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RESEARCH LETTER

Granivory in the Monte desert, Argentina: is it less intense than in other arid zones of the world?

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Abstract. In 1978, Mares and Rosenzweig assessed seed removal rates by granivores at a site in the northern Monte desert of Argentina, and concluded that granivory in South America is 'much depressed'. In this study, spatial and temporal patterns of seed removal by small mammals, ants, and birds in the central Monte desert were analysed, and results compared with data available from other arid zones of the world. Ants were found to be the most important granivores in spring–summer, while birds were more important in autumn–winter. No differences were found in seed removal rates between microhabitats in winter, but in the summer both ants and birds removed more seeds

from under the canopy of shrubs and trees than from exposed microhabitats. The impact of ants appeared to be lower in South America than in other continents, but removal by birds at the study site was only exceeded in North America, and removal by mammals only in North America and South Africa. Results indicate that granivory in South America is not abnormally depressed. Instead, current data suggest that seed removal in North America is exceptionally high, and that low levels are actually the norm for most arid zones.

Key words. Granivory, desert ecology, seed removal, South America, ants, birds, small mammals.

INTRODUCTION

Small mammals, ants and birds are the most important granivores in deserts, where seed consumption is thought to be ubiquitous (Guterman, 1994) because seeds constitute a diverse and abundant food (Brown, Reichman & Davidson, 1979; Reichman, 1979; Morton, 1985). Conversely, seed consumption has an important influence on soil seed banks (Reichman, 1979) and, ultimately, on the species composition, abundance and distribution of plants (Brown *et al.*, 1979; Inouye, Byers & Brown, 1980; Brown & Munger, 1985; Louda, 1989; Heske, Brown & Guo, 1993; Guo *et al.*, 1995; Mull & MacMahon, 1996).

Broadly similar environmental features operate in different deserts and, as a consequence, ecologists have long searched for patterns of convergent evolution in deserts worldwide (e.g. Orians & Solbrig, 1977; Mares & Rosenzweig, 1978; Morton, 1985; Kelt *et al.*, 1996). Some of these patterns have become paradigms of desert ecology (Kerley & Whitford, 1994). Recent research in several arid zones of the world, however, challenges the convergence paradigm (see Kerley, 1992; Mares, 1993; Morton, 1993; Kerley & Whitford, 1994).

In 1978, Mares and Rosenzweig assessed experimentally rates of seed removal by granivores at a location in the northern Monte desert of Argentina (Andalgalá), and compared results to similar data from the Sonoran desert in North America. The authors found lower removal rates in the Argentine site, and concluded that granivory is 'much depressed' in South America. Almost all the studies on granivory in warm deserts published since then have taken this statement as given (Abramsky, 1983; Morton, 1985; Brown & Ojeda, 1987; Kerley, 1991; Kerley & Whitford, 1994).

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To account for the differences between hemispheres, Mares & Rosenzweig (1978) proposed that the extinction of the marsupial family *Argyrolagidae* in South America had brought about an abrupt decline of seeds that, in turn, led to impoverished assemblages of granivorous ants. This historical explanation is untestable by manipulative experiments, but the suitability of the data that led to it may be re-examined. In particular, seed removal rates should be examined for consistency within continents, because granivorous assemblages may exhibit large geographic variation (e.g. Medel & Vásquez, 1994, Kelt *et al.*, 1996). Differences among habitats (Vásquez, Bustamante & Simonetti, 1995), and among microsites (a neglected factor in previous studies), therefore deserve close attention.

In the central Monte desert of Argentina, rates of seed removal were analysed in a year-round, replicated study, using seed-dish experiments similar to those used in earlier studies in other arid regions. Temporal (i.e. seasonal) and spatial patterns of seed removal by small mammals, ants, and birds are reported here. Seed removal rates in the central Monte desert are also related to previous data from other sites, in order to assess the degree of consistency in granivory among warm deserts of the world.

MATERIALS AND METHODS

Study site

The study was conducted in the Biosphere Reserve of Ñacuñán (34° 02' S, 67° 58' W), in the central Monte desert (Mendoza Province, Argentina). The predominant habitat in the reserve is an open woodland of *Prosopis flexuosa*, with extensive shrub (mainly *Larrea* spp.) and grass cover (*Pappophorum* spp., *Trichloris* sp., *Digitaria* sp., *Sporobolus* sp.). A more detailed description of the flora and general habitats of the reserve may be found in Roig (1981). Nomenclature of plants follows Roig (1981).

Ñacuñán has a dry temperate climate with cold winters. On average, 76% of annual rainfall occurs in spring and summer (mean \pm SE rainfall from October until March: 248 ± 15.2 mm, $n = 24$ years), determining the growing season. Climatic data were taken at the weather station of the reserve, 1–3 km away from the study plots. Rainfall values during the span of the experiment correspond to those of an average year in the central Monte desert.

Experimental design

Sampling design followed guidelines in Kelrick *et al.* (1986). Seeds were provided to granivores at two plots within the reserve. At each plot, seed-tray stations were arranged in a grid at 10 m intervals. Each seed-tray station consisted of three plastic petri dishes (9 cm diameter): a 'mammal' tray, a 'bird' tray, and an 'ant' tray. Vertebrate trays were glued to the top of long plastic cylinders (1 cm diameter) and set 2–3 cm above the ground surface to prevent access to ants. These trays were opened and closed by moving a petri dish top, secured with a rubber band, from one dish to the other at dawn and dusk, so seeds were only available to birds during daytime and to mammals at night (all non-herbivorous small mammals at Ñacuñán are nocturnal). Ant trays were buried with the lips of the dish wall flush with the soil surface, and covered with 6 mm mesh hardware cloth to prevent access by vertebrates. Several small twigs were added to facilitate the access of ants to the dish. All the trays were filled with 10 g of a commercial seed (*Setaria italica*), checked daily at dawn and dusk over a 48 h period, and replenished with preweighed packets of seeds before total depletion. The rate of seed removal by tray was determined by weighing the remainder of the seeds and by subtracting this value from the initial weight.

To assess seasonal variations in the intensity of seed removal by the three taxa, a total of twenty-five seed-tray stations were used in every season during 1994–95: autumn (May), winter (August), spring (November), and summer (February). Therefore, seventy-five trays were exposed to seed predators at any one time ($n = 300$). All seed-tray stations were located in exposed microhabitats, away from canopies of trees and shrubs. To assess spatial variation in seed removal, twenty-five seed-tray stations were placed in exposed microhabitats and twenty-five in microsites under the canopy of trees (*Prosopis flexuosa*) or shrubs (*Larrea divaricata*) during winter (August) and summer (February). In these cases, 150 trays were exposed at any one time ($n = 300$). Nine trays out of the total number were lost while processing in the field.

The sampling design relied on some assumptions. First, all seeds missing from trays result from removal by the respective granivores, and seed removal is accurately measured. Second, all granivore groups have an equal probability of finding the seed trays. Finally, commercial seeds are equally palatable to all granivores, and patterns of their removal simulate the use of native seeds in natural situations (Parmenter,

MacMahon & Van der Wall, 1984; Kelrick *et al.*, 1986). Similar sampling designs have been employed in other studies, so it was assumed that there was no idiosyncratic bias in this case. During the summer of 1993–94, a pilot survey was conducted to check the appropriateness of the sampling techniques. Ant trays were easily reached by the ants, and several caged individuals, representing most granivorous bird species at Ñacuñán, were able to consume seeds from 2 cm-elevated dishes. Ants were not observed in vertebrate trays. Several species of commercial seeds were provided to granivores, and *Setaria italica* showed the highest rates of removal by every taxon. These seeds are heavier (2.6 mg) than native *Setaria leucopila* (0.9 mg), but have a similar spherical shape. *Setaria leucopila* seeds are heavily preyed upon by birds and ants in Ñacuñán (Lopez de Casenave, Marone & Cueto, unpub. data and pers. obs.). Both birds and ants (including some small-sized species) were seen removing the commercial seeds provided.

Data analysis

Inter-taxa differences in mean removal rates within each season were evaluated with one-way ANOVA. Tukey's test was used for a posteriori comparisons. Both spring and summer data were reciprocally transformed ($y = 1/(x + 0.25)$) to homogenize variances (Zar, 1996). Mean removal rates in the different microhabitats were compared with *t* tests, or *t* tests for unequal variances in those cases in which the samples were heteroscedastic (Snedecor & Cochran, 1980).

RESULTS AND DISCUSSION

Temporal patterns of seed removal

Rates of seed removal by granivores in Ñacuñán varied with season (Fig. 1). Ants were the most important granivores in spring and summer but removed few seeds during autumn and winter. Conversely, birds, followed by mammals, were the most important consumers in autumn and winter, but removed fewer seeds in summer.

These within-taxon seasonal trends are roughly paralleled by changes in the abundance of granivorous populations throughout the year. Seed-eating birds were censused during the span of the experiment in three or four sites within 1 km from seed-tray plots (see Marone, Lopez de Casenave & Cueto, 1997 for

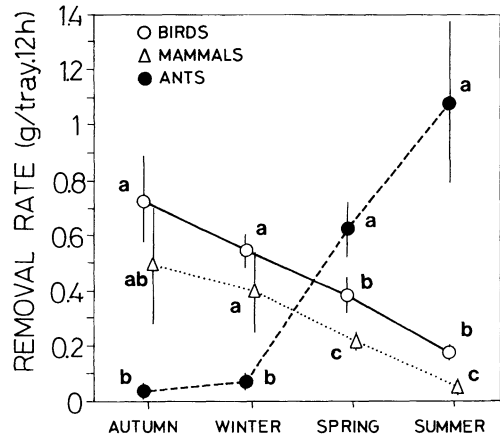


Fig. 1. Seasonal rates of seed removal by mammals, ants and birds in the central Monte desert. Values are means (\pm SE); $n = 25$ for every case except birds in autumn and mammals in autumn, with $n = 23$. Within a season, means with the same letter are not significantly different (Tukey's test, $P < 0.05$).

census methods). The highest abundance of these birds occurred in autumn (mean \pm SE = 2.01 ± 0.57 ind/ha) and winter (1.81 ± 1.01 ind/ha), and the lowest during spring (0.39 ± 0.11 ind/ha), with an increase in summer (1.53 ± 0.54 ind/ha), reflecting the presence of young (post-fledging) individuals following reproduction. These young birds could not be consuming seeds from experimental dishes, because seed removal rates by birds did not show an increase during the summer (Fig. 1). In Ñacuñán, the summed abundance of the three potential granivorous rodents (*Eligmodontia typus* Cuvier, *Graomys griseocephalus* Waterhouse, and *Calomys musculus* Thomas) is highest in autumn, decreasing gradually during winter and spring to a minimum in summer (see Table 1 in Ojeda, 1989), following the same trend as that of seed removal rates. Finally, although the abundance of ants was not measured directly, a marked decrease in activity and abundance between spring-summer and autumn-winter periods characterizes the ant fauna of Ñacuñán (Claver & Fowler, 1993; Lopez de Casenave, Cueto & Marone, pers. obs.), as has already been reported for other arid zones (Kerley, 1991; Thompson, Brown & Spencer, 1991; Vásquez *et al.*, 1995).

Seasonal patterns of seed removal at Ñacuñán, in the central Monte, differ from those reported for the northern Monte by Mares & Rosenzweig (1978). At Andalgalá, removal rates by ants were high in summer (January), maximal in autumn (May), and negligible

in spring (October–November). Seed consumption by birds was highest in spring and early summer (October to December), and removal by mammals peaked in summer (January). As those authors did not report seasonal changes in the abundance of granivores in their site, the causes of such differences between northern and central Monte desert remain unresolved.

Spatial patterns of seed removal

Spatial patterns have rarely been considered in experiments on seed removal (although see Brown *et al.*, 1975; Abramsky, 1983). This is surprising, considering the importance of differential use of microhabitats by desert rodents (reviewed by Price, 1978; Brown *et al.*, 1979; Price & Brown, 1983) and the distinct patterns of spatial distribution frequently reported for birds (Cody, 1985; Wiens, 1989, 1991) and ants (Crist & Wiens, 1994, 1996). In Ñacuñán, none of the three taxa showed a difference in rate of seed removal between microhabitats in winter (Fig. 2). In summer, however, both ants and birds removed more seeds from under the canopy of shrubs and trees than from exposed microhabitats, whereas seed removal by mammals did not differ between microsites (Fig. 2). These results strongly suggest a seasonal shift in the feeding microhabitats used by ants and birds.

The preference for protected microhabitats by ants and birds during the summer may result from thermoregulatory constraints. Open areas are exposed to high temperature and decreased humidity, and therefore they may be less suitable for ants, which have activity schedules ruled by ectothermy and other physiological constraints (see Holldobler & Wilson, 1990, and references therein). In cereal croplands of central Spain, harvester ants also forage in microsites with high shrub cover, but such a pattern might have arisen there as a consequence of the placement of nests under shrubs as a means to regulate nest temperature and humidity (Díaz, 1991, 1992). Desert birds may also be constrained by microclimatic influences such as sun exposure and soil temperature that may affect birds' thermal budget (Goldstein, 1984; Wiens, 1985; Walsberg, 1993; Wolf & Walsberg, 1996). Small mammals, on the contrary, appear to be less affected by the thermic environment largely because most of them restrict their activities to night-time (Bozinovic & Simonetti, 1992).

The background food distribution in the field could be another factor responsible for the increased use of protected microsites. In 1994, the standing crop of

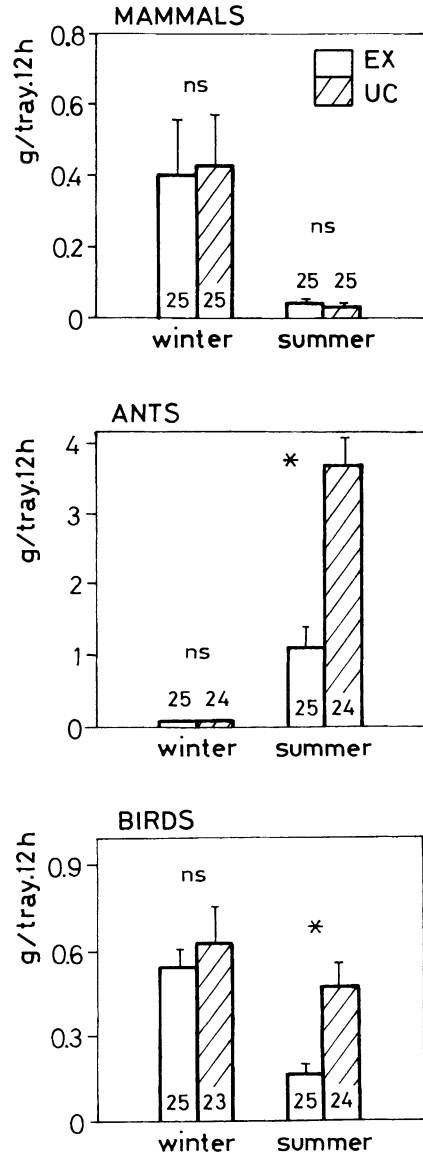


Fig. 2. Mean (± 1 SE) rates of seed removal by mammals, ants and birds in exposed microhabitats (EX) and in microhabitats under the canopy of trees or shrubs (UC) during winter and summer in the central Monte desert. The different scales used for each graph should be noted. Sample sizes are indicated in each bar. Asterisks indicate significant differences between microhabitats ($*P < 0.001$, ns, non significant, *t* tests, see Materials and methods).

seeds on the soil showed a strong decline toward the summer in Ñacuñán, when most seeds available to granivores remained in protected microhabitats (i.e. under the canopy of trees and high shrubs; Marone *et al.*, unpub. data). Therefore, granivores may increase their use of protected microhabitats for foraging during the summer, when overall seed supply is relatively scarce and the remaining seeds appear to be more abundant in protected sites.

Increased predation risk at exposed sites may also shape habitat selection patterns in both mammals (Kotler, 1984; Longland & Price, 1991; Lagos *et al.*, 1995) and birds (Lima, 1990; Lima & Valone, 1991). However, there is no reason to suppose that predation is more intense during summer than in other seasons in Ñacuñán. Instead, birds of prey are usually more abundant in the reserve during winter than summer (Marone, 1992). Therefore, predation risk is not likely to be responsible for the microhabitat patterns of seed removal shown here, although its role should be more rigorously assessed.

South American granivory in perspective

Available data about rates of seed removal by granivores in several arid zones of the world are depicted in Fig. 3. All data in this figure are average removal rates calculated over the year. Data from the Israeli desert (Abramsky, 1983) were not included because birds' removal rates were not assessed, and because they dealt exclusively with the summer. Their inclusion might confound potential comparisons, because rodents switch their diets in winter (Bar, Abramsky & Gutterman, 1984), and ants decrease foraging activities during the colder months. Significant seasonal variations in patterns of seed removal are frequently observed (e.g. Morton, 1985; Kerley 1991; Vásquez *et al.*, 1995; this study).

Removal rates by Ñacuñán granivores were averaged over both kinds of microhabitats. Differences in removal by ants and birds between microhabitats in Ñacuñán (Fig. 2) point out a potential bias in seed removal studies. Had only data from exposed microhabitats been taken from this site, overall seed removal by ants would have been dramatically underestimated (Fig. 3). Vásquez *et al.* (1995) also showed that different habitats at the same site can hold different rankings of granivores. The comparison of seed removal rates among geographically disparate sites should be made with caution, because the precise allocation of effort to every microhabitat is often

unreported, and results may depend dramatically on such allocation.

Whatever sample designs were used, rates of removal by every taxon appear to be higher in the central Monte than in other South American sites. Indeed, removal rates by birds at Ñacuñán is only surpassed in North America, and removal rates by mammals only in North America and South Africa. The impact of ants appears to be lower than on other continents, as previously suggested by Mares & Rosenzweig (1978), although removal rates from protected sites alone is roughly similar to that in Australia.

Overall, South American removal rates by ants appear to be lower than in other deserts in spite of the assemblages of harvester ants being more diverse and abundant than their North American and Australian counterparts (Medel, 1995). Food habits of South American harvester ants, however, appear to be more generalized than in North America (Medel & Vásquez, 1994; Medel, 1995), and this might explain, at least partially, their reduced consumption of seeds.

Removal by mammals, on the other hand, is consistently low within the Southern Hemisphere sites in comparison to North America and possibly to the Northern Hemisphere as a whole, since Abramsky's (1983) data suggest a similar high consumption by mammals in Israel. This pattern may be related to the paucity of granivorous rodents in southern continents (Kerley & Whitford, 1994; Vásquez *et al.*, 1995), and also to the more omnivorous food habits of South American small mammals (Kelt *et al.*, 1996).

Finally, birds are variable in their relative importance with respect to the other two taxa. Previous workers felt that their results were an underestimation of the impact of granivorous birds, because of sampling inadequacies (Mares & Rosenzweig, 1978; Morton, 1985; Kerley, 1991) or because they did not observe birds at the feeding trays (Brown *et al.*, 1975; Abramsky, 1983). Birds were regularly seen at the seed-tray plots in Ñacuñán, and they visited a high proportion of trays, as judged by husk remains as well as tracks around dishes. Indeed, the results suggest that birds have an important impact in relation to other taxa (see also Parmenter *et al.*, 1984; Thompson *et al.*, 1991; Guo *et al.*, 1995), and do not support those authors who view birds as unimportant seed-eaters in desert ecosystems (e.g. Brown *et al.*, 1975; Mares & Rosenzweig, 1978; Abramsky, 1983).

Current data on inter-continental differences in the impact of desert granivores suggest, as Kerley & Whitford (1994) pointed out for small mammals, that

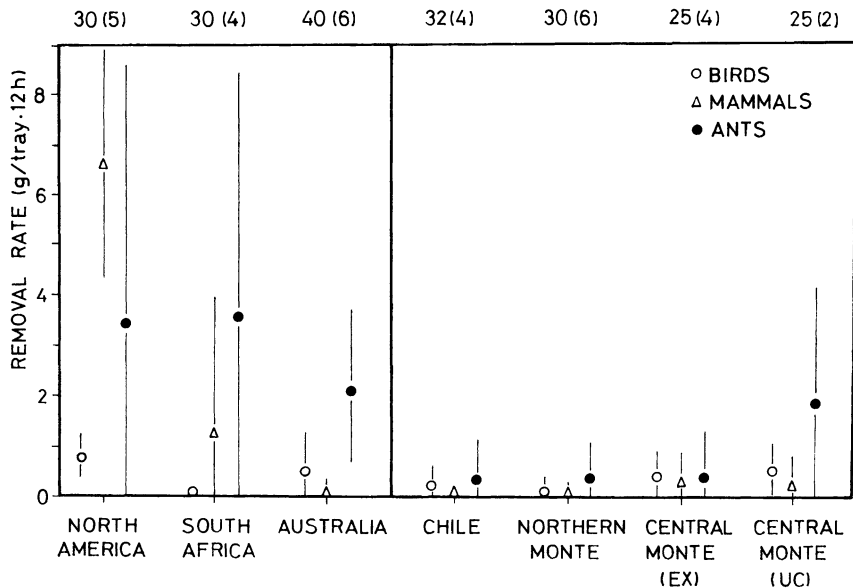


Fig. 3. Mean (\pm SD) rates of seed removal in several arid regions of South America (right side) and elsewhere in the world (left side). Also shown is the number of seed-tray stations used in each region, with the number of temporal samples in parentheses. Data for all the regions except Australia (four sites) and South Africa (two sites) are from single locations. Data for all the regions except Chile (from Vásquez *et al.*, 1995) and central Monte (this study) were redrawn from Kerley & Whitford (1994). EX, exposed microhabitats; UC, microhabitats under the canopy of trees or shrubs

granivory in North America differs from that of the Southern Hemisphere. Low levels of seed removal actually appear to be the norm, whereas granivory in North American deserts is exceptionally high. From this perspective, granivory in South America does not seem to be abnormally depressed, as had previously been suggested (Mares & Rosenzweig, 1978; Abramsky, 1983; Morton, 1985). Future research should seek to explain why granivory is so prominent in North America instead of focusing on explanations about the reduced levels of granivory in other deserts. Clearly, more comparative studies are required to rule out particular explanations and to advance on the knowledge of patterns and mechanisms associated with granivory in deserts.

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