fig. 1b). The substrate from which birds foraged was the main factor that



**Fig. 1.** Ordination diagrams of bird species during the non-breeding season on the space defined by (a) their attack methods and (b) their foraging sites in a correspondence analysis. Open circles are bird species and closed circles are foraging behaviour; acronyms of foraging behaviour as in Table 3. Bird species: AB = *Asthenes baeri*, CP = *Columbina picui*, CPY = *Cranioleuca pyrrhophia*, DD = *Diuca diuca*, LA = *Lepidocolaptes angustirostris*, LP = *Leptasthenura platensis*, MC = *Melanerpes cactorum*, PM = *Picooides mixtus*, PT = *Poospiza torquata*, PL = *Pseudoseisura lophotes*, RL = *Rhinocrypta lanceolata*, SA = *Saltator aurantirostris*, SB = *Stigmatura budytoides*, SM = *Saltatricula multicolor*, UC = *Upucerthia certhioides*, ZC = *Zonotrichia capensis*.

**Table 3. Foraging behaviour of birds during the non-breeding season in arid scrublands in the central Monte Desert**

Number of foraging observations (*N*) for each species is given in parentheses. Bird species: AB = *Asithenes baeri*, CP = *Columbina picui*, CPY = *Crantoleuca pyrrhophia*, DD = *Diuca diuca*,

LA = *Lepidocolaptes angustirostris*, LP = *Leptasthenura platensis*, MC = *Melanerpes cactorum*, PM = *Picooides mixtus*, PT = *Pospiza torquata*, PL = *Pseudoseisura lophotes*,

RL = *Rhinocrypta lanceolata*, SA = *Saltator aurantirostris*, SB = *Stigmatura budyoides*, SM = *Saltatricula multicolor*, UC = *Upucerthia certhioides*, ZC = *Zonotrichia capensis*

	Acronyms	AB (20)	CP (25)	CPY (20)	DD (76)	LA (29)	LP (65)	MC (50)	PM (10)	PT (57)	PL (9)	RL (10)	SA (25)	SM (25)	SB (118)	UC (9)	ZC (52)	
<b>Attack behaviour</b>																		
Perching, ground	pg	70.0	100.0	—	86.8	3.4	—	—	2.0	7.0	55.6	100.0	28.0	60.0	5.9	77.8	90.4	
Perching, foliage	pf	25.0	—	25.0	5.3	6.9	44.6	—	—	24.6	11.1	—	48.0	12.0	46.6	22.2	1.9	
Perching, branch	pb	5.0	—	20.0	—	10.3	10.8	30.0	16.0	7.0	—	—	—	—	3.4	—	1.9	
Perching, trunk	pt	—	—	40.0	—	75.9	35.4	20.0	56.0	28.1	33.3	—	20.0	8.0	19.5	—	5.8	
Perching, grass	pp	—	—	—	7.9	—	—	—	—	33.3	—	—	—	20.0	0.8	—	—	
Perching, between the foliage	pe	—	—	—	—	—	—	—	—	—	—	—	—	—	0.8	—	—	
Hanging, foliage	hf	—	—	10.0	—	—	7.7	—	—	—	—	—	—	—	—	—	—	
Hanging, branch	hr	—	—	5.0	—	—	1.5	—	—	—	—	—	—	—	—	—	—	
Hanging, trunk	ht	—	—	—	—	3.4	—	—	2.0	—	—	—	—	—	—	—	—	
Hammering, branch	mb	—	—	—	—	—	—	10.0	2.0	—	—	—	—	—	—	—	—	
Hammering, trunk	mt	—	—	—	—	—	—	40.0	22.0	—	—	—	—	—	—	—	—	
Hovering, foliage	vf	—	—	—	—	—	—	—	—	—	—	—	—	—	17.8	—	—	
Hovering, trunk	vt	—	—	—	—	—	—	—	—	—	—	—	—	—	1.7	—	—	
Sallying, between foliage	se	—	—	—	—	—	—	—	—	—	—	—	4.0	—	1.7	—	—	
Sallying, open space	so	—	—	—	—	—	—	—	—	—	—	—	—	—	1.7	—	—	
<b>Foraging sites</b>																		
Ground	g	70.0	100.0	—	89.5	3.4	—	—	2.0	7.0	55.6	100.0	32.0	72.0	5.1	66.7	90.4	
Herb or grass	h	—	—	—	—	—	1.5	—	—	10.5	—	—	—	—	—	—	—	
Short shrub	s	5.0	—	5.0	7.9	3.4	13.8	—	—	22.8	11.1	—	12.0	16.0	11.9	22.2	3.8	
Tree or shrub, <1 m	t1	20.0	—	35.0	1.3	41.4	16.9	10.0	16.0	12.3	—	—	12.0	4.0	16.1	11.1	—	
Tree or shrub, 1–2 m	t2	5.0	—	30.0	1.3	27.6	35.4	30.0	34.0	19.3	—	—	16.0	—	17.8	—	1.9	
Tree or shrub, 2–3 m	t3	—	—	20.0	—	17.2	20.0	30.0	30.0	14.0	22.2	—	12.0	4.0	17.8	—	1.9	
Tree or shrub, >3 m	t > 3	—	—	10.0	—	6.9	12.3	30.0	18.0	14.0	11.1	—	12.0	4.0	11.9	—	1.9	
Lower air, <1 m	l1	—	—	—	—	—	—	—	—	—	—	—	—	—	5.1	—	—	
Lower air, 1–2 m	l2	—	—	—	—	—	—	—	—	—	—	—	—	—	2.5	—	—	
Lower air, 2–3 m	l3	—	—	—	—	—	—	—	—	—	—	—	—	—	0.8	—	—	
Medium air, 1–2 m	m2	—	—	—	—	—	—	—	—	—	—	—	—	—	3.4	—	—	
Medium air, 2–3 m	m3	—	—	—	—	—	—	—	—	—	—	—	—	—	1.7	—	—	
Medium air, >3 m	m > 3	—	—	—	—	—	—	—	—	—	—	—	4.0	—	5.9	—	—	

explained species dispersion in the foraging space delimited by axes 1 and 2. Foraging height was less important than substrate in the spatial segregation of the whole assemblage.

Axis 1 split the species that foraged on the ground from those that used the vegetation. Species that scored high on axis 1 were *Rhinocrypta lanceolata* and three granivorous species (*Columbina picui*, *Diuca diuca* and *Zonotrichia capensis*, Rufous-collared Sparrow), which obtained their food from the ground ( $\geq 90\%$  of their foraging records; Table 3). On the other side of the diagram were five insectivorous species (*Picoides mixtus*, *Melanerpes cactorum* (White-fronted Woodpecker), *Cranioleuca pyrrhophia*, *Lepidocolaptes angustirostris*, and *Leptasthenura platensis*) that captured prey from trees and shrubs ( $\geq 85\%$  of the samples).

*Stigmatura budytoides* scored high on the second axis, because it took prey from the air (Fig. 1b). *Poospiza torquata* was split from the other wintering species owing to its use of the herb layer. Unlike other granivores at Telteca, this species rarely foraged on the ground (Table 3).

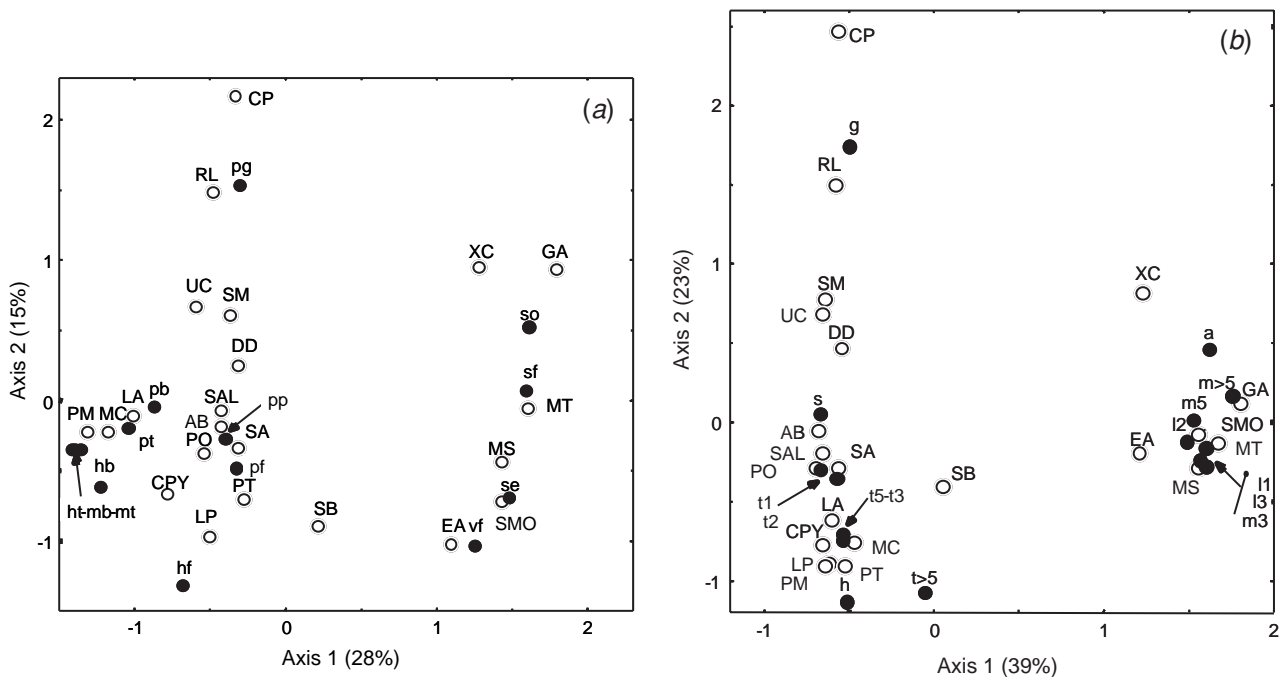
#### Breeding season (October to January): attack behaviour

Axes 1 and 2 of the correspondence analysis explained 43% of the variation observed in attack methods of the 22 species considered (Table 2). Two well-defined groups of species

emerged on the first axis. The species that composed one of these groups captured insects using aerial manoeuvres, independent of the food substrate from which food taken (Fig. 2a). Six of seven tyrant flycatchers are included in this group, with the exception of *Stigmatura budytoides*, which showed a bimodal response on the first axis. This last species took prey by hovering and sallying as well as by perching from the foliage (Table 4).

The second group of species included *Picoides mixtus*, *Melanerpes cactorum* and *Lepidocolaptes angustirostris*. They foraged while perching on thick branches and trunks. The two species of woodpeckers also foraged by hammering trunks and branches, or by hanging and taking prey from the bark. These behaviours comprised 93% or more of the attack manoeuvres of the three species (Table 4).

The species of tyrant flycatchers were split on the ordination axis 2 (Fig. 2a). *Empidonomus aurantioatrocristatus* and *Xolmis coronatus* (Black-crowned Monjita) scored high on the second axis. *Empidonomus aurantioatrocristatus* had a stereotyped attack manoeuvre characteristic of many species of tyrant flycatchers (Fitzpatrick 1985): it sallied after flying insects in open spaces, usually over the canopy. *Xolmis coronatus* also perched on exposed branches to detect prey, although it captured them in long sallies or by descending briefly to the ground.



**Fig. 2.** Ordination diagram of bird species during the breeding season on the space defined by (a) their attack methods and (b) their foraging sites in a correspondence analysis. Open circles are bird species and closed circles are foraging behaviour; acronyms of foraging behaviour as in Table 4. Bird species: AB = *Asthenes baeri*, CP = *Columbina picui*, CPY = *Cranioleuca pyrrhophia*, DD = *Diuca diuca*, EA = *Elaenia albiceps*, GA = *Empidonomus aurantioatrocristatus*, LA = *Lepidocolaptes angustirostris*, LP = *Leptasthenura platensis*, MC = *Melanerpes cactorum*, MS = *Myiarchus swainsoni*, MT = *Myiarchus tyrannulus*, PM = *Picoides mixtus*, PO = *Poospiza ornata*, PT = *Poospiza torquata*, RL = *Rhinocrypta lanceolata*, SA = *Saltator aurantioatrocristatus*, SB = *Stigmatura budytoides*, SM = *Saltator multicolor*, SMO = *Sublegatus modestus*, SAL = *Synallaxis albescens*, UC = *Upucerthia certhioides*, XC = *Xolmis coronatus*.

**Table 4. Foraging behaviour of birds during the breeding season in the central Monte Desert**

Number of foraging observations (N) for each species is given in parentheses. Bird species: AB = *Asthenes baeri*, CP = *Columbina picui*, CPY = *Craniolenta pyrrhophia*, DD = *Diuca diuca*, EA = *Elaenia albiceps*, GA = *Empidonomus aurantioatrocristatus*, LA = *Lepidocolaptes angustirostris*, LP = *Leptasthenura platensis*, MC = *Melanerpes cactorum*, MS = *Myiarchus swainsoni*, MT = *Myiarchus tyrannulus*, PM = *Picoites mixtus*, PO = *Poospiza ornata*, PT = *Poospiza torquata*, RL = *Rhinoerypta lanceolata*, SA = *Salpator aurantirostris*, SB = *Stigmatura budyoides*, SM = *Salpatria multicolor*, SMO = *Sublegatus modestus*, SAL = *Synallaxis albescens*, UC = *Upucerthia certhioides*, XC = *Xolmis coronatus*

	AB (24)	CP (22)	CPY (21)	DD (48)	EA (19)	GA (31)	LA (26)	LP (36)	MC (43)	MS (21)	MT (30)	PM (17)	PO (13)	PT (65)	RL (16)	SA (27)	SB (72)	SM (42)	SMO (36)	SAL (14)	UC (16)	XC (13)
<b>Attack behaviour</b>																						
Perching, ground	pg	16.7	95.5	-	31.3	-	-	-	-	-	-	-	7.7	1.5	68.8	11.1	2.8	42.9	5.6	21.4	37.5	23.1
Perching, foliage	pf	70.8	4.5	38.1	56.3	21.1	-	69.4	4.7	9.5	3.3	-	69.2	86.2	12.5	81.5	59.7	45.2	2.8	71.4	25.0	-
Perching, branch	pb	4.2	-	23.8	4.2	-	23.1	8.3	25.6	-	-	23.5	7.7	4.6	12.5	3.7	4.2	9.5	-	-	31.3	-
Perching, trunk	pt	4.2	-	14.3	2.1	-	73.1	-	20.9	-	-	23.5	15.4	-	6.3	-	-	-	-	7.1	6.3	-
Perching, grass	pp	4.2	-	-	2.1	-	-	-	-	-	-	-	-	1.5	-	-	-	-	-	-	-	-
Hanging, foliage	hf	-	-	14.3	-	-	-	22.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hanging, branch	hb	-	-	-	-	-	-	-	4.7	-	-	11.8	-	-	-	-	-	-	-	-	-	-
Hanging, trunk	ht	-	-	-	-	-	-	-	4.7	-	-	5.9	-	-	-	-	-	-	-	-	-	-
Hammering, branch	mb	-	-	-	-	-	-	-	16.3	-	-	29.4	-	-	-	-	-	-	-	-	-	-
Hammering, trunk	mt	-	-	-	-	-	-	-	20.9	-	-	5.9	-	-	-	-	-	-	-	-	-	-
Hovering, foliage	vf	-	-	-	2.1	57.9	-	-	-	38.1	23.3	-	-	3.1	-	-	25.0	2.4	33.3	-	-	-
Sallying, foliage	sf	-	-	-	-	-	-	-	-	4.8	3.3	-	-	-	-	-	-	-	5.6	-	-	7.7
Sallying, between foliage	se	-	-	-	-	5.3	-	-	-	9.5	16.7	-	-	1.5	-	-	5.6	-	41.7	-	-	7.7
Sallying, open space	so	-	-	-	2.1	15.8	100.0	3.8	-	2.3	53.3	-	-	1.5	-	3.7	2.8	-	11.1	-	-	61.5
<b>Foraging sites</b>																						
Ground	g	16.7	95.5	-	31.3	-	-	-	-	-	-	-	7.7	1.5	68.8	11.1	2.8	42.9	5.6	14.3	37.5	23.1
Herb or grass	h	-	-	-	-	-	-	-	-	-	-	-	-	1.5	-	-	-	-	-	-	-	-
Short shrub	s	8.3	-	-	8.3	-	-	2.8	-	-	-	-	7.7	1.5	-	3.7	2.8	7.1	-	14.3	6.3	-
Tree or shrub, <1 m	t1	29.2	-	19.0	14.6	-	46.2	-	7.0	-	-	5.9	15.4	7.7	11.1	5.6	14.3	-	-	7.1	25.0	-
Tree or shrub, 1-2 m	t2	25.0	4.5	33.3	25.0	5.3	23.1	30.6	18.6	4.8	-	23.5	61.5	26.2	6.3	40.7	22.2	21.4	2.8	28.6	31.3	-
Tree or shrub, 2-3 m	t3	16.7	-	23.8	4.2	5.3	7.7	30.6	25.6	-	3.3	29.4	-	27.7	6.3	22.2	19.4	7.1	-	28.6	-	-
Tree or shrub, 3-5 m	t5	4.2	-	23.8	12.5	10.5	19.2	33.3	37.2	-	-	41.2	7.7	23.1	18.8	7.4	16.7	7.1	-	7.1	-	-
Tree or shrub, >5 m	t > 5	-	-	-	-	-	-	2.8	9.3	4.8	-	-	-	4.6	-	-	1.4	-	-	-	-	-
Lower air, <1 m	l1	-	-	-	-	-	-	-	-	23.8	20.0	-	-	-	-	-	6.9	-	13.9	-	-	7.7
Lower air, 1-2 m	l2	-	-	-	2.1	31.6	12.9	-	-	23.8	26.7	-	-	3.1	-	-	11.1	-	25.0	-	-	15.4
Lower air, 2-3 m	l3	-	-	-	-	6.5	-	-	-	14.3	6.7	-	-	1.5	-	-	4.2	-	16.7	-	-	-
Medium air, 1-2 m	m2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Medium air, 2-3 m	m3	-	-	-	-	10.5	9.7	3.8	-	14.3	3.3	-	-	-	-	-	1.4	-	22.2	-	-	-
Medium air, 3-5 m	m5	-	-	-	-	36.8	22.6	-	-	9.5	26.7	-	-	1.5	-	3.7	4.2	-	8.3	-	-	23.1
Medium air, >5 m	m > 5	-	-	-	2.1	19.4	-	-	-	4.8	10.0	-	-	-	-	-	-	-	5.6	-	-	7.7
Higher air	a	-	-	-	-	29.0	-	-	2.3	-	3.3	-	-	-	-	-	1.4	-	-	-	-	23.1

Among non aerial-foraging species, *Columbina picui*, *Rhinocrypta lanceolata*, and to a lesser degree *Upucerthia certhioides*, *Saltatricula multicolor* and *Diuca diuca*, had high scores on the second axis, foraging mainly from the ground (Table 4). Interpretation of the foraging behaviour of species that score low on the second ordination axis is difficult. They include tyrant flycatchers that hovered to capture prey (*Elaenia albiceps*, White-crested Elaenia) or sallied among the foliage (*Sublegatus modestus*, Scrub Flycatcher). The two species of *Myiarchus* (*Myiarchus swainsoni*, Brown-crested Flycatcher; *Myiarchus tyrannulus*, Swainson's Flycatcher) showed a bimodal response curve on axis 2; they caught prey by sallying in open areas and by hovering and sallying between the foliage. *Leptasthenura platensis* and *Cranioleuca pyrrhophia* clustered together because they were the only species that captured food from foliage while hanging from thin branches. Finally, in the diagram delineated by axes 1 and 2 (Fig. 2a), there is a central group of species characterised by birds that foraged by perching from the foliage (86–56% of observations; Table 4). This group comprises *Synallaxis albescens* (Pale-breasted Spinetail), *Asthenes baeri*, *Poospiza torquata*, *Saltator aurantiirostris*, *Poospiza ornata* (Cinnamon Warbling-Finch), *Leptasthenura platensis*, *Stigmatura budytoides* and *Diuca diuca*.

#### Breeding season: foraging sites

Species ordination on axis 1 is similar to the first ordination axis of the attack behaviour. Aerial-foraging tyrant flycatchers were split from those species that foraged on vegetation or on the ground (Fig. 2b). *Stigmatura budytoides*, a species that captured prey in the air or on plants was situated between both groups of species on axis 1.

A gradient of foraging heights was expanded along the second axis. Species that walked on the ground looking for food, such as *Columbina picui* and *Rhinocrypta lanceolata*, scored high on the second axis. The opposite edge of the diagram was composed of species that foraged on shrubs and trees. From 81% to 97% of the behavioural records of these species (i.e. *Leptasthenura platensis*, *Picoides mixtus*, *Melanerpes cactorum*, *Poospiza torquata* and *Cranioleuca pyrrhophia*) was on trees and shrubs more than 1 m in height (Table 4).

Finally, several species that captured most of their food close to the ground (*Asthenes baeri*, *Synallaxis albescens*, *Poospiza ornata* and *Saltator aurantiirostris*) were arranged close together on the first two axes. Another three species related to this group were *Saltatricula multicolor*, *Upucerthia certhioides* and *Diuca diuca*. However, they differed by foraging more on the ground than on plants (Table 4).

#### Relationships between foraging behaviour components

During the breeding season, between-species differences in attack manoeuvres were positively related to changes in the

type of substrate from which food was taken (Mantel test,  $r = 0.43$ ,  $P = 0.001$ ) and with foraging site of the bird ( $r = 0.46$ ,  $P = 0.003$ ). The congruence between food substrates and foraging sites was lower in the breeding season ( $r = 0.52$ ,  $P = 0.0001$ ) than in the non-breeding season ( $r = 0.92$ ,  $P = 0.0001$ ). However, the attack manoeuvres of the wintering assemblage showed a small, but significant, correlation with food substrates ( $r = 0.35$ ,  $P = 0.002$ ) and foraging sites ( $r = 0.21$ ,  $P = 0.007$ ).

#### Plant species used

To analyse the use of plant species by foraging birds, I included all samples from Telteca in which food was taken from shrubs or trees. Food items could be a part of the plant, such as seeds or sap, or prey located on them. Foraging frequency by the whole bird assemblage (Fig. 3) differed among plant species in summer and winter (Kruskal–Wallis test, winter:  $H_{(5,48)} = 19.8$ ,  $P = 0.0014$ ; summer:  $H_{(5,108)} = 44.8$ ,  $P < 0.0001$ ). Relative frequency of plant species used by foraging birds shifted slowly between seasons (Fig. 3), although the woodland species, *Prosopis flexuosa*, was the most frequently used plant throughout the year. During the breeding and non-breeding seasons, *P. flexuosa* was used with similar frequency by foraging birds compared to the rest of plant species pooled together ( $G = 1.15$ , d.f. = 1,  $P > 0.1$ ). The most notable seasonal change in use was observed on *Capparis atamisquea* ( $G = 6.46$ , d.f. = 1,  $P < 0.02$ ). The increase in the relative importance of these shrubs in summer coincided with their fruiting period, when some birds (e.g. *Poospiza ornata*, *Diuca diuca*, *Saltatricula multicolor*) ate the arils of their seeds.

Although all bird species foraged mainly on *Prosopis flexuosa*, there were marked differences among them. The two woodpecker species and *Lepidocolaptes angustirostris* obtained most of their food from the trunks and branches of *Prosopis flexuosa* (Fig. 3), whereas *Elaenia albiceps* hovered to capture insects at flowers. Conversely, many species, such as *Saltatricula multicolor*, *Saltator aurantiirostris*, *Poospiza torquata*, *Stigmatura budytoides*, *Leptasthenura platensis*, *Asthenes baeri*, *Diuca diuca* or *Synallaxis albescens* used a broad spectrum of shrub and tree species (Fig. 3a, b). Finally, the importance of *Geoffroea decorticans* for *Cranioleuca pyrrhophia* reflects the preference of this bird for foraging within the small woodlands of *Geoffroea decorticans* growing in the flooding areas (P. G. Blendinger, personal observation).

#### Behavioural variability within functional groups

Based on diet (Blendinger 2000) and the correspondence analysis of foraging behaviours, bird species were divided into three comprehensive functional categories: (1) granivores–insectivores (hereafter granivores); (2) surface insectivores; and (3) aerial insectivores (Blendinger, in press). Attack behaviours and foraging sites of each functional group varied significantly within breeding and non-breeding



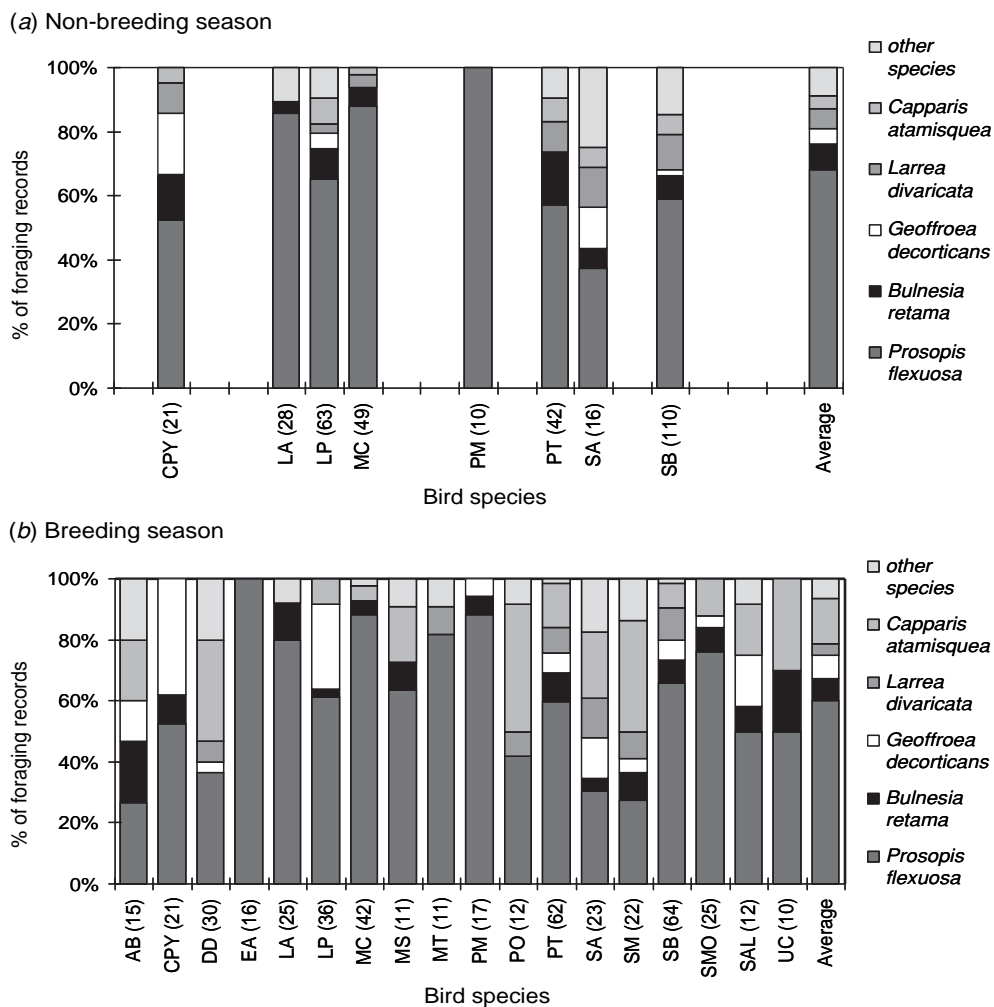
seasons (Table 5). In all cases, attack behaviours varied more than the sites where birds foraged. Among granivorous species, behavioural differences were related to the food items consumed (Fig. 4) and probably with resource availability. In winter, granivores consumed larger amounts of seeds than in summer, when their diet included more insects, reflecting the increase in arthropod abundance then (G. Debandi and P. G. Blendinger unpublished data).

Species lying near the edge of the ordination diagrams might be expected to have a narrower range of foraging behaviours than the other members of the assemblage. During the breeding season, a granivore (*Columbina picui*), an aerial insectivore (*Empidonomus aurantioatrocristatus*)

and a substrate insectivore (*Lepidocolaptes angustirostris*) showed the highest scores (Fig. 5a). Differences among species were less marked in the non-breeding season: *Lepidocolaptes angustirostris* and *Melanerpes cactorum* showed high scores in the attack behaviour space; *Columbina picui* and *Rhinocrypta lanceolata* were specialised in the use of foraging sites; and *Picoides mixtus* was specialised in both components of foraging behaviour (Fig. 5b).

**Discussion**

Groups of species with similar foraging behaviour can be defined by their foraging sites and attack behaviour. Among



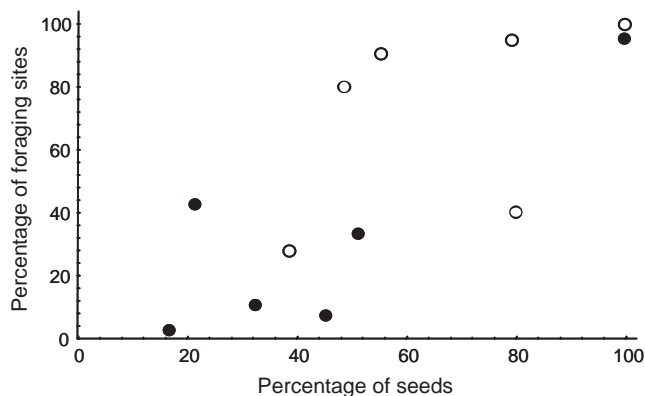
**Fig. 3.** Relative frequency of use of shrub and tree species by foraging birds during (a) the non-breeding season and (b) the breeding season; including only species with ten or more foraging records in trees and shrubs. Sample size for each bird species is indicated in parentheses. Plant species included as ‘other species’ are, in decreasing order: *Lycium tenuispinosum*, *Tricomaria usillo*, *Ximena americana*, *Bougavillea spinosa*, *Lycium chilense*, *Prosopis alata*, *Prosopis argentina*, *Ephedra boelckei* and *Atriplex lampa*. Bird species: AB = *Asthenes baeri*, CPY = *Cranioleuca pyrrhophia*, DD = *Diuca diuca*, EA = *Elaenia albiceps*, GA = *Empidonomus aurantioatrocristatus*, LA = *Lepidocolaptes angustirostris*, LP = *Leptasthenura platensis*, MC = *Melanerpes cactorum*, MS = *Myiarchus swainsoni*, MT = *Myiarchus tyrannulus*, PM = *Picoides mixtus*, PO = *Poospiza ornata*, PT = *Poospiza torquata*, SA = *Saltator aurantiostris*, SM = *Saltatricula multicolor*, SB = *Stigmaturota budytoides*, SMO = *Sublegatus modestus*, SAL = *Synallaxis albescens*, UC = *Upucerthia certhioides*.

**Table 5. Differences in foraging behaviour within functional groups (*G* test of heterogeneity)**

	Attack behaviour			Foraging sites		
	<i>G</i>	d.f.	<i>P</i>	<i>G</i>	d.f.	<i>P</i>
Breeding season						
Granivores	74.7	20	<0.001	86.5	30	<0.001
Surface insectivores	261.4	32	<0.001	145.9	32	<0.001
Aerial insectivores	221.1	24	<0.001	173.9	30	<0.001
Non-breeding season						
Granivores	195.0	20	<0.001	179.6	30	<0.001
Surface insectivores	248.7	32	<0.001	184.9	32	<0.001

the birds from Telteca, the main factor distinguishing bird species was the dichotomy between whether birds foraged on the ground or above it. Similarly, in bird assemblages from temperate forests and woodlands of North America and Australia, species could be separated on their vertical stratification during foraging (Holmes *et al.* 1979; Ford *et al.* 1986; Holmes and Recher 1986; Recher and Davies 2002). At Telteca, three groups of bird species were defined according to three broad types of food substrate (ground, air and vegetation), and by foraging sites. Nevertheless, composition and structure of the assemblage changed with season, demonstrating the importance of conducting year-round studies in seasonal environments.

The interpretation of foraging behaviour is scale-dependent. Studies covering different seasons may reach different interpretations than those from single-season studies, because the former includes behaviours of species faced with changing resources (Block 1990; Cale 1994; Wilson and Recher 2001). A shortcoming of this study is that I could not examine annual changes in foraging behaviour because samples obtained for many species were small. Foraging behaviour is likely to change from one year to the next, as bird abundance or resource persistence and reliability varies. In the Monte Desert, annual changes in seed supply (Marone *et al.* 1998; Blendinger and Ojeda 2001) and arthropod abun-



**Fig. 4.** Relationships between seed proportion in the diet of granivores and the percent of foraging observations on ground and grasses during the breeding season (closed circles) and non-breeding season (open circles).

dance (Debandi 1999) have been documented, and are likely to influence the components of foraging behaviour.

The most notable difference between seasons was the presence of birds that capture prey in the air during the breeding season. All species in this group are migrants and insectivores, and belong to the same family (Tyrannidae). These species ate flying insects, a resource much more abundant in the rainy and warmer summer period. *Stigmaturo budytoides*, the only resident species in this group, dramatically changed its attack behaviour according to strong seasonal variations in flying insect supply. Miles (1990a) found that insectivorous species showed greater temporal variation in foraging behaviour in desert shrublands than in deciduous temperate forest from North America. In the Monte Desert, seasonal changes in resource availability had a stronger effect on aerial insectivores than on other functional groups of birds, resulting in changes in foraging behaviour of resident species and, potentially forcing departure of more specialised aerial foragers.

A second group of species was characterised by foraging on the ground. Despite the similarity in foraging behaviours, species in this group belong to very different functional groups. *Columbina picui* and *Rhinocrypta lanceolata* searched for and consumed their food on the ground, overlapping almost completely in attack behaviour and foraging site. However, *Columbina picui* is a strict granivore whereas *Rhinocrypta lanceolata* consumes insects and, occasionally, small fruits. Other species, such as *Diuca diuca*, *Saltatricula multicolor*, *Upucerthia certhioides* and *Asthenes baeri*, foraged mainly on the ground in winter, but changed to more arboreal foraging behaviour during the breeding season.

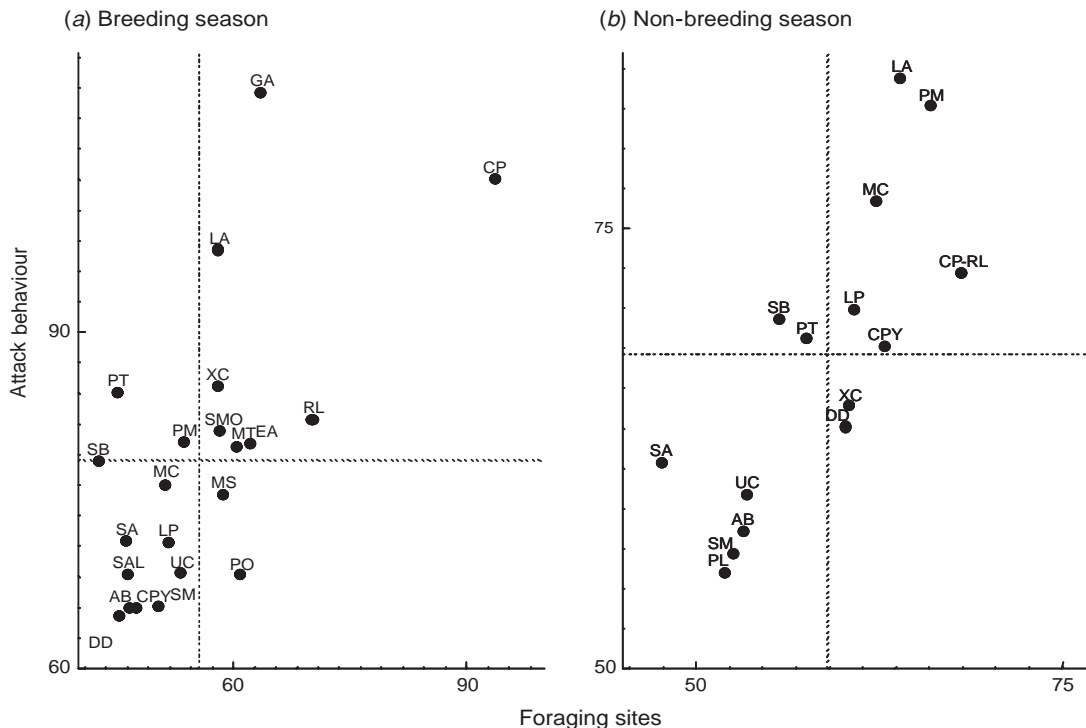
The third group of species was more heterogeneous than the other two groups. It included species that obtained most of their food from vegetation by perching, hanging or hammering. During the non-breeding season, these species used holes made by *Melanerpes cactorum* to obtain sap (Genise *et al.* 1993; Blendinger 1999). Birds that searched for food on branches and trunks formed a subgroup of species, although they differed in foraging postures and movements, and occupied different foraging strata. Similarities in foraging behaviour among the five species of this subgroup (*Picoides mixtus*, *Melanerpes cactorum*, *Lepidocolaptes*

*angustirostris*, *Cranioleuca pyrrhophia* and *Leptasthenura platensis*) diminished during the breeding season.

Analysis of species-specific foraging behaviour could explain the increase in species richness and bird abundance observed in woodland patches of *Prosopis flexuosa* compared with the dune shrubby matrix in Telteca (P. G. Blendinger, personal observation). In the more humid and protected inter-dune lowlands, *Prosopis flexuosa* forms a canopy three times taller than the remaining plant cover, and facilitates recruitment of many other plant species (Rossi and Villagra 2003), thereby increasing local vegetation diversity. Many bird species, mostly migratory insectivores, reportedly prefer mimosoid tree species such as *Acacia* and *Prosopis* as foraging substrates (Greenberg *et al.* 1997). These authors suggested that high abundance and species number of birds in mimosoid woodlands is likely to be a consequence of high densities of foliage arthropods attracting foliage insectivores (Greenberg *et al.* 1997). However, most bird species at Telteca, even those belonging to different functional groups, foraged on *Prosopis flexuosa*. The use of this tree species throughout the year was remarkable, considering that the resources exploited changed markedly between seasons, with insects dominating in summer and sap

in winter. Those species that foraged from trunks and branches were closely linked to the presence of *Prosopis flexuosa* trees. These species included the two woodpeckers and *Lepidocolaptes angustirostris*, which were present throughout the year and which are absent from other areas in the Monte Desert where *Prosopis* trees have been removed by logging (P. G. Blendinger personal observation). During the winter dry season, *Prosopis flexuosa* is important for species that frequented holes made by *Melanerpes cactorum* to obtain sap (Blendinger 1999). Sap is a major food source for *Melanerpes cactorum* during the dry season. Holes drilled by woodpeckers enable other species to use the sap, facilitating access to a food rich in water and sugar during the season when availability of such resources are limited. A similar switch to food items rich in sugar was observed in Australian dry forests and woodlands during part of the year (e.g. Holmes and Recher 1986).

Also working in an arid environment, Tomoff (1974) found that the number of substrates and foraging sites used by the bird assemblage increased with the physiognomic complexity of the vegetation. At Telteca, however, resources associated with a single species of tree appear to be as important for foraging birds as physiognomic heterogeneity.



**Fig. 5.** Diagram of mean Euclidean distance (dashed line) between bird species in attack behaviours and foraging sites. Bird species: AB = *Asthenes baeri*, CP = *Columbina picui*, CPY = *Cranioleuca pyrrhophia*, DD = *Diuca diuca*, EA = *Elaenia albiceps*, GA = *Empidonomus aurantioatrocristatus*, LA = *Lepidocolaptes angustirostris*, LP = *Leptasthenura platensis*, MC = *Melanerpes cactorum*, MS = *Myiarchus swainsoni*, MT = *Myiarchus tyrannulus*, PL = *Pseudoseisura lophotes*, PM = *Picoides mixtus*, PO = *Poospiza ornata*, PT = *Poospiza torquata*, RL = *Rhinocrypta lanceolata*, SA = *Saltator aurantirostris*, SB = *Stigmatura budytoides*, SM = *Saltatricula multicolor*, SMO = *Sublegatus modestus*, SAL = *Synallaxis albescens*, UC = *Upucerthia certhioides*, XC = *Xolmis coronatus*, ZC = *Zonotrichia capensis*.

Further studies are needed to determine the relative importance of both factors. In a more mesic locality in the Monte Desert, Marone (1991) found that inter-habitat gradients of tree and shrub cover partially explained the spatial segregation of species during the breeding season. Thus, the information available suggests that in the Monte Desert, habitat complexity and presence of *Prosopis* trees are two main factors that contribute to the spatial segregation of bird species, providing different opportunities for searching and finding food.

Interspecific differences in foraging sites and food substrates were strongly interrelated, although their congruence with differences in attack behaviours was lower. Bird species were segregated primarily by the substrate from which they obtained food, suggesting that spatial heterogeneity, tree species composition, and availability of foraging substrates were important axes of environmental variation that determined assemblage structure. Species that clustered together owing to their foraging behaviour may have distinct trophic habits. Complementary studies on their diet are necessary to identify species that might interact negatively. For example, detailed studies on the diet of granivorous species through the Monte Desert (Blendinger 2000) found that, independent of similarities in their foraging behaviour, the changes in the diet of coexisting species was explained more by individual responses and morphological restrictions than by direct interactions among species. The present study suggests that seasonal changes in availability of food resources, presumably mediated by physical factors such as temperature and precipitation, were also important factors that allowed species coexistence and caused variation in functional groups of birds, as defined by their foraging behaviour.

### Acknowledgments

This study was supported by a doctoral grant of the National Council for Science and Technology (CONICET) of Argentina, and was partially supported by a CONICET grant (PIP No. 4684). Harry Recher and Van Remsen provided helpful advice on the manuscript. Thanks to Ricardo Ojeda, Manuel Nores, Jorge Gonnet, Stella Giannoni and John Blake for comments on a first draft; to Adriana Rubinstein, Susana Peluc and Dolores Juri for their assistance in the field; and to the Department of Natural Resources of Mendoza for logistical support at Telteca.

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Manuscript received 13 October 2003, accepted 4 October 2004