

Granivory rates by rodents, insects, and birds at different microsites in the Patagonian steppe

Patricia J. Folgarait and Osvaldo E. Sala

Folgarait, P. J. and Sala, O. E. 2002. Granivory rates by rodents, insects, and birds at different microsites in the Patagonian steppe. – *Ecography* 25: 417–427.

We studied the rates of seed removal by different granivores, in different microsites, at different times, in a Patagonian shrub steppe in South America. Granivory rates of exotic (*Phalaris canariensis*) and native (*Mulinum spinosum*) seed species were an order of magnitude lower than those reported for another cool desert from North America with comparable climatic conditions. Insects and rodents removed the greatest amount of seeds in comparison to birds. In general, there were no differences in seed removal across microsites, except at one sampling time (when rodents and insects removed more seeds from bare soil and beside tussocks in comparison to positions beside shrubs, while birds took similar amounts of seeds from all microsites). The length of the experiment differentially affected the granivory rate of different groups. Removal rates (per day) were significantly greater, and exhibited lower variability, when seeds were left for a longer period of time in the field (a month) than for a few days. Insects were more efficient at finding the seeds rapidly and rodents at depleting them; birds could not find or deplete many seeds in short periods of time. Rates of granivory decreased slightly but significantly as the summer progressed mainly due to a reduction of seed removal by birds and rodents but not by insects. Granivores removed an order of magnitude less native seeds than exotic seeds. These differences seemed to be related to palatability as *M. spinosum* seeds have more phenols, toxic concentrations of iron and copper, and lower dry matter digestibility, phosphorous, and nitrogen content, in comparison to *P. canariensis* seeds.

P. J. Folgarait (pfolgariat@unq.edu.ar), Unidad de Investigación en Interacciones Biológicas, Centro de Estudios e Investigaciones, Univ. Nacional de Quilmes, Roque Saenz Peña 180, 1876 Bernal, Buenos Aires, Argentina. – O. E. Sala, IFEVA, Cátedra de Ecología, Fac. de Agronomía, Univ. de Buenos Aires, Av. San Martín 4453, Buenos Aires 1417, Argentina.

Granivores are important elements of arid and semi-arid ecosystems (Brown et al. 1979, Brown and Ojeda 1987, Brown and Heske 1990, MacMahon et al. 2000). They can remove up to 80% of the annual seed production (Chew and Chew 1970, Soholt 1973), and directly (Davidson 1977, Reichman 1979, Inouye et al. 1980, Brown et al. 1986, Samson et al. 1992, Guo et al. 1995) or indirectly (Inouye 1981, Davidson et al. 1984, Samson et al. 1992) affect richness, distribution, and abundance of plants. Rates of seed removal and the relative importance of each granivore group vary among arid regions (Mares and Rosenzweig 1978, Morton 1985, Kerley

1991, Kelt et al. 1996, Lopez de Casenave et al. 1998) and several reasons may account for these differences. In arid environments, seeds vary in size, shape, presence of projections, thickness of the coat, chemical composition, amount and timing of dissemination (Kelrick and MacMahon 1985, Brown and Ojeda 1987), and granivores vary in their ability to handle different seeds (Pulliam and Brand 1975, Price and Brown 1983). Environmental, historical, and biogeographical factors may also determine the differences in granivory found across arid and semi-arid regions of the world (Mares and Rosenzweig 1978, Mares 1993, Kelt et al. 1996, Folgarait et al. 1998).

Accepted 21 June 2001

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ISSN 0906-7590

In an experiment specifically designed to compare granivory rates between Sonora (North America) and Monte (southern South America), Mares and Rosenzweig (1978) found greater granivore activity at the North American site. In hot deserts, rodents and ants are the most important granivores; rodents dominate in the Northern Hemisphere and ants in the Southern Hemisphere (Morton 1985, Kerley 1991). Granivory varies in space at a fine scale too, across habitats or microhabitats (Bowers 1990, Thompson et al. 1991, Crist and MacMahon 1992). Rates of seed consumption in deserts vary in time as well, within (Kelrick et al. 1986) and across seasons mainly due to a reduction of activity of ants during winter (Mares and Rosenzweig 1978, Kerley 1991, Vásquez et al. 1995, Lopez de Casenave et al. 1998) and birds during autumn or summer (Morton 1985, Vásquez et al. 1995, Lopez de Casenave et al. 1998). In a recent comparison of granivory rates across seven deserts throughout the world, Folgarait et al. (1998) showed that levels of granivory could be explained by temperature range. They suggested that granivory rate increases with climate continentality. These conclusions have been drawn, however, from studies comparing removal rates of exotic seeds. Parmenter et al. (1984) and Kelrick et al. (1986) demonstrated that granivory rates of exotic seeds are usually greater than those of native seeds.

Similarities in climate between North and South America offer a great opportunity to learn about the consequences of the differences in evolutionary history on community organization in arid environments. Although Patagonia (Nearctic) belongs to a different floristic realm than climatically equivalent areas such as the Great Basin in North America (Holarctic), both have similar environmental controls that account for their convergence in plant functional types (C3 and C4 grasses and shrubs), soil organic carbon, and above-ground net primary production (Paruelo et al. 1998). The Patagonian steppe occupies 50 000 km² in South America and is a cold semi-arid region. Vegetation structure is arranged in two modules: tussock grasses in a matrix of bare ground, and shrubs surrounded by a dense ring of grasses (Soriano et al. 1994). This patchy structure of the plant community probably influences the animals living in it by providing different amount of resources and protection against predators and weather. Besides the horizontal heterogeneity just described, there is an important vertical heterogeneity in root distribution and use of resources between shrubs and grasses (Sala et al. 1989). Shrubs are deep rooted, obtain most of the water from deep soil layers, and show a clear phenological pattern with a dormant period in autumn and winter and an active period in spring and summer. In contrast, grasses are shallow rooted, obtain water and nutrients from upper layers, and always have some green tillers ready to reassume growth when conditions become favorable. Contrary to

the accumulated knowledge on plant ecology that exists from the Patagonian steppe, hardly anything is known about the ecology of the wild animals of this region, in particular the granivores.

This study has the goal to gain information on granivory for a cold semi-arid region, the Patagonian steppe in Argentina, South America. Our overall objective was to evaluate granivory rates in the Patagonian steppe, major players, and spatial and temporal variability. In particular, we had the following questions. 1) What is the granivory rate in the Patagonian steppe for exotic and native seeds? 2) What is the relative contribution to seed removal of insects, rodents, and birds for exotic and native seeds? 3) What are the differences in granivory rates among different microhabitats, such as those represented by shrubs, tussock grasses, and bare soil, for exotic and native seeds? 4) Do granivory-rate estimates differ between short- and long-term experiments? 5) Are granivory rates different throughout the growing season? 6) Is there any relationship between the chemical composition of native and exotic seeds and their consumption? To address these objectives, we offered seeds in feeding trays that allowed exclusive access by one group of granivores: insects, rodents, or birds. Trays were located beside shrubs, grass tussocks, and on bare ground. Exotic seeds were offered for different lengths of time and at different months during the spring-summer, that is the season when seeds are naturally available at our field site and most of the granivores seem active. Native seeds of *Mulinum spinosum* were offered immediately after the peak of production in the field, at the end of the summer (Soriano et al. 1976, Soriano and Sala 1983).

Materials and methods

Study site

Our field site at Río Mayo is located in the SW of Chubut, Argentina, at 45°25'S, 70°16'W, 500 m a.s.l. It corresponds to the Patagonian phytogeographical Province (Soriano 1956, Cabrera and Willink 1980), Occidental District (Soriano 1956). This steppe is characterized by strong winds from the west, a mean annual temperature of 8°C, and a mean annual precipitation of 172 mm with 62% of the total annual rainfall concentrated during winter time (Beltrán 1997). Soils have a glacial/volcanic origin with coarse texture (Paruelo et al. 1987).

Based on coarse-scale maps of geographical distribution of fauna in Argentina (Folgarait unpubl.), we estimated the potential presence of the following granivores in our site: among insects, 3 species of *Pogonomyrmex* ants, 1 species of *Solenopsis*, 1 species of *Pheidole*, 6 species of Tenebrionidae beetles; among rodents, 3 species of Muridae; and among birds, 3

species of Emberezidae, 3 species of Tinamidae, and 1 species of Columbidae.

Sampling design

In order to assess if granivory rates differ among different groups of animals, we offered seeds of an exotic seed, *Phalaris canariensis* ("canary seeds"), and of a native seed, *M. spinosum*, in feeding trays that excluded insects, rodents, or birds. We used canary seeds because we wanted to compare our results from those by Mares and Rosenzweig (1978) who made comparisons between US and Argentina of granivory rates by ants, rodents, and birds. We have chosen *M. spinosum* as the native seed because it is the dominant shrub at our field site, representing 44% of the shrub cover (Fernández et al. 1991), and its fruits are consumed by sheep in the summer (Bonvisuto et al. 1983). Seed removal was assessed on basis of weight differences during the experiment.

In order to evaluate granivory of exotic and native seeds in different microhabitats, we located feeding trays at three microsites, beside shrubs, beside tussock grasses, and in patches of bare ground (we could not locate trays underneath the shrubs because their canopy reached the ground leaving no space to set the feeding trays). In order to investigate differences between short- and long-term experiments, we repeated the same experiment for a 4- and a 41-d period for exotic seeds. To find out if granivory rates differ throughout the season, we repeated the experiment in spring and summer with exotic seeds. To start comparing consumption of exotic and native seeds we repeated the experiment at the end of the summer but with *M. spinosum* seeds.

We chose 36 individuals of the shrub *M. spinosum* of modal size that were farther than 3 m from each other within a 1-ha enclosure to domestic herbivores. We had 12 replicates of each of the three granivore feeding trays in each microsite giving a total of 108 feeding trays (except for the second experiment – see below – for which we used half of the replicates). Feeding trays were randomly located among microsite positions and replicates. On 23 November 1995, we put 5 g of canary seeds in each feeding tray and we weighed the seeds remaining after 4 d (indicated as "short-term" in Results). Immediately after, on 28 November we filled half of the trays with 5 g of canary seeds and left them for 41 d (indicated as "long-term-spring" in Results). On 8 January 1996, using 10 g of canary seeds in all trays, we initiated the long-term-summer experiment which was left for 39 d. All exotic seeds were collected from the trays immediately after each of the time periods had passed, and were taken to the laboratory for weight measurements. We put 2 g of *M. spinosum* seeds in February and left them for 32 d. On 19 March, all the feeding trays were covered with their lids to stop the

experiment. Seeds were taken out from the field on 23 April when we collected the feeding trays that were taken to the laboratory for measuring the remnant weight.

Seeds of *P. canariensis* and of *M. spinosum* were chemically analyzed using flame photometry and atomic absorption spectrometry (Dean and Rains 1971) for their chemical elements, Kjeldahl (Anon. 1997) for total nitrogen, Prussian Blue assay (Price and Butler 1977 but substituting ferric ammonium sulfate for ferric chloride) for total phenols, and fiber analysis (Goering and Van Soest 1970) for dry matter digestibility.

Feeding-trays design

We did not offer seeds in isolated petri dishes, as most studies do, because of the strong winds characteristic of Patagonia; therefore, we had to hold the petri dishes within other containers (see below). Other studies used diurnal removals of seeds from uncovered petri dishes to account for bird feeding rates and nocturnal removal to account for rodent feeding rates. We used different types of cages surrounding feeding trays of birds and rodents because at our field site there seem to be diurnal and nocturnal rodents (Monjeau pers. comm.), and because we were not able to daily check the traps in the long-term feeding experiments (see below). Seeds were not replenished in the field but were never found empty.

Only insect access

Each tray consisted of two containers, one within the other (Fig. 1). The larger container (8 cm height and 6.4 cm diameter) was used to anchor the trays in the loose sandy soils to prevent them from being blown away or removed by animals. It was pushed upright 2 cm in the soil to diminish the effect of wind. The smaller container or petri dish (2 cm height and 6 cm diameter) which contained the seeds, was covered with a coarse wire mesh (1.5 × 1.5 cm) that prevented access by rodents and birds and was glued with a non-smelly substance that provided a rough surface (along 5 cm) for the insects to climb. We tested these trays in the field prior to the start of our experiments and found that insects were able to get in and out of the feeding devices without problems.

Only rodent or bird access

Each tray consisted of two containers, one within the other, and both within a cage. The larger container (7.5 cm height and 11 cm diameter) was used to anchor the feeding tray in the soil and contained a mixture of water (60%), oil (10%), and detergent (30% approximately) that prevented the access of insects to the inner container (same size as the petri dish in the insect-access trays) that had the seeds. This liquid showed little

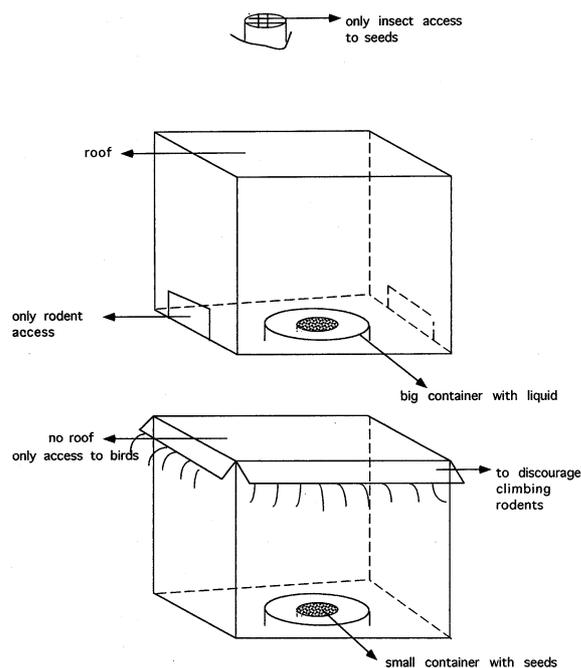


Fig. 1. Three kinds of feeding trays that allow consumption only by insects (top), only by rodents (middle), and only by birds (bottom).

evaporation, did not deter rodents (see Results), trapped insects very efficiently, and did not seem to have affected insect populations (see Results). The larger container was pushed upright 2 cm from the soil to diminish the effect of the wind. The smaller container was glued to a styrofoam column (5 cm height) in the middle of the larger container, separated from it by a gap of liquid wide enough (2.5 cm) to prevent insects from reaching the inner container but narrow enough to allow the rodents to eat from outside of the bigger container (Fig. 1).

The compound tray was buried in the middle of a cage (40 × 40 × 40 cm) made with wire mesh (1.5 × 1.5 cm, in case of rodents, and 1.0 × 1.0 mm in case of birds). The rodent-access cages had two openings on the sides (15 × 8 cm). The bird-access cages had no lateral openings but had no roof, and to discourage climbing rodents we folded the walls of the cages in a 90° angle towards outside, and we left at the end of these foldings, lines of wire sticking out. The cage was held to the soil by burying part of the wire framework of the cage, and by using wire-made stakes (Fig. 1). We saw birds getting in and out of the bird-access cages and, although we have not seen rodents getting in and out of the rodent-access cages, we found signs of their activity (such as rodent feces and trays taken out from the sandy soil).

Statistical analyses

We used for most cases (except one) non-parametric Kruskal-Wallis and Mann-Whitney tests (results shown as χ^2 -approximations, JMP Statistical Package, SAS, Cary, USA) because data were heteroscedastic even after transformation; therefore, these results are reported as median and ranges (25 and 75% quartiles). Data from the second experiment for exotic seeds did not violate the assumptions of parametric analyses and therefore we used a two factor ANOVA; these results were reported as means and standard deviations (in the text) or standard errors (in the graphs) (JMP Statistical Package, SAS, Cary, USA). (Results from overall granivory rates, as well as those used for comparison with a North American site were reported as means to facilitate comparisons across studies.) Those traps that were broken or out of place at the end of each experiment were not considered in the statistical analyses (see Results for final sample sizes used). Using regressions between number of seeds and weight, we were able to transform these numbers to mass ($y = 0.00645X + 0.00033$, $R^2 = 0.996$, $p < 0.01$ for exotic seeds, and $y = 0.0032X + 0.0002$, $R^2 = 0.999$, $p < 0.01$ for native seeds) and account for those cases of seed spillage besides the trays and seeds found in the liquid of the feeding tray. It was necessary to correct the data in this way in order to consider them as non-removed seeds. We did not control for changes in seed weight due to wetting in the field; however, rainfalls (<15 mm for any of the sampling months) were very low during the sampling time, and we always found the seeds dry and with normal size. We made six blank cages with no entrances (4 in bare soil and 2 besides shrubs), which had inside 1 rodent/bird tray and 1 insect tray to evaluate the effect of wind in removing *M. spinosum* seeds (much lighter than the exotic seeds). Although in some cases we found some seeds that were blown away, most of these seeds remained in the liquid of the feeding trays or on the surrounding soil and we were able to recover all the seeds.

Results

1) What are the granivory rates in the Patagonian steppe?

Exotic seeds

In the short-term experiment only $3.27\% \pm 8.84$ seeds/tray were removed after 4 d, while in the long-term-spring experiment $85.25\% \pm 9.05$ of seeds/tray were collected after 41 d, whereas in the long-term-summer experiment $60.96\% \pm 31.96$ of seeds/tray were taken away after 39 d.

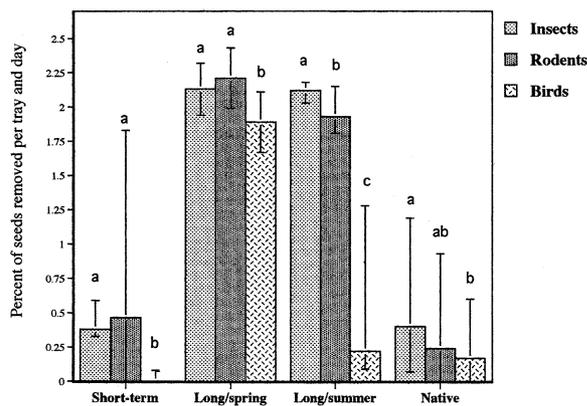


Fig. 2. Percent of seeds removed by different granivores: insects, rodents, and birds, for the short-term experiment (N = 30, 30, 33, respectively), long-term experiment performed in late spring (N = 19, 19, 16, respectively), the long-term experiment performed in the middle of the summer (N = 36, 33, 36), and the native seed experiment (N = 36, 36, 35). Medians and quartiles are reported for all cases except for the long-term-spring experiment where means and SE are reported. Bars followed by different letters differ at $p < 0.01$ within sampling periods.

Native seeds

Granivores removed only $12.43\% \pm 12.94$ of *M. spinosum* seeds/tray after 32 d.

2) Do insects, rodents, and birds have similar rates of seed removal?

Exotic seeds

Different groups of granivores removed significantly different amounts of exotic seeds per tray and day independently of the length of the experiment ($\chi^2 = 29.5$, DF = 2, N = 93, $p < 0.001$ for short-term experiment) or the month of the season (SS = 468.33, F-ratio = 4.07, DF = 2, N = 54, $p < 0.023$ for long-term-spring experiment, and $\chi^2 = 56.98$, DF = 2, N = 105, $p < 0.001$, for long-term-summer experiment). Insects and rodents removed similar amounts of seeds, and both significantly more than birds in the short-term as well as in the long-term-spring experiment (Fig. 2).

For the long-term-summer experiment, insects removed significantly more seeds than rodents, and the latter significantly more than birds (Fig. 2).

Native seeds

We also found significant differences in the rates of *M. spinosum* seed removal, per tray and day, among granivore taxa ($\chi^2 = 6.55$, DF = 2, N = 106, $p < 0.038$, Fig. 2). Insects showed significantly greater rates of seed removal than birds ($\chi^2 = 6.13$, DF = 1, $p < 0.01$) whereas rodents collected similar ($\chi^2 = 0.35$, DF = 1, $p < 0.55$) amounts than insects and birds ($\chi^2 = 0.05$, DF = 1, $p < 0.81$). Insects and rodents showed similar patterns of seed consumption although the former seemed to discover feeding trays faster than rodents whereas birds seemed to have greater difficulties at finding the resources offered (Table 1).

3) Are granivory rates similar for different microhabitats, such as shrubs, tussock grasses, and bare soil?

Exotic seeds

Granivory rates differed among microsites (SS = 384.24, F-ratio = 3.34, DF = 2, $p < 0.044$) for the long-term-spring experiment. Fewer exotic seeds were removed beside shrubs in comparison to bare soil but similar amounts were harvested from tussock grasses and bare soil, and from shrubs and tussocks (Fig. 3). A significant interaction term (SS = 752.88, F-ratio = 3.27, DF = 4, $p < 0.019$) showed that birds removed seeds from all microsites in similar amounts, rodents removed less beside shrubs and similar amounts in bare ground and beside tussocks, while insects removed fewest seeds beside shrubs, slightly more beside tussocks and more seeds in bare soil. We did not find significant differences in the rates of seed removal among the three microsites for the short-term experiment ($\chi^2 = 0.30$, DF = 2, $p > 0.86$) as well as for the long-term-summer experiment ($\chi^2 = 1.45$, DF = 2, $p > 0.48$) (Fig. 3).

Table 1. Percentage of feeding trays used by each granivore group according to the amount of seeds collected by insects (I), rodents (R) and birds (B) for the short-term (SHTexotic) and long-term-summer (LTSexotic) experiment performed with *P. canariensis* seeds and for the long-term experiment performed with *M. spinosum* seeds (Native).

Amount (%) of seeds removed	SHTexotic			LTSexotic			Native		
	I	R	B	I	R	B	I	R	B
0	0	40.00	70.95	0	0	8.33	11.11	33.33	34.28
0.1–10	100.0	40.00	29.05	0	0	44.44	25.00	19.46	34.34
10.1–20	0	6.66	0	0	0	8.33	27.78	13.88	17.11
20.1–30	0	3.33	0	0	0	2.78	25.00	19.46	5.71
30.1–65	0	10.00	0	2.78	18.18	25.00	11.42	13.88	8.57
65.1–90	0	0	0	83.33	66.67	2.78	0	0	0
>90	0	0	0	18.89	15.15	5.55	0	0	0

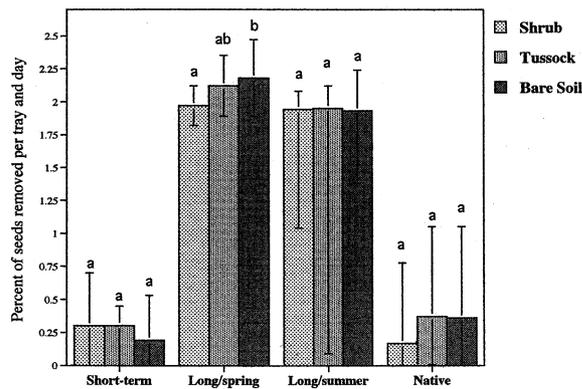


Fig. 3. Percent removal of seeds at different microsites: shrub, tussock, and bare soil, for the short-term experiment (N = 30, 28, 35, respectively), long-term experiment performed in late spring (N = 18, 17, 19, respectively), for the long-term experiment performed in the middle of the summer (N = 35 for each microsite), and the native seed experiment (N = 35, 36, 36). Medians and quartiles are reported for all cases except for the long-term-spring experiment where means and SE are reported. Bars followed by different letters differ at $p < 0.01$ within sampling periods.

Native seeds

There were no significant differences among microsites in rates of native seed removal, for all granivores together ($\chi^2 = 2.49$, DF = 2, $p < 0.288$, Fig. 3), as well as for each group separately (for rodents: $\chi^2 = 3.29$, DF = 2, $p < 0.193$; for insects: $\chi^2 = 4.84$, DF = 2, $p < 0.089$; for birds: $\chi^2 = 0.31$, DF = 2, $p < 0.856$).

4) Do estimates of granivory rate differ between short and long-term experiments?

On a daily basis, granivores removed a significantly lower percentage of seeds during the short-term experiment (0.817% seeds/tray/day) in comparison with the long-term-spring experiment that was performed immediately afterwards (2.08% seeds/tray/day) ($\chi^2 = 54.93$, DF = 1, $p < 0.0001$). Birds were not able to find most of the trays after 4 d while after a month, birds removed up to 65% of the seeds from 33% of the trays (Table 1). After 4 d, insects had found all the trays but only removed < 10% of the seeds offered. Rodents, on the contrary, did not find 40% of the trays but have consumed between 10 and 65% of seeds from 20% of the trays after 4 d. When seeds were left in the field for a month, insects and rodents found all the trays, and they removed from > 60% of these trays between 65 and 90% of the seeds offered (but none ever removed 100% of the seeds offered).

5) Are granivory rates different throughout the growing season?

Removal rates per tray and day were significantly

smaller ($\chi^2 = 10.20$, DF = 1, $p < 0.0014$) for the long-term-summer experiment (1.56% seeds/tray/day) than for the long-term-spring experiment (see question 4). These changes mainly were accounted for by a huge decrease in seed removal by birds ($\chi^2 = 14.67$, DF = 1, $p < 0.0001$), although the rates of rodents also decreased ($\chi^2 = 6.76$, DF = 1, $p < 0.0093$), while insects maintained their levels of granivory ($\chi^2 = 0.56$, DF = 1, $p < 0.456$). The pattern of seeds discovered and depleted by each group of granivores did not differ greatly between both long-term experiments (Folgarait unpubl.).

6) How were the chemical characteristics of *Mulinum spinosum* in comparison to *Phalaris canariensis* seeds?

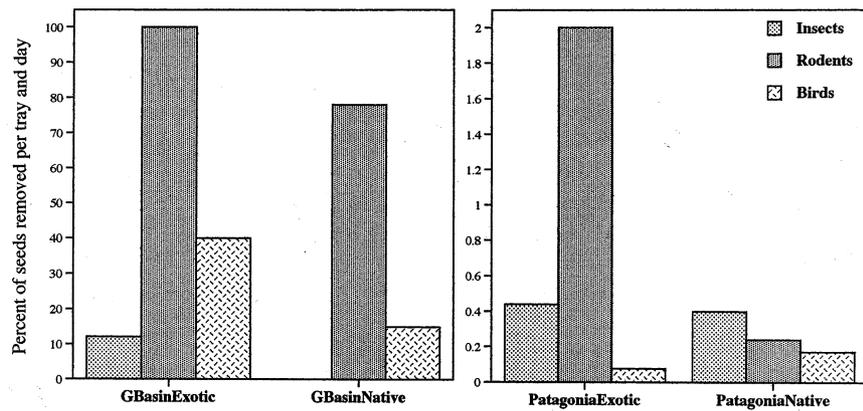
Mulinum spinosum seeds have higher values of phenolic compounds, very high values of Fe and Cu, and lower values of dry matter digestibility, P and N content in comparison to *P. canariensis* (Table 2), all of which could reduce the attractiveness of these seeds. *Mulinum spinosum* seeds also had more water content, K, Na, Mg, and Ca in comparison to *P. canariensis*.

Mulinum spinosum seeds were not preferred very much by any of the granivores because none of the granivores removed > 65% of the seeds after 32 d (Table 1). Rodents or birds did not remove seeds from a third of all the trays while insects collected from 90%

Table 2. Morphological and chemical characteristics of native seeds of *M. spinosum* and exotic seeds of *Phalaris canadensis*. Chemical results shown in % (g/100 g) except for total phenols (Mmoles gallic acid/g) and Fe and Cu (ppm). N = 3; each sample being a composite sample of randomly collected (in case of *Mulinum*) or bought (in case of *Phalaris*) batches of seeds.

Characteristic	<i>Mulinum spinosum</i>	<i>Phalaris canadensis</i>
Shape	circular	elliptic
Surface	smooth	smooth
Seed projections	none	none
Elaiosomes	none	none
P	0.190 ± 0.001	0.427 ± 0.003
N	1.064 ± 0.014	1.819 ± 0.024
K	2.430 ± 0.011	0.513 ± 0.011
Na	0.119 ± 0.000	0.059 ± 0.002
Ca	0.740 ± 0.010	0.033 ± 0.001
Mg	0.223 ± 0.005	0.143 ± 0.006
Fe	3568.00 ± 0.00	51.00 ± 0.00
Cu	329.67 ± 1.53	11.87 ± 0.21
Total phenols	13.41 ± 0.74	0.79 ± 0.09
Humidity	13.45 ± 0.14	8.75 ± 0.00
Cellulose	27.84 ± 0.61	7.57 ± 0.43
Lignin	10.41 ± 0.13	4.11 ± 0.09
Ashes	18.40 ± 0.03	5.60 ± 0.01
Dry matter digestibility	36.08 ± 1.84	67.20 ± 3.91

Fig. 4. Percent removal of seeds by insects, rodents, and birds for the Intermountain Great Basin (means taken from Parmenter et al. 1984 and pers. comm.; considering 5 g/tray/day in each of the 2 d) and for Patagonia (means from short-term removal experiment). At the North American site, millet (*Panicum miliaceum*) was offered as the exotic seed, and a mixture of *Purshia tridentata*, *Oryzopsis hymenoides*, and *Artemisia tridentata* were offered as native seeds; at this site insects refer to ants exclusively. Note that the y axes differ between sites.



of them. Again, insects and rodents removed similar amounts of seeds from similar number of trays whereas birds removed <10% of seeds from a third of the trays.

Discussion

Granivory rates and granivores

Our study showed much lower granivory rates than those found at North American sites. These results agree with Mares and Rosenzweig's (1978) studies in hot deserts, which found that granivory rates of exotic seeds were one order of magnitude lower in South America (Monte, Argentina) than in North America (Sonora). A better comparison, however, is to look at the granivory rates of seeds at sites with similar climatic conditions to the Patagonian steppe such as the Intermountain Great Basin of North America (Paruelo et al. 1995). There are still enormous differences in seed removal rates for exotic seeds (51% of seeds removed per tray/day; Parmenter et al. 1984) as well as for native seeds (31% removed per tray/day; Parmenter et al. 1984) (Fig. 4). Despite using different designs of trays, seed removal rates between Patagonia and the Intermountain Great Basin are so great that should reflect real tendencies in granivory in favor of the North American site.

Why are seed removal rates so much greater in the Intermountain Great Basin? There is similarity in abiotic conditions between the two sites (Goodall and Perry 1979). Both are at similar latitudes (41°N, 40°S), have the same warmest annual mean temperature (17°C), and receive similar solar radiation (120 and 140 kcal cm⁻² yr⁻¹ for Patagonia and Great Basin, respectively). Both sites receive most of the precipitation in winter, and have the same variability of annual precipitation (20%), although most of the annual precipitation (226 mm) is received as snow at the Great Basin due to

its higher altitude (2100 m). A comparison between the Patagonian steppe (Fernández et al. 1991, Jobbágy and Sala 2000) and several North American steppes such as high altitude sites in Washington and Idaho (West 1983) and low altitude sites in Oregon and New Mexico (Jobbágy and Sala 2000) shows that productivity is comparable in Patagonia (56–79 g m⁻² yr⁻¹) and at the Great Basin of North America (range 24–50 and 80–250 g m⁻² yr⁻¹, respectively). Plant life-forms are also very similar between North and South American sites. Both shrub steppes share some of the dominant grass genera (*Poa*, *Bromus*, *Stipa*), percentage of soil covered by shrubs, and amount of bare ground (Soriano and Sala 1983, Parmenter et al. 1984).

The contrasting granivory rates between sites in North and South America do not seem to be accounted for by differences in biological diversity. Great Basin and Patagonian sites presumably have similar richness of rodents (3 species) and of birds (7 species). However, the Patagonian steppe has greater diversity of ants (5 species instead of 1, all from the same subfamily Myrmicinae), that does not seem to have a compensatory effect on increasing granivory rates (Folgarait et al. 1998). Despite sharing one subfamily of rodents between the Great Basin (Sigmodontinae) and Patagonia, most of the rodents potentially present at our field site (i.e. *Eligmodontia morgani*, *Abrothrix* sp. and *Olygoryzomys* sp.; Lozada et al. 1996, Monjeau et al. 1997) seem to be omnivores (Monjeau 1989) whereas one species from the Great Basin is potentially a seed specialist (*Perognathus parvus*) while the others are omnivores (Kelrick et al. 1986).

Differences in levels of granivory between Patagonia and the Great Basin could not be explained by differences in granivore activity related to sampling period as both studies were performed during the summer-autumn when animals were most active. Folgarait et al. (1998) in a world-wide comparison of granivory across deserts found that thermal amplitude (the difference

between extreme annual mean temperature) correlates with levels of granivory and proposed that selection for granivory may have been greater for those desert areas with broader temperature range and high continentality (high land/ocean ratios). They hypothesized that harsh thermal conditions shut down resource availability at certain times of the year and that granivory is the best feeding strategy to cope with this variability in food production because seeds can be stored easily. The thermal amplitude is greater for the Great Basin North American site (although mean temperature is similar) because the minimum annual mean temperature is lower for the Great Basin (-8°C) than for Patagonia (3°C).

Our seed removal experiments showed that insects and rodents are the most important granivores, while birds are less so. Our results contrast somehow with what is known for hot arid areas, where rodents are by far the most important group in the Northern Hemisphere and ants in the Southern Hemisphere (Mares and Rosenzweig 1978, Morton 1985, Kerley 1991). The nature of our experiment requires that we used devices that allowed differential access for the different animal groups. We were not able to evaluate that all devices had similar effects on each group. However, careful observations suggest that birds, which were the least important granivore, freely moved in and out of the devices. Folgarait et al. (1998) suggested that wide thermal amplitudes select for the granivore syndrome, and that the identity of the granivore was the result of historical circumstances and physiological preadaptations. Then, granivory rates in Patagonia may be much lower than at the Great Basin possibly because of a combination of recent lineages of potential granivores and little selective pressure in favor of granivory (Folgarait et al. 1998); this in turn can explain the abundance of omnivores in South America (Kelt et al. 1996).

***Phalaris canariensis* and *Mulinum spinosum* seeds**

Our native-seed removal experiment showed that granivores at this Patagonian steppe have a low consumption of *M. spinosum* seeds in comparison to exotic seeds offered. *Mulinum spinosum* seeds were consumed less (0.28% of seeds per tray and day) than exotic seeds (1.56% of seeds per tray and day) offered at the same field site. We were not able to compare them statistically as we were not able to offer both types of seeds simultaneously; however, removal rates of exotic seeds were an order of magnitude higher than for native seeds suggesting a greater preference for exotic seeds by native granivores. A similar pattern for a comparable site in the Intermountain Great Basin cool desert was also found (Kelrick et al. 1986) with greater preference for exotic seeds (high in percentage of soluble carbohydrates) over 6 native species. Even among native seeds, granivore preferences can differ quite a lot (Hay and Fuller 1981,

Kelrick et al. 1986). For example, at our field site, the percentage of *M. spinosum* seeds removed was lower than that for (native) *Bromus pictus* ($70.5\% \pm 20.4$ from January to April or daily $0.91\% \pm 0.26$; Aguiar 1991). Although, *B. pictus* was eaten more than *M. spinosum*, the removal rate per tray and per day of the former is still lower than the rate reported for exotic seeds.

Why were native *M. spinosum* seeds eaten less than exotic *Phalaris* seeds? Some properties of the seeds may explain this pattern. Both types of seeds were smooth, and had no elaiosomes or projections. *Mulinum* seeds were circular and flat (like a coin) whereas *Phalaris* seeds were elliptical with volume (like a rugby ball), and these differences in seed morphology could have affected handling time by granivores (Pulliam and Brand 1975, Lemen 1978). However, most differences occurred in chemical characteristics. *Phalaris* seeds had a higher nutritive value than *M. spinosum* seeds due to their greater digestibility, protein and phosphorous content, and due to their lower concentration of phenolic compounds. Interestingly, levels of Fe and Cu in *M. spinosum* were beyond the maximum tolerable levels of minerals known for domestic mammals and birds (McDowell 1992), and this result by itself could explain the low seed removal of *M. spinosum* seeds found in this study.

Other studies have shown that granivore preferences were correlated with assimilation efficiency (Soholt 1973, Whitford 1978, Withers 1982, Price 1983). In fact, at the Intermountain Great Basin (Kelrick and MacMahon 1985, Kelrick et al. 1986) 7 different native seeds were offered to rodents, ants, and birds, and granivore preferences was correlated to the concentration of soluble carbohydrates and water in the seeds. Our results on cellulose, lignin, and ashes showed that *Mulinum* values were similar to the least preferred seed at Kelrick et al.'s study (*Artemisia tridentata*) and *Phalaris* to the most preferred seed (*Purshia tridentata*). They argued that the greater the amount of structural carbohydrates in the seeds the greater the allocation of water to fecal excretion by the granivore. In turn, this could seriously affect the assimilation and water efficiency of vertebrates from arid environments (Schmidt-Nielsen 1964) and could determine consumption decisions by desert granivores (Morton and MacMillen 1982). The low consumption of *M. spinosum* seeds by native granivores may help to explain the dominance of this shrub at this steppe.

Granivory in different microsites

Seeds were removed either equally from different microsites (in the short-term and long-term-summer experiment for exotic seeds, and long-term-summer experiment for native seeds) or less besides shrubs by rodents and insects (in the long-term-spring experiment).

Despite the greater abundance of seeds present underneath or close to shrubs (Reichman 1984, Kemp 1989, Aguiar and Sala 1994, Folgarait unpubl.), Patagonian granivores do not seem to prefer this type of microsite over bare ground or scattered tussocks for feeding. Few studies have explored granivory rates in different microsities in desert areas, and most of them showed a lack of preference among microhabitats (Abramsky 1983, Lopez de Casenave et al. 1998). These results are surprising since it has been shown several times that the activity of granivores varies among different microsities (Price 1978, Brown et al. 1979, Wiens 1985, Crist and Wiens 1994).

There could be many factors that interact with animal foraging decisions (Sih 1980, Kotler 1984) and the final pattern of seed consumption may not reflect exclusively seed availability. There is lack of information on the natural history of the granivores at our field site; therefore, our interpretations should be taken with caution until more information is gathered. However, the following three non-exclusive reasons, could explain in part the lack of microsite preferences for seed collection. 1) Opportunity cost of foraging. The opportunity cost of foraging could be low in summer when food abundance is maximal reducing the differential microsite attractiveness. Therefore, microsite specificity may occur at other times of the year when the opportunity cost of seeds is larger and the microhabitat differences greater, or otherwise with preferred seeds (Hay and Fuller 1981, Crist and MacMahon 1992). 2) Differential predation. Foraging decisions also could be modeled by the risk of being eaten while foraging (Bowers 1990). Although there is no information on possible predator's abundance, the absence of snakes and lizards in the area, and the high historical hunting pressure on wild cats as well as foxes in the region, suggest a low predation risk for granivores. A general low predation rate in the Patagonian steppe suggests that differential predation may not account for granivory differences among microsities. 3) Granivory pressure. Folgarait et al. (1998) suggested that granivory rates in Patagonia are very low because may not represent a competitive advantage under these abiotic conditions. If this is the case, then we were dealing at our field site with omnivores instead of granivores, so their use of space may not need to be related to seed availability. Studies on foraging regimes and activity patterns of these "granivores" and their predators, included in their microsite-dependent food webs, may be able to elucidate these hypotheses.

The effects of length of experiment

Removal rates of seeds from our short-term experiment were significantly lower, on a daily basis, than our long-term experiments. Birds were the most sensitive

group to the length of the experiment; they found only few trays in the short-term experiment and most of them in the long-term experiment. Other studies also showed that the length of time that seeds are left in the trays is relevant in order to measure seed removal by birds (Mares and Rosenzweig 1978, Morton 1985). Short-term experiments may bias removal rates towards rodents as they locate and deplete resources very rapidly (Reichman 1979, Abramsky 1983), as it is the case for the Intermountain Great Basin (Parmenter et al. 1984). In this study, insects seem to be faster at finding the seeds while rodents seem to be more efficient at depleting them (Table 1). At the Intermountain Great Basin, rodents found 100% of the trays after 2 d whereas birds and ants found a small percentage. The smaller granivory rates found in the long-term-summer experiment than in the spring one suggested that granivores may have not learned the constant position of the trays through time. Other authors (on consecutive months: Kelrick et al. 1986, across seasons: Mares and Rosenzweig 1978, Morton 1985, Kerley 1991, Vásquez et al. 1995, Lopez de Casenave et al. 1998) gathered data in a similar way keeping the position of the trays constant.

Seasonality of seed removal

As the summer progressed, granivory by birds and rodents significantly decreased at our site, suggesting that many sampling periods or longer ones should be considered even within a season. Kelrick et al. (1986) also showed different granivory rates between consecutive months during the summer of a cold desert in North America. In our case, the differences in bird seed removal could be explained by migration patterns. The lower percentage of seed removal by rodents could be related to the life cycle of females who lactate during the summer (Monjeau pers. comm.) and might be less mobile. The fact that insect granivory rates were constant through time reflects either the rapid development of several cohorts during the summer or the presence of adult insects throughout the sampling time. To better understand the patterns found, it will be useful to have a greater knowledge of the natural history of each group, their diets, and to trap the animals alive as granivory data are being collected.

Acknowledgements – We are indebted to the help obtained in the field to set up the experiment and/or to collect part of the data to M. Aguiar, E. Jobbágy, M. Oesterheld, P. Roset, J. Tumio, and J. Vrsalovic, and for the intense help obtained in the lab by D. Primrose, and J. Folgarait. M. Nogués kindly closed our field trays. G. Somma de Feré kindly performed most of the chemical analyses of the seeds, and provided lab space and equipment to perform the total phenols assay. We also thank A. Monjeau, E. Jobbágy, M. Aguiar, M. Price, T. Crist, B. Kotler, and M. Mönkkönen for their comments on the manuscript or useful conversations about the data, and to B. Parmenter for answering our many queries about his data.

This Project was supported by Cross-site LTER Project, Univ. of Buenos Aires, National Research Council of Argentina (CONICET), FONCyT, and the Inter American Institute for Global Change Research. Finally, we thank CONICET for providing support to PJF.

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