Research

Can seed-eating birds exert top-down effects on grasses of the Monte desert?

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Granivorous animals can exert major effects on the abundance and diversity of plants when they are selective as well as efficient consumers. However, even under such conditions granivore impact will ultimately depend on whether environmental stress obscures plant-animal interactions. We studied diet and seed selection patterns of seed-eating birds to corroborate whether they are selective consumers in the central Monte desert of Argentina. Overall, 83% of seeds in bird stomachs were grass seeds, whereas only 30% of available seeds were from grass species. Therefore, we conclude that avian granivory is highly selective. We developed a set of a priori expectations to test whether birds are efficient consumers (i.e. whether they reduce seed reserves significantly), through short-term mechanism-explicit enclosure experiments. Birds decreased the number of selected grass seeds by >50%, and also reduced the amount of non-selected grasses and selected forbs when selected grass seeds were scarce in the habitat. Thus, consumption was context-dependent, varying with the composition of background seed reserves. The corroboration of foraging plasticity through mechanism-explicit trials seems to be crucial to correctly assign direct and indirect effects of seed predation in long-term enclosure experiments. The comparison of average grass seed reduction caused by bird predation with mean declines of grass seedlings caused by senescence (ca 95%) allowed us assess top-down (e.g. seed availability) vs bottom-up control (e.g. rainfall) on grass recruitment. Despite moderate to high seed predation, the number of grass seeds that remains in the soil in spring would not limit seed germination and seedling recruitment. By contrast, safe-site availability and drought may be important factors limiting grass recruitment, at least in the undisturbed habitats of the Biosphere Reserve of Ñacuñán.

Predators can exert major effects on prey abundance and diversity if they are both selective and efficient (Jaksic and Marone 2007). A selective consumer takes their prey in different proportions than those present in the habitat within size limits imposed by the predator/prey size ratios and the handling capability of the consumer, whereas an efficient predator significantly reduces prey abundance at least at some time in some patches (Jaksic 1989). Small and medium-sized granivorous birds often feed on seeds of herbaceous plants during autumn and winter in desert areas and continue foraging on seeds, along with insects and fruits in the breeding season (Wiens and Dyer 1976, Morton and Davies 1983, Lopez de Casenave et al. 2008). Despite this, a long standing assumption is that birds do not significantly alter the fate of seeds in arid and semiarid ecosystems (Chambers and MacMahon 1994, Báez et al. 2006). This assumption implies that birds are not efficient consumers, but it seldom has been verified or tested (Marone et al. 2000a).

The hypothesis that seed-eating birds are selective consumers is plausible (Morton and Davies 1983, Marone et al. 1998a, Garnett et al. 2005), but remains largely

unexplored given the difficulties of assessing seed availability under field conditions for long periods. Our first goal here is to assess whether seed-eating birds are selective consumers in the central Monte desert of Argentina. We will depict the species-specific composition of granivorous bird diet along with the composition of soil seed reserves, in order to test the hypothesis that the more common Emberizidae species take seeds in different proportions than present in the habitat and, specifically, that birds effectively select grass seed species (Marone et al. 1998a, Cueto et al. 2006).

Indirect evidence of birds as efficient seed consumers has accumulated during the last decade in several South American deserts. Birds removed major proportions of experimentally offered seeds in the central (Lopez de Casenave et al. 1998) and austral Monte desert (Saba and Toyos 2002), and in an arid thorn scrub community of north-central Chile (Kelt et al. 2004). Even in arid North America, where small mammals are usually considered the primary seed consumers, birds also can be efficient foragers (Thompson et al. 1991, Guo et al. 1995). In contrast, data on top-down effects of birds on seeds and plants under field

conditions – especially in situations where the natural composition and size of soil seed bank is monitored – are still lacking. Our second goal is to assess the hypothesis that seed-eating birds cause a significant decline in the number of seeds that they consume in natural settings of the central Monte desert. We look for such effects by using enclosure experiments to test a set of a priori predictions as to which seeds would be more strongly affected by bird foraging. Predictions come from two sources: the results of experiments that combined choice and non-choice trials to infer seed preferences by birds (Cueto et al. 2006), and information on seed selection reported in this paper.

Despite three decades of intensive research on seed predation, rather little is known about its importance in plant demography (Worthy et al. 2006). Studies on when and where plant recruitment is limited by bottom-up forces such as rainfall or number of safe-sites, or by top-down forces such as seed limitation induced by consumption (Maron and Simms 1997, Meserve et al. 2003) are increasing in arid and semiarid ecosystems, with recent emphasis on bottom-up control of primary production and food web processes (Báez et al. 2006, Holmgren et al. 2006, Peters et al. 2006). Whether seed-eating animals still may affect plant populations is unclear partly because few studies have assessed the impact of predation on the number of soon-to-germinate seeds simultaneously with the seed-to-seedling transition (Maron and Simms 2001). Despite likely moderate to high seed predation in the central Monte desert, Marone et al. (2000b) asserted that the prevalence of bottom-up control of grass populations is probable because grass recruitment is mostly restricted to exceptional wet years with high seed production and germination. However, this assertion needs to be carefully evaluated, and the final goal is to compare the mean seed reduction caused by bird predation (goal 2) with the average decay of seedlings provoked by senescence (a bottom-up effect).

Methods

Study site

We conducted studies in the open *Prosopis flexuosa* woodland of the Biosphere Reserve of Ñacuñán, central Monte desert, Argentina (34°03′S, 67°54′W). This extensive habitat has a tree stratum made up of scattered individuals of *Prosopis flexuosa* and *Geoffroea decorticans* within a dense matrix of tall shrubs (>1 m; *Larrea divaricata, Capparis atamisquea, Condalia microphylla, Atriplex lampa*), and low shrubs (<1 m; *Lycium* spp., *Verbena aspera, Acantholippia seriphioides*). Grass cover is 25–50%. The most common Poaceae species are C₄-perennial grasses: *Pappophorum* spp., *Trichloris crinita, Setaria leucopila, Digitaria californica, Sporobolus cryptandrus, Aristida mendocina, Diplachne dubia* and *Neobouteloua lophostachya*. Most forbs are annual or biennial. These include *Chenopodium papulosum, Phacelia artemisioides, Descurainia* sp., *Glandularia mendocina, Sphaeralcea miniata, Conyza* spp., *Parthenium hysterophorus, Lappula redowskii, Heliotropium mendocinum* and *Plantago patagonica*. The climate is dry and temperate, with cold winters. Around 75% of the annual rainfall occurs in the warmer months of October to March, which coincides with the growing season. Average rainfall in the growing season is 266 mm (n = 32 year). The bulk of grass and forb seeds disperse and enter the soil in late summer and early autumn months (Marone et al. 1998b).

Seed abundance in the soil

We analysed the composition of soil seed banks in winter (early August) and spring (October) of 1993 through 1998, with the exception of winter 1995. Samples were taken over three (1993 and 1994) and four (1995–1998) 2-ha plots (200 × 100 m) arranged within the open woodland. One third (1993 and 1994) and one fourth (from 1995 on) of the sampling effort was allocated to each plot (n = 73 on every date). The 73 replications were allocated proportionally to the cover of five microhabitats in the open woodland in order to obtain a weighted average at the habitat scale: beneath trees (12), beneath tall shrubs (24), beneath low shrubs (9), grassy areas (12), and bare soil (16). We extracted soil cores by using a cylindrical sampler, 3.2 cm diameter and 2 cm deep. About 80% of seeds are found in the upper 2 cm of soil (Marone et al. 1998b), and 80% of medium sized and heavy grass seeds are found in the upper 1 cm of soil (Marone unpubl.). Sampler contents were air-dried in the laboratory, and sifted through a sieve of 0.27 mm mesh. The finer fraction was discarded, and the coarser fraction was washed in the same sieve under water pressure. After drying the remains, we searched seeds under a stereoscopic microscope, recording and identifying those that did not crumble when probed with forceps (Marone et al. 1998b).

Bird diet

Six Emberizidae species are usually common at Ñacuñán, at least in some seasons: *Poospiza torquata* (mean weight 10.5 g), *Poospiza ornata* (12.7 g), *Phrygilus carbonarius* (16.1 g), *Zonotrichia capensis* (19.2 g), *Saltatricula multicolor* (22.4), and *Diuca diuca* (25.0 g) (Lopez de Casenave 2001). We assessed the granivorous fraction of bird diet by counting seeds in the digestive tract of mist-netted individuals. Birds were caught year-round during 20 field trips between winter 1993 and summer 2000 (nine trips in autumn or winter, and 11 trips during spring or summer). We obtained the content of the digestive tract by using the flushing method, which allows the effective collection of different food items (Zach and Falls 1976, Zann and Straw 1984, Rosenberg and Cooper 1990). When the technique failed, we collected the water and partial contents which were regurgitated by birds. In addition, we also collected droppings while handling birds, and incorporated them into corresponding samples. Finally, we removed the entire digestive tract of a few individuals that died during the study. We preserved all tract contents in alcohol, and different seed items were taxonomically identified and sorted in the laboratory under a dissecting microscope. Therefore, although our primary technique was flushing, we attempted to obtain maximum information from each individual by combining several procedures. Since our goal was to depict the granivorous fraction of bird diet,

the remains of arthropods and fleshy fruits were not considered in analyses.

The contribution of seeds of every plant species to the individual diet was expressed as the percentage of seeds in relation to the total number of seeds contained in every stomach. We then obtained the diet of each bird species by averaging the individual values, as suggested by Rosenberg and Cooper (1990), excluding samples lacking quantifiable seed remains. Given variable sample size between seasons in some species, and seasonal variation in diets, we first calculated the seasonal diet (by averaging individual values within a season), and then averaged the diets of each species from mean seasonal values.

Enclosure experiments

Experiment 1

In early April 2001 we installed a series of field exclosures to determine whether autumn-winter granivores cause a decline in the soil seed bank (and the magnitude of the decline, if any). Seed removal in autumn and winter can be attributed mainly to birds and only secondarily to rodents (Lopez de Casenave et al. 1998). Seed removal by invertebrate granivores, especially seed-eating ants, is almost nil in autumn and winter (Lopez de Casenave et al. 1998, Pol and Lopez de Casenave 2004). There were 25 exclosures allocated to three 2-ha plots (8, 8 and 9 stations in each plot) within the open woodland. Each station consisted of two small depressions, placed 1–3 m apart in open areas of bare soil located at least 1 m from any perennial plant. Depressions were artificially generated by removing the top 4–5 cm layer of soil from an area of 300–500 cm^2, then replenishing the hole with >10 cm deep soil coming from the vicinity (the number of seeds in deep soil is negligible; Marone et al. 1998b), and pressing a petri dish (9 × 2 cm deep) against the soil surface to create a depression. We considered that all seeds recorded at the end of the trial were the product of seed set and dispersal during the study period (April–September 2001, ca 5 months). One depression in every station was covered with a 20 × 20 cm, 6 mm square mesh, hardware cloth elevated 1 cm to prevent access by vertebrates (=exclosure). Seed size of grasses and forbs is well below 6 mm, so we assume that all seeds can pass through the mesh. The other depression (control) was left open access to vertebrates. In September we extracted the soil from depressions by using one half of a 4.5 cm circular sampler, 1 cm deep (31.8 cm^2). We pushed the sampler into the soil, and then slid a metal scoop under its bottom edge to isolate the soil within. In the laboratory, soil samples were searched for seeds following the previously-described procedure (Seed abundance in the soil).

Experiment 2

From early April through September 2002 we carried out a similar field experiment in the same habitat. It consisted of 35 stations, each one with two 9 cm Ø × 2 cm deep depressions, constructed as above. Depressions were located in open areas, no more that 20–30 cm from tussock grasses. Exclosures and controls were as in experiment 1. Given that seven stations suffered some kind of damage in the 2001 experiment, usually the loss of the hardware cloth due to excavation by animals, we utilized a higher number of

replications in 2002. Further, we located depressions in a slightly different microhabitat (near source grasses) in order to facilitate seed entrapment. In early September 2002 we extracted soil cores from every depression by using a circular sampler, 9 cm Ø × 1 cm deep (63.6 cm^2). Soil samples were searched for seeds at the laboratory.

We used one-tailed, paired t-tests on square-root transformed data ($y = (x + 0.5)^{0.5}$) to evaluate if the amount of seeds in the open depressions was lower than in the enclosed ones. The high number of zeros for some of the pairs of depressions, particularly in 2001, compromised the normality of the data. In such cases the t-test may not be the most appropriate analysis. Hypotheses testing renders, however, the same results when using the non-parametric paired Wilcoxon test and we, thus, reported only the t-test outcome.

Grass seedling recruitment

From October 1993 through August 1995 we recorded the proportion of emerging grass seedlings that reached the juvenile or adult phase at the end of the growing season (May) in two habitat types of the Ñacuñán Reserve: open woodland and *Larrea cuneifolia* scrubland (in this last habitat we did not count emerging seedlings in spring-summer 1993–1994). The complete analysis of the temporal and spatial dynamics of seed emergence and seedling survival of grasses and forbs in open woodland has been published (Marone et al. 2000b); here we specifically report the proportion of grass seedlings that reached the juvenile or adult stage and distinguish it from the proportion that died due to senescence or animal activity (herbivory or soil disturbance). We carried out seedling sampling on 1-m^2 quadrats (25 or 30 in open woodland, 20 in scrubland), in which we detected and mapped the seedlings as soon as they emerged. Grass seedlings could not be identified to species level and were therefore combined. Quadrats were recensused every 15–30 days from October to May, and every 45 days in the winter. At each census date, we recorded phenological changes, seedling mortality and its plausible cause as well as any new emergence. In every habitat type we located a third of the quadrats over any of three 2-ha plots, randomly positioning them (separated at least by 5 m) along a transect. Since most of the surviving (perennial) grasses did not fruit but remained as juveniles during the same season that they had emerged (Marone et al. 2000b), we probably overestimated the number of grass seedlings that reached the reproductive stage.

Results

Seed abundance in the soil

Total number of grass and forb seeds found in soils of the open woodland in the winter and spring of 1993–1998 are shown in Table 1. On average, forb seeds represented 68% (winter) and 71% (spring) of total herbaceous seeds. Table 2 includes the relative abundances (percentages) of the 20 most common seed species found in Ñacuñán's soil. They here are considered as an indicator of seed availability for bird species. On average, *Ch. papulosum* (a forb) and

Table 1. Average number of forb and grass seeds m^{-2} in soils of open *Prosopis* woodland in the winters and springs of 1993–1998 (there were no data for the winter of 1995). The interannual means ($\pm$SE) are also shown. Rainfall corresponds to total precipitation during the previous growing season (October–March).

Year	Rainfall (mm)	Winter seed bank		Spring seed bank	
		Forb seeds	Grass seeds	Forb seeds	Grass seeds
1993	269	15268	7122	9892	5333
1994	124	6356	4310	6236	3663
1995	289	–	–	5589	2777
1996	177	5572	1346	5094	1022
1997	295	6662	1925	4959	851
1998	453	7293	4311	9355	3442
Mean$\pm$SE		8230$\pm$664	3803$\pm$377	6854$\pm$366	2848$\pm$280

S. cryptandrus (a grass) accounted for almost 75% of total seed abundance. Of the remaining species, only two forbs (*P. artemisioides*, *Descurainia* sp.) and two grasses (*Pappophorum* spp., *D. californica*) surpassed 2% of relative abundance. These six plant species combined accounted for >90% of total seed abundance in the soil.

Bird diet

Grass seeds dominated in most stomach contents (Table 3): 100% (*S. multicolor* and *Ph. carbonarius*), 98.7% (*P. torquata*), 80.0% (*D. diuca*), 78.3% (*P. ornata*) and 51.5% (*Z. capensis*). Overall, diets of *S. multicolor, P. torquata, Ph. carbonarius, D. diuca* and *P. ornata* were composed of >75% grass seeds. Only *Z. capensis* had a more mixed diet, with a variable fraction of forb seeds. The most common grass seeds found in bird stomachs were *S. cryptandrus, Pappophorum* spp., *S. leucopila, T. crinita, D. californica* and *D. dubia*. Only the forb *Ch. papulosum* surpassed 5% of overall mean diet. All other seed species

contributed <3% to bird diets, and often considerably less (Table 3).

To assess whether seed-species abundance determines bird diet in the field, we evaluated the correspondence between these two variables by using the 95% confidence interval for the concordance correlation coefficient (Zar 1996 p. 401). Birds were widely selective foragers (the 95% CI [−0.135, 0.539] did not approach 1; Fig. 1). Consumption of all common grass seeds was greater than expected by seed abundance, whereas several forb seeds – the abundant *Ch. papulosum* and *P. artemisioides* seeds among them – were consumed less than expected (Fig. 1).

Enclosure experiments

A priori predictions

We utilized previous results of seed preference experiments (Cueto et al. 2006) combined with data on seed selection by birds under field conditions (Table 2, 3, Fig. 1) to classify herbaceous seeds according to their vulnerability to birds. *Z. capensis, S. multicolor, D. diuca* and *P. ornata* are the most

Table 2. Relative abundance (percentages) of seed species in the soil in winter and spring. Most species included are found in bird stomachs, and constituted >99% of total seed bank in each sampling occasion. The mean percentage ($\pm$SE) of every species for the whole study period is given in the last column.

	1993		1994		1995	1996		1997		1998		Mean$\pm$SE
	Win	Spr	Win	Spr	Spr	Win	Spr	Win	Spr	Win	Spr	
Grasses												
Sporobolus cryptandrus	11.3	11.9	22.5	23.9	21.8	12.3	9.2	13.5	10.3	16.3	12.8	15.1$\pm$1.6
Pappophorum spp.	10.8	10.3	4.9	6.4	6.7	5.4	3.9	3.4	1.2	6.6	6.8	6.0$\pm$0.8
Digitaria californica	3.3	4.1	1.9	3.1	2.2	0.7	1.1	2.8	2.0	9.0	3.9	3.1$\pm$0.7
Trichloris crinita	3.1	4.5	3.0	0.9	0.4	0.5	0.6	1.4	0	1.5	1.2	1.6$\pm$0.4
Setaria leucopila	1.1	2.1	4.8	0.9	0.8	0.7	0.3	0.4	0.6	1.9	1.6	1.4$\pm$0.4
Diplachne dubia	1.3	1.8	2.2	0.7	0.4	0	0.6	0.2	0.3	0.9	0.1	0.8$\pm$0.2
Aristida mendocina	0.1	0.3	1.0	0.2	0.6	0	0	0.2	0	0.2	0.1	0.2$\pm$0.1
Neobouteloua lophostachya	0.1	0	0.2	0.9	0.2	0	0	0.2	0	0.4	0	0.2$\pm$0.1
Bouteloua spp.	0	0	0.2	0	0	0	0.8	0.2	0.3	0	0	0.1$\pm$0.1
Eragrostis spp.	0	0	0	0	0	0	0	0	0	0	0	0
Forbs												
Chenopodium papulosum	59.6	57.5	45.7	52.8	58.2	66.3	69.1	60.3	66.9	54.6	54.6	58.7$\pm$2.1
Phacelia artemisioides	5.6	4.1	5.6	3.8	1.8	5.4	5.3	5.0	2.0	1.5	2.0	3.8$\pm$0.5
Descurainia sp.	0.3	0.7	2.5	3.4	3.0	3.2	3.1	4.4	3.8	1.6	11.3	3.4$\pm$0.9
Glandularia mendocina	0.1	0.2	1.6	0.5	2.2	3.0	1.4	3.6	6.2	1.0	1.6	1.9$\pm$0.5
Sphaeralcea miniata	0.7	1.1	1.4	1.5	1.0	1.5	3.3	1.0	3.5	0.7	1.1	1.5$\pm$0.3
Conyza spp.	1.2	0.8	1.3	0.3	0.2	0.2	0.3	1.0	0	0.9	1.6	0.7$\pm$0.2
Parthenium hysterophorus	0.1	0.1	0.2	0	0	0.2	0.3	0.8	0	1.2	0.6	0.3$\pm$0.1
Lappula redowskii	0.5	0.3	0.5	0.1	0.2	0	0.3	0.6	0.3	0.3	0.1	0.3$\pm$0.1
Heliotropium mendocinum	0.1	0	0	0	0	0.5	0	0.4	1.7	0.6	0.1	0.3$\pm$0.1
Plantago patagonica	0	0	0	0	0	0	0.3	0.6	0.9	0.6	0	0.2$\pm$0.1

Table 3. Mean percentage of grass and forb seeds in the digestive tracts of birds in year–round samples from 1993–2000. Acronyms: *Poospiza torquata* (PTOR), *Poospiza ornata* (PORN), *Phrygilus carbonarius* (PHRY), *Zonotrichia capensis* (ZONO), *Saltatricula multicolor* (SALT), and *Diuca diuca* (DIUC). The mean consumption ($\pm$SE) of every seed for all six bird species is given in the last column.

	PTOR	PORN	PHRY	ZONO	SALT	DIUC	Mean$\pm$SE
Grasses							
Sporobolus cryptandrus	32.5	18.1	20.5	23.2	36.0	0	21.7$\pm$5.2
Pappophorum spp.	24.1	2.8	7.7	5.8	23.9	39.4	17.3$\pm$5.8
Setaria leucopila	9.5	38.9	9.3	21.2	3.5	18.2	16.8$\pm$5.1
Trichloris crinita	18.4	6.4	28.7	2.4	15.6	2.1	12.3$\pm$4.3
Digitaria californica	8.7	5.7	13.1	0.5	4.3	10.7	7.2$\pm$1.9
Diplachne dubia	2.5	0	11.0	0.6	7.7	4.6	4.4$\pm$1.7
Aristida mendocina	1.5	2.3	5.7	0.6	2.1	2.8	2.5$\pm$0.7
Neobouteloua lophostachya	0	0	0	0.6	5.7	0	1.0$\pm$0.9
Eragrostis spp.	0.6	0	0	0	0.1	0	0.1$\pm$0.1
Bouteloua spp.	0.4	0	0	0	0	0	0.1$\pm$0.1
Forbs							
Chenopodium papulosum	0	18.8	1.4	25.7	0.9	0	7.8$\pm$4.7
Glandularia mendocina	0	0	2.1	15.1	0.2	0	2.9$\pm$2.5
Lappula redowskii	0	1.3	0	0	0	9.2	1.7$\pm$1.5
Parthenium hysterophorus	0	0	0	0.8	0	7.4	1.4$\pm$1.2
Sphaeralcea miniata	0	0	0	1.2	0	5.6	1.1$\pm$0.9
Descurainia sp.	0	5.7	0	0	0	0	0.9$\pm$0.4
Heliotropium mendocinum	0	0	0.5	2.3	0	0	0.5$\pm$0.4
Conyza spp.	1.7	0	0	0	0	0	0.3$\pm$0.1
No. of stomachs	44	22	11	96	37	15	
No. of seeds	1268	246	65	3666	716	151	

abundant bird species that eat seeds directly from the soil at Ñacuñán (Lopez de Casenave et al. 2008), and laboratory experiments which tested preferences among eight seeds (four forbs, four grasses) indicated that these birds have clear preferences for three grasses (*S. leucopila*, *Pappophorum* spp. and *D. californica*) and avoid two forbs (*P. artemisioides* and *P. patagonica*). *S. multicolor*, *D. diuca* and *P. ornata* also avoids *Ch. papulosum* seeds, which is less-preferred by
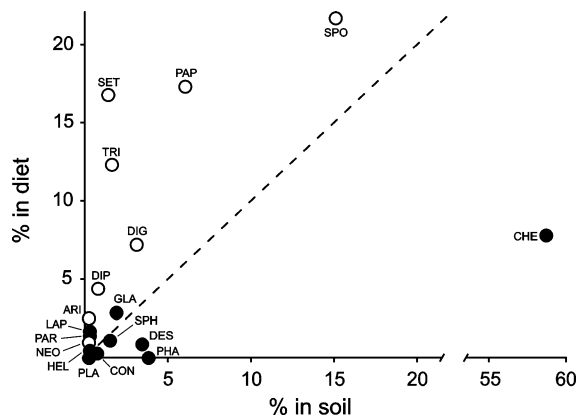

Fig. 1. Relation between the relative abundance, expressed as percentages, of total herbaceous seeds in the soil bank and in bird diets. Black dots correspond to forb species and open dots to grass species. Broken line represents the plane of equivalence of the occurrence in soil and in diet for each seed species. Acronyms: *Setaria leucopila* (SET), *Pappophorum* spp. (PAP), *Digitaria californica* (DIG), *Trichloris crinita* (TRI), *Sporobolus cryptandrus* (SPO), *Aristida mendocina* (ARI), *Diplachne dubia* (DIP), *Neobouteloua lophostachya* (NEO), *Chenopodium papulosum* (CHE), *Phacelia artemisioides* (PHA), *Descurainia* sp. (DES), *Glandularia mendocina* (GLA), *Sphaeralcea miniata* (SPH), *Conyza* spp. (CON), *Parthenium hysterophorus* (PAR), *Lappula redowskii* (LAP), *Heliotropium mendocinum* (HEL), *Plantago patagonica* (PLA).

Z. capensis. Only one forb seed (*P. hysterophorus*) appears to be strongly preferred (*Z. capensis*) or less-preferred by some sparrows (*D. diuca*, *S. multicolor*), whereas the remaining grass seed employed in the experiments (*S. cryptandrus*) is less-preferred by *Z. capensis* and *P. ornata*, and avoided by *S. multicolor* and *Diuca diuca* (Cueto et al. 2006). These results are generally consistent with patterns of seed selection in the field (Fig. 1). We then classified seeds into "selected species" if the ratio between percentage in the diet and percentage in the soil seed bank was greater than 2, and "non-selected species" if the ratio between percentage in the diet and the soil seed bank was less than 2 (Table 2, 3, Fig. 1). Patterns of seed vulnerability relative to avian predation were: (1) "selected grasses": *S. leucopila*, *A. mendocina*, *T. crinita*, *N. lophostachya*, *D. dubia*, *Pappophorum* spp., *D. californica*; involving the three grass seeds preferred in laboratory experiments; (2) "non-selected grasses" included *S. cryptandrus*, which had been avoided by two sparrows and less-preferred by the other two; (3) "selected forbs", with *L. redowskii*, *P. hysterophorus* and *G. mendocina*; the second species was the only one tested for preferences, and preferred or moderately consumed by several sparrows; (4) "non-selected forbs": *Ch. papulosum*, *S. miniata*, *Conyza* spp., *H. mendocinum*, *Descurainia* sp.; only *Ch. papulosum* had been tested in the laboratory and avoided by three out of four bird species; and (5) a group of relatively abundant seed species in the soil (>0.1%) which never appeared in bird stomachs and were avoided in laboratory trials (*P. artemisioides* and *P. patagonica*) were included into a "non-consumed species" category. Thus, rare and anecdotal seed species were not considered for analyses.

In sum, diet and seed preference data rendered clearcut results and we predicted the following for field experiments: (a) selected seeds, especially selected grasses, will be less abundant in control sites, (b) non-selected seeds (grasses and forbs) will be less abundant in control sites only if
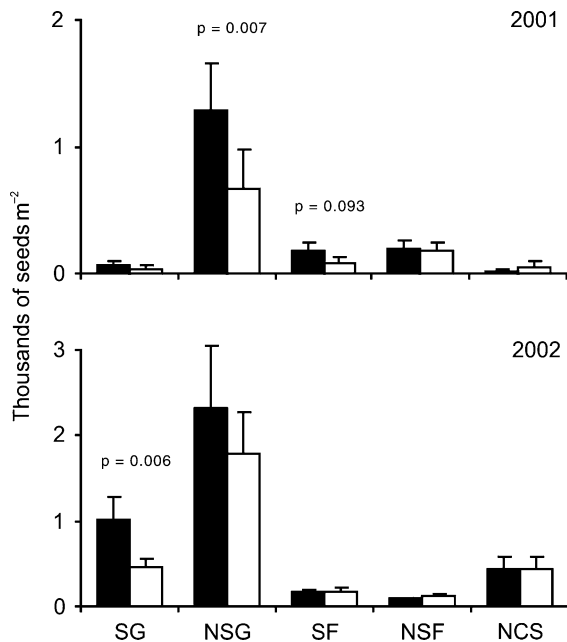
Fig. 2. Number of seeds m^{-2} in enclosure experiments carried out in 2001 and 2002 in open *Prosopis* woodland of the central Monte desert. Open bars reflect seed number in control conditions (with access to autumn-winter granivores) and black bars in treatment conditions (granivores excluded). Seed acronyms: SG (selected grasses), NSG (non-selected grasses), SF (selected forbs), NSF (non-selected forbs), NCS (non-consumed seeds). p-values of one-tailed, paired t-tests between enclosure and control (2001: DF = 17; 2002: DF = 30) are shown only when p < 0.1.

selected seeds are scarce or rare in the soil seed bank, and (c) seeds of non-consumed species will not differ significantly between control and treatment conditions.

Effects on soil seed bank

During 2001 only 18 out of 25 stations could be included in the analyses. Seed numbers of selected grasses were very low in exclosures and controls making statistical comparison uncertain (t = 1.000, p = 0.166, n = 18; Fig. 2). By contrast, seed numbers of non-selected grasses were high and more abundant in granivore exclusions (t = 2.756, p = 0.007), while the number of selected forb seeds showed

a slight tendency for more abundance in exclosures (t = 1.376, p = 0.093). The abundance of non-selected forb seeds (t = 0.369, p = 0.358) as well as non-consumed seeds (t = −0.497, p = 0.687) were similar between treatments (Fig. 2). Low numbers of selected grass seeds were not expected in depressions since precipitation in the previous growing season (2000–2001; 354.2 mm) was 35% above the mean. Low seed number should be plausibly attributed to failed dispersal instead of production. In 2000 and 2001 there was an unusual invasion of forbs in open woodland (family Asteraceae), most likely due to high autumn rains. These forbs covered extensive areas of previously bare ground, hindering grass seed dispersal. To avoid this problem, in 2002 – after moderately high rainfall (302.0 mm, 15% over the average) – we located experimental soil depressions nearer grass tussocks to ensure seed entrapment. During the second experiment, 31 stations remained active. The number of seeds of selected grasses was about an order of magnitude higher than in 2001, and it was higher in granivore exclusions (t = 2.689, p = 0.006, n = 31; Fig. 2). Foraging effect on non-selected grass seeds was not as notable as in the first experiment (t = 1.156, p = 0.128). The amount of selected forb (t = 0.370, p = 0.357) and non-selected forb seeds (t = 0.078, p = 0.469), as well as the number of non-consumed seeds (t = −0.089, p = 0.535) did not differ between exclosures and controls (Fig. 2).

Grass seedling recruitment

The proportion of grass seedlings that reached maturity or juvenile stage in both habitats was very low (Table 4). Further, we did not record seedling emergence at all in the autumn of 1995 (both habitats). Germination and grass survival was highest during the spring-summer 1994–1995 (8.60 and 3.75 seedlings m^{-2} in open woodland and scrubland, respectively). At the end of that growing season 5% (open woodland) and 8% (scrubland) of seedlings successfully "recruited" (28% of them fructificated but the rest only reached the juvenile stage). Thus, at least 95% in woodland and 92% in scrubland of emerged seedlings were lost before recruitment, and 99% and 91% of them, respectively, due to senescence provoked by drought.

Table 4. Number of emerging grass seedlings (mean ±SD) that reached the juvenile or madure phase at the end of the growing season (May 1994 and 1995) in two habitat types of the Reserve of Ñacuñán: open woodland and *Larrea cuneifolia* scrubland (we did not count emerging seedlings in the spring summer 1993–1994). The number of seedlings that died due to the activity of animals (herbivory or soil perturbation) or to senescence provoked by dry conditions are also included. Most of the surviving grasses remained as juveniles by the end of the growing season and, thus, figures in last column probably overestimates grass recruitment.

Period	Total emergence	Dead by senescence	Dead by animals	Adult or juvenile stage
Open woodland				
Spring–summer 1993–94 (n = 25)	1.84 ± 3.90	1.72 ± 3.96	0.12 ± 0.44	0
Autumn 1994 (n = 30)	1.40 ± 2.67	1.40 ± 2.67	0	0
Spring–summer 1994–95 (n = 30)	8.60 ± 10.40	8.10 ± 10.61	0.03 ± 0.18	0.47 ± 1.14
Autumn 1995 (n = 30)	0	0	0	0
Scrubland				
Autumn 1994 (n = 20)	0.05 ± 0.22	0.05 ± 0.22	0	0
Spring–summer 1994–95 (n = 20)	3.75 ± 6.37	3.15 ± 6.45	0.40 ± 0.88	0.20 ± 0.89
Autumn 1995 (n = 20)	0	0	0	0

Discussion

Seed-eating birds are highly selective in their diet. They heavily consume the less abundant grass seeds despite clear species-specific differences in morphology and size among them. For example, lighter *S. cryptandrus* seeds (ca 0.07 mg) were eaten as well as medium-sized *Pappophorum* spp. seeds (ca 0.35 mg), and heavier *S. leucopila* seeds (ca 0.75 mg). Caryopses in elongated diaspores with conspicuous awns (e.g. *T. crinita* and *A. mendocina*) were eaten together with those in round-shaped diaspores with smooth outlines (e.g. *S. leucopila*). Birds ate kernels that usually require no husking (e.g. *S. cryptandrus*) along with caryopses surrounded by hairy glumes or long projecting awns that require husking (e.g. *Pappophorum* spp. and *D. californica*).

The five more consumed seed species were all grasses and made up 75% of mean bird diet (Table 3, Fig. 1). This pattern of seed selection in the field coincided with seed preferences in the laboratory (Cueto et al. 2006; *T. crinita* was not tested for preferences). *S. leucopila*, *Pappophorum* spp. and *D. californica* were preferred by all bird species, whereas *S. cryptandrus* was less preferred (*Z. capensis*, *P. ornata*) or avoided (*S. multicolor*, *D. diuca*). Accordingly, the former species were all higly selected and *S. cryptandrus* was not selected by birds in the field (ratio = 1.4; Table 2, 3). Its high consumption is likely due to the combination of greater availability (Table 2) and flexible feeding behaviour of Ñacuñán's birds (Cueto et al. 2006). High consumption of grass seeds by birds has been reported in other locations, including several deserts (Morton and Davies 1983, Read 1994, Crowley and Garnett 1999, Garnett et al. 2005). Morton and Davies (1983) suggested that greater abundance or stability of grass seeds in the soil could account for the predominance of grass seeds in bird diet. This does not necessarily apply to Ñacuñán, however, where the mostly transient grass seed bank is less abundant that the persistent forb seed bank (Marone et al. 1998b). Certainly, grass seeds share other features that might make them relatively easy to harvest by birds; some of them are not firmly attached to a protective coat (Morton and Davies 1983), allow maximise seed processing speed owing to beak morphology and seed-handling techniques (Díaz 1990, Lopez de Casenave 2001), or have a relatively low incidence of secondary chemical compounds such as tannins or alkaloids (Díaz 1996). All these plausible mechanisms of seed selection should stimulate experiments devised to build general – although possibly hierarchical and context dependent – theory on the causes of seed preferences. Such kind of theory is needed to explain numerical as well as functional responses of birds given the remarkably versatile and opportunistic behaviour of most animal consumers (Jaksic and Marone 2007).

Although there is cogent evidence of the impact seed predation has on seedling recruitment of some focal desert scrubs that produce a moderate amount of seeds (Maron and Simms 1997, 2001), the impact of birds on grass and forb recruitment is less clear. On the one hand, grasses and forbs can produce huge amounts of seeds (Marone et al. 1998b) making top-down control unlikely. On the other hand, the effect of avian consumers has not been always assessed in granivory studies (Marone and Horno 1997), especially when phenomenological long-term enclosure experiments were involved. These experiments (sensu Peckarsky 1998) are essential for realistic pattern recognition and are often devised to detect the effects of one species (e.g. a granivore) on some response variable (e.g. the abundance of a seeding species). Consumers are usually excluded and overall changes in the response variable are adjudicated to manipulation (Brown 1998, Meserve et al. 2003). These phenomenological experiments have some practical problems like the difficulty to exclude birds from big areas (Thompson et al. 1991). Further, they often lack a priori mechanismic hypotheses that connect manipulated and response variables, making very difficult to distinguish phenomena derived from direct and indirect effects (Dunham and Beaupre 1998). These limitations can be solved, however, by combining phenomenological with short-term mechanism-explicit experiments (Werner 1998), which are devised to test causal hypotheses on consumer effects. For example, the behaviour of the tiny *S. cryptandrus* seeds in our trials could have appeared as astonishing in a phenomenological experiment since it varied markedly between years (Fig. 2), but bird natural history information (i.e. seed selection and preferences) provided us specific predictions that could be verified in the field: direct effects of birds on selected grasses when they are abundant (2002, Fig. 2), and a greater effect of birds on non-selected grass seeds and perhaps selected forb seeds when selected grasses are scarce (2001, Fig. 2). Mechanismic-explicit experiments contribute to identify direct and indirect ("context-dependent") effects of birds on target seeds and, thus, they may help to interpret phenomenological experiment results.

Seed predation reduced non-selected grass seeds by 49% (from about 1300 to 670 seeds m^{-2}) in 2001, and selected grass seeds by 55% (from about 1040 to 470 seeds m^{-2}) in 2002 (Fig. 2). Such figures are similar to previous indirect calculations, based on seed production and soil seed bank composition at Ñacuñán (Marone et al. 2000b). All these reductions are important, and therefore, birds may be considered efficient consumers. On this basis a negative impact of birds on most grass species (and perhaps a positive indirect effect on non-consumed forb species) can be expected. However, even if the Monte desert's birds are both efficient and selective, their impact on plant populations will ultimately depend on whether environmental stress obscures plant-animal interactions (Maron and Simms 2001).

At the end of the 1994–1997 dry cycle, Ñacuñán's soil seed banks suffered strong numerical reductions: <900 grass seeds m^{-2} remained in the soil (Table 1). Even in a period of very scarce seed reserves, the extrapolation of the number of emerging seedlings in the more mesic 1993–1995 period (3.24–8.60 seedling m^{-2} in the open woodland, 0.05–3.75 seedling m^{-2} in the scrubland; Table 4) indicates that the percentage of germinated seeds was very low; <1% of total grass seed available. Despite high winter seed predation, seed availability does not seem to limit seedling recruitment in the following growing season. By contrast, post-emergence mortality due mainly to senescence was very high (>95%, Table 4), suggesting that drought and safe-site availability (Maron and Simms 1997, Gutiérrez and Meserve 2003) may be important factors limiting grass recruitment in the Monte. Other kinds of evidence lead to similar conclusions. From the 422 grass seedlings that emerged during our study, 83 of them

(20%) did so in spring months, 296 (70%) in summer months, and 43 (10%) in autumn months. Given that grass seed dispersal usually begins in early summer (Marone et al. 1998b), a major fraction of emerging grass seedlings (i.e. those germinating in summer or autumn) could have come from newly produced seeds instead of from seeds that survived bird predation in the previous autumn and winter. Laboratory germination trials showed that high proportions of several grass seed species (e.g. *T. crinita*, *A. mendocina* and *Pappophorum* spp.) are viable and capable of germinating as soon as they disperse (Marone et al. 2000b).

A scenario in which: (a) summer seed production of the main grass species in bird diet (Table 3) is usually very high ($25-60 \times 10^6$ seeds ha^{-1}; Marone et al. 1998b); (b) birds strongly select seeds of several grass species for feeding (Cueto et al. 2006; this paper) and consume 50–60% of them in autumn-winter (Marone et al. 1998a; this paper); and (c) <1% of the remaining grass seeds germinate (Marone et al. 2000b; this paper) and <5% of these seedlings survive the growing season (this paper) suggests that grass population dynamics is more likely to be under bottom-up than top-down control in undisturbed habitats of the central Monte desert. This general conclusion must be cautious, however, and more research is needed since there are circumstances in which top-down effects may still be important. Birds may affect the spatial distribution of plants as a consequence of their seed preferences (Cueto et al. 2006) and selection of foraging sites (Milesi 2006), combined with the tendency of some seed species or group of species to co-occur in the seed bank at microhabitat scale (Marone et al. 2004). Short-term, enemy-mediated, indirect effects on seeds (Chaneton and Bonsall 2000) may affect the composition and spatial distribution of mature plant communities (e.g. the relative enrichment of forb seeds as well as the context-dependent enrichment of the less-selected seeds; Fig. 2). Further, results for the particular environmental conditions within the reserve of Ñacuñán could change in the more extensive semi-natural matrix of the Monte desert outside it. If granivory pressure is still high in disturbed habitats, where cattle grazing markedly reduces grass seed availability (Gonnet 2001), we can not rule out top-down effects of seed-eating animals on plants.

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