Articles

Litter and seed burying alter food availability and foraging efficiency of granivorous birds in the Monte desert

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We assessed experimentally if the main granivorous bird species that feed on the ground in the central Monte desert are able to detect and consume seeds buried in the soil or trapped within litter. Understanding seed vulnerability to birds allows 1) a better understanding of how seed abundance translates into seed availability, a necessary step to assess seed limitation scenarios, and 2) whether birds alter the distribution of soil seeds through their consumption. Rufous-collared sparrows found and consumed high proportions of buried seeds, though less seeds were eaten at increasing depths. In contrast, many-colored chaco-finches, common diuca-finches and cinnamon warbling-finches did not find buried seeds. All bird species fed on every substrate offered but, as a whole, birds reduced by 50% their seed consumption in *Prosopis* litter, and by 30% in *Larrea* litter, compared to consumption in bare soil. This effect was less notable for rufous-collared sparrows, whose 'double scratch' foraging method would contribute to its great diet breath and abundance in the Monte desert. As birds do not reach a fraction of seeds buried and trapped by litter, seeds readily available for them may be scarcer than previously estimated through soil seed bank studies. Furthermore, since the four bird species detect and consume seeds from littered microhabitats, seed consumption by them surely affects the seasonal dynamics of the soil seed bank in all microhabitat types of the Monte desert.

The difference between resource abundance and resource availability impacts our ability to assess the degree to which consumer populations are food limited (Hutto 1990, Newton 1998). Available food is a complex function of food abundance and its actual accessibility to the consumer (Coleman 2008), and the translation from abundance into availability depends on particular combinations of both components (Wiens 1984).

The vulnerability of immobile prey usually depends on microhabitat or background structure and is therefore context dependent (Gordon 2011). It is well known that foliage architecture modifies the chances of capturing prey by arthropod-feeding birds (Parrish 1995, Whelan 2001, Park et al. 2008). Whittingham and Markland (2002) also found that seed accessibility for birds foraging on the ground declines with substrate complexity. Jones et al. (2006) showed that microhabitat structure modifies seed detection, and Baker et al. (2009) reported that microhabitat complexity reduces feeding rate by reducing predator–prey encounter rates. Foraging efficiency of seed-eating birds may also depend on seed burial. Whalen and Watts (2000) found that seed burial has a species-specific impact on emberizid birds: those doing 'bilateral scratch' or 'double scratch' (i.e. quickly moving both legs backwards

and forwards simultaneously; Harrison 1967, Greenlaw 1977) are able to recover buried seeds, while those unable to develop such foraging techniques only consume the unburied seeds (Whalen and Watts 2000).

Granivorous birds of the Biosphere Reserve of Ñacuñán, central Monte desert, Argentina, forage mainly on grass seeds (Marone et al. 2008), which they prefer – especially the medium or large grass seeds – over similar sized forb seeds (Cueto et al. 2006). Most grass seeds enter the soil bank through open, bare soil or grassy microhabitats during primary dispersal, but the seeds are not found in these microhabitats by the beginning of the next growing season (Marone et al. 2004). On average, seed loss from January to August (summer to winter in the Southern Hemisphere) exceeds 75% of seed dispersal in open micro-habitats (Marone et al. 2004), largely due to seed burial, redistribution by wind or water to littered microhabitats, and consumption by granivores. Whether granivorous birds can still consume their target seeds when trapped within litter or buried in the ground is an unresolved question, which is essential to determine the fraction of seeds that is actually available to different bird species (i.e. to evaluate how seed abundance translates into availability), and the potential impact of bird consumption on the

seasonal dynamics of the soil seed bank and, consequently, the importance of bottom–up and top–down effects in the granivore–seed system (Marone et al. 2008).

We assessed experimentally the extent to which the main granivorous bird species that feed on the ground in the central Monte desert can detect and consume seeds buried in the soil or trapped within litter. We predict that increasing microhabitat substrate complexity and increasing seed depth in soil will reduce foraging efficiency for all bird species, up to a point when seeds will result unavailable. Second, if species-specific morphological and behavioral features do limit which seeds are available to the birds, we expect that those species that are capable of using 'double scratching' with their legs will have access to more seeds, both in the soil and trapped within litter. Finally, if birds use visual cues to explore potential foraging patches and use leave–stay rules during their exploitation, we expect untrained birds to search for hidden seeds only if accessible seeds on the surface are previously found and consumed.

Methods

Study site and bird species

We captured granivorous birds with mist-nets and cage-traps in the open *Prosopis flexuosa* woodland located in the Biosphere Reserve of Ñacuñán (34°03′S, 67°54′W). This habitat has a tree stratum composed of scattered individuals of *P. flexuosa* and *Geoffroea decorticans* within an extensive shrub stratum (mainly *Larrea divaricata*). The herbaceous stratum is dominated by grass species (the most abundant are *Pappophorum* spp., *Digitaria californica*, *Trichloris crinita*, *Aristida* spp., *Sporobolus cryptandrus* and *Setaria leucopila*). Most forb species are annuals (e.g. *Chenopodium papulosum*, *Phacelia artemisioides*, *Sphaeralcea miniata*, *Parthenium hysterophorus*, *Lappula redowskii*, *Plantago patagonica*); their cover is usually lower than grass cover but highly variable from year to year (Marone 1991). Ñacuñán has a dry temperate climate, with cold winters and hot summers. On average, >75% (263 mm, n = 31 yr) of the annual rainfall occurs in spring and summer (October–March).

Granivorous bird species used in experiments were: cinnamon warbling-finch (*Poospiza ornata*, body weight: 13 g), rufous-collared sparrow (*Zonotrichia capensis*, body weight: 19 g), many-colored chaco-finch (*Saltatricula multicolor*, body weight: 22 g) and common diuca-finch (*Diuca diuca*, body weight: 25 g). These species mainly search for seeds on the soil, as members of a ground-foraging guild (Lopez de Casenave et al. 2008).

Experimental design

All captured birds were kept in individual cages (30 × 20 × 20 cm) for <10 d in an indoor room under natural photo-period with ad libitum color polymorphic foxtail millet (*Setaria italica* seeds; size = 2.6 × 1.5 × 1.1 mm, weight = 2.4 mg) and vitamin-enriched water.

Individual birds were tested in an observational cage (40 × 40 × 40 cm, with a single horizontal perch). They were moved from their cage to the observational cage in darkness and, after one minute, a hidden observer turned on a light and the bird was allowed to feed for a period of time, depending upon the specific experimental setup. Each trial was preceded by two hours of food deprivation, with water available.

Every bird received a single testing and training session in the observational cage, which consisted of allowing the bird to feed from a petri dish with 250 mg of foxtail millet seeds in the center of the experimental arena. Individuals that did not feed for one hour were not tested further and released. In total, 38 birds (10 cinnamon warbling-finches, 10 rufous-collared sparrows, 10 many-colored chaco-finches, and 8 common diuca-finches) fed during this first session, were tested in the experiments and then immediately released near their capture site.

Seed depth experiments

In order to vary the depth of soil in the foraging environment, we used a circular piston (diameter = 10 cm) within a cylinder located under the observational cage that allowed the modification of the distance between the top of the piston and the floor of the experimental arena by changing the length of the piston rod. Scattered seeds on the surface of the piston were covered with the necessary amount of sifted sand to level with the rest of the experimental arena. We performed two types of experiments.

Experiment A

We offered foxtail millet seeds at different depths: 0 mm (surface), 4 mm, 8 mm, 16 mm and 32 mm. In the first trial, each individual was offered 50 foxtail millet seeds on the surface. In the following tests, 45 buried foxtail millet seeds were offered at increasing depths, with five seeds remaining on the surface in order to trigger feeding in the patch (Whalen and Watts 2000). In each trial, an individual subject was allowed to feed during a 3 min trial, after which the soil was sifted and all remaining seeds were recovered. The five seeds on the surface differed from the buried seeds in color (i.e. dark vs pale) to permit their identification. Trials continued, during which the depth of offered seeds continued to increase, if at least one individual of each focal species had consumed buried seeds in the previous series of trials (i.e. at a smaller depth). We tested five cinnamon warbling-finches, five rufous-collared sparrows, five many-colored chaco-finches, and four common diuca-finches.

Experiment B

To evaluate the importance of seeds at the surface as indicators of the presence of buried seeds, we carried out an experiment following a similar protocol as in Experiment A, in which surface seeds were not offered and 50 seeds were buried at 4 mm depth. In this case, trials lasted 10 min to guarantee that birds had enough time to search for seeds. We tested four rufous-collared sparrows and four many-colored chaco-finches.

We analyzed data with one factor repeated measures ANOVA (Zar 1996), because all depths were tested with the same individual bird, therefore constituting a repeated measure (Zar 1996). A Tukey multiple comparison test

(Day and Quinn 1989) was used to detect at which depths birds consumed more seeds.

Substrate experiments

We used an experimental design that combined both choice and non-choice experiments to detect absolute and relative substrate preferences by the four granivorous species. This combined protocol can overcome the limitations and biases of using only one of the experimental designs, which is crucial when the species under study has partial or conditional preferences (e.g. the use of an item depends on the availability of other options; Cueto et al. 2001). Substrate options were bare soil (sifted sand from Ñacuñán soil), *Larrea* litter (from under the canopy of *Larrea divaricata* shrubs), and *Prosopis* litter (from under the canopy of *Prosopis flexuosa* trees). These are the three most common substrates that granivorous birds confront when searching for seeds on the ground. In the Ñacuñán landscape, horizontal plant cover is < 50%, with *Larrea divaricata*, and *Prosopis flexuosa* accounting for approximately 33 and 6% of the ground cover, respectively (Milesi 2006). We collected naturally accumulated litter under *Larrea* shrubs and *Prosopis* trees, and kept it in plastic bags until used. *Larrea* litter was shallow (depth < 1 cm), mainly formed by small leaves and twigs, whereas *Prosopis* litter was bigger and thicker (around 2 cm), mostly formed by pieces of its leaves (small pinnas and long raquises), twigs and small branches.

In choice experiments, we presented the three substrate options simultaneously. The experimental arena was a circular tray (38 cm in diameter and 3 cm high), formed by three 120° sectors ('pizza portions'). The 'bare soil portion' was covered with 0.5-cm deep sifted sand, the '*Larrea* portion' with a 1 cm bed of *Larrea* litter, and the '*Prosopis* portion' with a 2 cm bed of *Prosopis* litter. We used local photographs as guides to build the litter portions realistically. In each trial, 20 seeds of foxtail millet were scattered randomly on each portion and an individual bird was allowed to feed during 3 min (following the same procedure explained above). At the end of each trial, we sifted each substrate to remove all remaining seeds and recorded the number of seeds consumed. Non-choice experiments were similar, except that the three sectors had the same substrate. In both choice and non-choice experiments we tested five cinnamon warbling-finches, five rufous-collared sparrows, five many-colored chaco-finches, and four common diuca-finches.

Following the recommendations of Roa (1992) and Lockwood (1998), we used two-way ANOVA with repeated measures on one factor (Zar 1996) to analyze choice data, given that the substrate treatments were offered simultaneously and therefore were not independent. The second factor was the granivorous bird species. We used the same statistical test for the analysis of non-choice data, because we tested all substrates with the same individual bird, therefore constituting a repeated measure (Zar 1996). A Tukey multiple comparison test with Kramer modification for unbalanced design (Day and Quinn 1989) was used to evaluate the substrates in which birds consumed more seeds. The greenhouse-geiser procedure (lower bound epsilon correction) was applied to adjust the degrees of freedom of within-subject effects when data violated the symmetry assumption (Winer 1971). Given that we had an unequal number of replicates per cell, we used the type III method to compute the sum of squares (Shaw and Mitchell-Olds 1993).

We also applied a graphical analysis to integrate the results of choice and non-choice experiments, which allows visual detection of preferred, avoided, and less-preferred substrate types (Cueto et al. 2001, 2006). The average percentage of seeds consumed by each granivorous bird species in each substrate type was represented on the x (non-choice) and y (choice) axes of a 2D scatterplot. For each species, each substrate type was assigned to one of three groups: 1) preferred (seed consumption > 75% in both kinds of experiments), 2) avoided (seed consumption < 25% in both kinds of experiments), and 3) less-preferred (seed consumption between 25 and 75% in choice experiments, and > 25% in non-choice experiments). All values are reported as averages ± SD. All tests were considered statistically significant when $p < 0.05$.

Results

Seed depth experiments

In Experiment A (seeds at increasing depths) all birds consumed most seeds offered at the surface (0 mm depth, Table 1): > 80% by rufous-collared sparrow, many-colored chaco-finch and common diuca-finch, and > 50% by cinnamon warbling-finch. With buried seeds we obtained a contrasting pattern. Many-colored chaco-finch, common diuca-finch and cinnamon warbling-finch did not extract buried seeds (although they did consume the few seeds at the surface). By contrast, rufous-collared sparrow found and consumed an large proportion of the buried seeds, though with decreasing efficacies at increasing depths ($F_{4,16} = 191.6$, $p < 0.0001$, Table 1): 95% of seeds at 4 mm depth, 75% of seeds at 8–16 mm depth, and < 1% of seeds at 32 mm depth (only one individual consumed three seeds at this depth).

In Experiment B (only buried seeds) none of the rufous-collared sparrows or many-colored chaco-finches consumed any seeds, although they did consume many surface seeds during the single training session.

Substrate experiments

The four granivorous bird species showed the same pattern of substrate use when searching for and consuming seeds in both choice and non-choice experiments (non significant interaction effects, Table 2, Fig. 1). Overall, birds ate more seeds in bare soil, intermediate numbers of seeds in *Larrea* litter and fewer seeds in *Prosopis* litter (significant substrate effect: Table 2, Fig. 1; Tukey multiple comparison test, $p < 0.05$). Bird species differed in the amount of seeds consumed: in both experimental designs, rufous-collared sparrow ate more seeds than the other three species (significant species effect: Table 2, Fig. 1; Tukey multiple comparison test, $p < 0.05$).

The integration of both experimental approaches allows for a better evaluation of the whole pattern (Fig. 2). Bare soil

Table 1. Average number ($\pm$ SD) of foxtail millet pale seeds consumed in seed burying experiments by four granivorous bird species of the central Monte desert, Argentina. An en dash indicates that the experiment was not run because no individual extracted seeds in previous trials at smaller depths. See Methods for a detailed description of Experiments A (buried seeds at increasing depths, with some seeds on surface) and B (only buried seeds). The number of individuals tested is shown between brackets. Depth treatments denoted by different superscript letters were statistically different (Tukey multiple comparison test, $p < 0.05$).

		Depth (mm)				
	Species	0	4	8	16	32
Experiment A	Rufous-collared sparrow [5]	44.8 $\pm$ 0.5[a]	44.4 $\pm$ 0.9[a]	34.8 $\pm$ 4.8[b]	36.0 $\pm$ 4.1[b]	0.6 $\pm$ 1.3[c]
(45 pale seeds at depth +	Many-colored chaco-finch [5]	42.0 $\pm$ 1.9	0	–	–	–
5 dark seeds on surface)	Common diuca-finch [4]	35.6 $\pm$ 9.8	0	–	–	–
	Cinnamon warbling-finch [5]	26.4 $\pm$ 9.5	0	–	–	–
Experiment B	Rufous-collared sparrow [4]	39.5 $\pm$ 13.9	0	–	–	–
(50 buried pale seeds)	Many-colored chaco-finch [4]	43.3 $\pm$ 12.8	0	–	–	–

substrate was preferred by three out of four bird species (it was less-preferred by cinnamon warbling-finch). *Larrea* litter was preferred by rufous-collared sparrow and less-preferred by the other three species. *Prosopis* litter was less-preferred by the four bird species. Notably, the four granivorous bird species used the three types of substrate offered.

Discussion

The main granivorous birds of the Monte desert showed a contrasting response to seeds offered in different substrates and at different depths. Many-colored chaco-finch, common diuca-finch and cinnamon warbling-finch did not detect buried seeds or were unable to extract them. During the experimental sessions, birds readily consumed seeds on the surface and then crisscrossed the experimental arena without intentionally displacing soil with their beaks or legs. If this is their usual behavior in the field, then buried seeds, even when a few millimeters depth, are not part of the available soil seed bank for these species. In contrast, rufous-collared sparrows 'double scratched' the soil, recovering up to 80% of the seeds at a depth of 16 mm or less in just three minutes. One individual even consumed some seeds at 32 mm depth, showing the efficacy of 'double scratching' to recover buried seeds (Whalen and Watts 2000).

An interesting result is that rufous-collared sparrows only started 'double scratching' when some seeds were available on the soil surface (Experiment A vs B). It appears that there must be some visible seeds to trigger rufous-collared sparrow foraging. At that point, this species has the particular ability to start searching for more seeds below. In field experiments with rufous-collared sparrows feeding on natural substrates within aviaries, Milesi (2006) found that birds do not follow indirect environmental cues of seed abundance at the microhabitat scale, but rather explore everywhere and decide where to stay foraging while (enough) seeds are found. Our lab experiments support this idea, since rufous-collared sparrows only started scratching for hidden seeds once a potentially profitable patch was detected.

Rufous-collared sparrow has greater diet breath compared to that of specialized – graminivorous – species like many-colored chaco-finch in the central Monte desert (Marone et al. 2008). Some physiological mechanisms contribute to explain this ecological characteristic. Rufous-collared sparrow forages on seeds regardless of starch content, which is usually high in grass seeds, and tolerates dietary phenolics owing to its detoxification capability (Ríos et al. 2012a, b). Besides these physiological capacities, behavioral mechanisms like 'double scratching' might also facilitate the generalized diet of rufous-collared sparrow. As in other deserts worldwide, the soil seed bank at Ñacuñán is highly heterogeneous in space, with many seeds accumulating with the litter in natural depressions and below shrubs and trees (Marone and Horno 1997, Marone et al. 2004). Although the tiny grass seed of *Sporobolus cryptandrus* reaches soil depths >2 cm, the bulk of grass seed species lie on the soil surface or in the first millimeters of the soil (Marone unpubl.). Furthermore, only 2% of seeds buried deeper than 2 cm are medium or large grass seeds, but 98% of buried seeds are forb seeds (Marone et al. 1998). This pattern suggests that under field conditions most grass seeds remain on soil surface, available for the four bird species, but that numerous forb seeds are buried in the soil where they remain available

Table 2. Summary of the two-factor analysis of variance with repeated measures on one factor for choice and non-choice substrate experiments with four granivorous bird species of the central Monte desert, Argentina. Probabilities for within-substrate effects in the non-choice substrate experiments have been adjusted with the Lower Bound Epsilon correction ($\varepsilon = 0.729$). (MS = mean squared.)

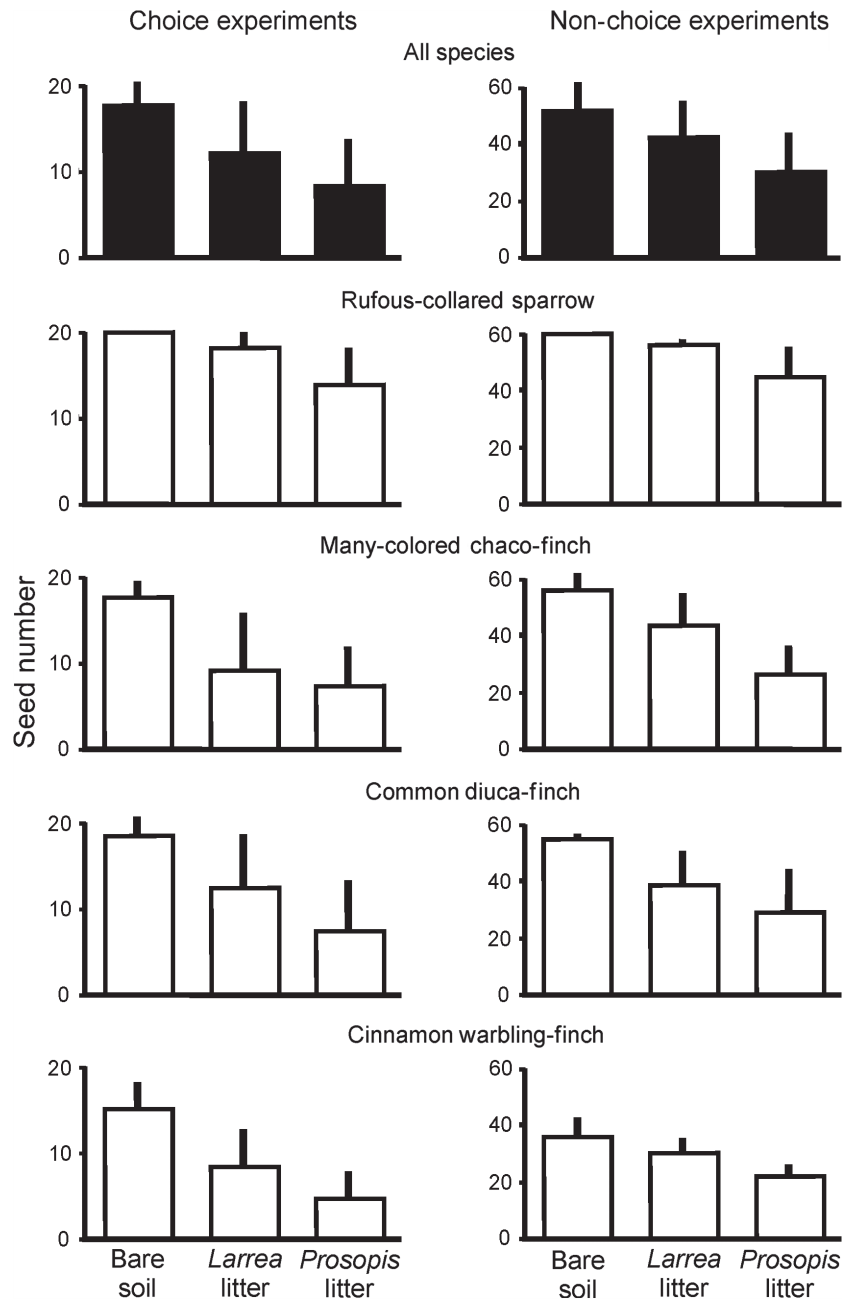|		Choice substrate experiments			Non-choice substrate experiments		
Source of variation	DF	MS	F	p	MS	F	p
Between species							
Species	3	168.6	8.13	0.0018	1475.5	15.20	< 0.0001
Individual (Species)	15	20.7			96.5		
Within species							
Substrate	2	431.6	29.21	< 0.0001	2070.0	37.46	< 0.0001
Substrate $\times$ Species	6	11.8	0.80	0.58	82.1	1.56	0.19
Substrate $\times$ Individuals (Species)	30	14.8			55.3		

Figure 1. Average number of seeds consumed in choice and non-choice substrate experiments by all species (black bars) and by each of the four granivorous bird species (white bars) of the central Monte desert, Argentina. Whiskers indicate standard deviations.

only to rufous-collared sparrows. For example, the seeds of *Chenopodium papulosum* and *Glandularia mendocina*, which constitute >40% of the rufous-collared sparrow's diet (Marone et al. 2008), were abundant below 2 cm deep into the soil (Marone et al. 1998). The 'double scratching' capacity of rufous-collared sparrows allows them to acquire seeds unavailable to the other species, showing that their repertoire of physiological as well as behavioral abilities enhances their resource base. We conjecture that the abundance of this generalist species is greater in autumn-winter in Ñacuñán than that of the rest of the birds with more restricted diets and behavioral abilities due to a greater availability of seeds to rufous-collared sparrows (Lopez de Casenave et al. 2008, Marone et al. 2008).

Substrate complexity had clear but weaker effects than seed burying on bird foraging. All species fed on every substrate offered, but *Prosopis* and *Larrea* litters reduced the bird's efficiency to detect or to extract seeds. As a whole, birds reduced their seed consumption by 50% in *Prosopis* litter, and by 30% in *Larrea* litter, compared to bare soil. This effect, however, differed in magnitude among species. Again, it was less adverse in the species with the behavioral option to 'double scratch', the rufous-collared sparrow. Microhabitat structural complexity modifies seed foraging rates in the species study here, as in other granivorous birds (Whittingham and Markland 2002, Jones et al. 2006, Baker et al. 2009), but the magnitude of the effect seems to depend on the behavioral toolkit of each species.
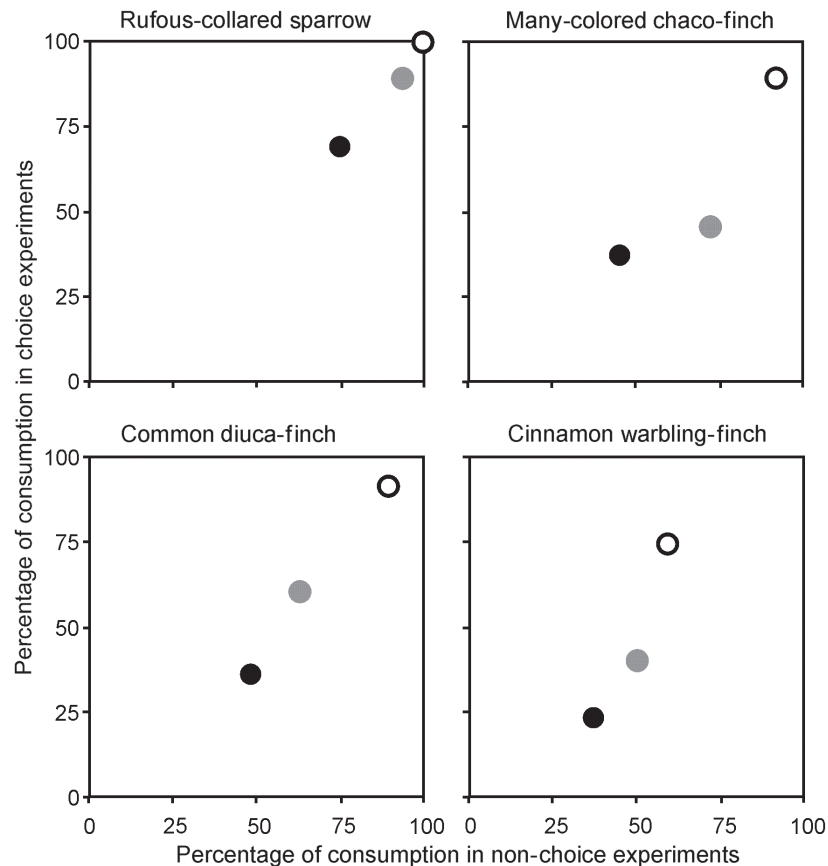
Figure 2. Scatter plots integrating the results of non-choice (x-axis) and choice (y-axis) experiments of substrate type by four granivorus bird species of the central Monte desert, Argentina. Data is the average percentage of seeds consumed in each experiment type in bare soil (open circles), *Larrea* litter (grey) and *Prosopis* litter (black) substrates.

Our results have practical implications for bait removal studies of granivory and its top-down effect at the community level. For example, studies following the GUD approach (Brown 1988, 1999) usually offer trays with seeds mixed in sandy substrates (Brown 1988, Garb et al. 2000). This technique could underestimate granivory rates in areas like the central Monte desert, where only seeds left at surface would be accessible to all seed-eating bird species. Such GUD experiments may measure only the effect of rufous-collared sparrows on seeds. In worldwide comparative studies, the avian granivores in the Monte's bird community may appear less important as they may actually be. Dispersing seeds over structured surfaces to increase searching costs or times (e.g. commercial turf: Whittingham and Markland 2002; artificial stubble: Butler and Gillings 2004, Jones et al. 2006, Baker et al. 2009; artificial grass: Tsurim et al. 2010; natural plant litter: this study) may prove more appropriate, though the relationship between increase in search time with decreasing seed densities (and time in the patch) remains to be tested for these visual seed foragers (Hayslette and Mirarchi 2002).

The restrictions on foraging at depth and from complex substrates studied here contribute to a better evaluation of the relationship between seed abundance and seed availability in the soil seed bank. Classic estimates of seed abundance in Ñacuñán considered the whole palatable seed bank up to 2 cm deep (Marone and Horno 1997, Marone et al. 2004). However, several species did not seem able to access buried seeds, and all of them decreased their foraging rate when searching for seeds within litter. Seed availability for bird species appears to be less than previously estimated and, in this context, seed shortages could be more likely than that previously considered, making plausible the hypothesis of occasional food limitation for granivorous birds in undisturbed scrublands and open woodlands of the central Monte desert (Marone 1992).

Our results also have implications for assessing the role of birds in the removal and redistribution of grass seeds over different microhabitats after primary dispersal in the Monte desert. Most seed loss during secondary dispersal has been imputed to consumption by birds (Marone et al. 2000, 2004), established as the main granivores during autumn–winter (Lopez de Casenave et al. 1998). Our results support that hypothesis, since all birds easily consumed the seeds offered on the bare soil surface, the type of substrate characteristic of the open microhabitas where 75% of grass seeds land during primary dispersal. Moreover, rufous-collared sparrow is the most abundant bird species during the grasses' primary dispersal season (Marone et al. 1997), does not restrict its foraging to particular microhabitats (Milesi et al. 2008), and is not strongly affected by litter presence or normal seed burying (this work). Since the

other three species do not avoid exploring and foraging from littered microhabitats (Milesi et al. 2008, this work), where they experience moderate decreases in their foraging efficiency (this work), seed consumption by birds surely affects the seasonal dynamics of the soil seed bank in all microhabitat types of the Monte desert.

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