

Granivory in the Chilean matorral: extending the information on arid zones of South America

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Comparative studies of granivory intensity across different arid and semi-arid regions of the world have assumed homogeneity of conditions over large geographical areas, despite the existence of evident heterogeneities at local and regional scales. For South America, previous evidence from the Monte desert, Argentina, showed that granivory intensity is low compared with other continents and that seed removal rates by taxon (granivore ranking) are in decreasing order: ants > birds = small mammals. In this work, we examined the assumed generality of this pattern for another South American region, the Chilean matorral. We studied the differences between sparse and dense habitats of the matorral in granivory intensity throughout the year. Although total seed removal did not differ between habitats, differences among granivores did occur. Ants were the most important seed removers in both habitats, although they did not differ from birds in the sparse habitat. Further, ants were the most important seed consumers during summer, but their seed removal rate is almost negligible the rest of the year. Birds maintained an intermediate rate of seed consumption through the year. Granivory intensity by small mammals was very low in both habitats during the whole year. The granivore ranking obtained for the Chilean matorral was: ants > birds > mammals, in dense habitat; and ants = birds > mammals, in sparse matorral. Ant abundance is correlated with seed removal throughout the year. This relationship was not found in the other taxa. We discuss possible causes for the differences among habitats, taxa, and seasons, as well as distinct granivore rankings from different continents.

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Introduction

Granivory by ants, birds, and small mammals has been used to assess convergent evolution across communities from different arid and semi-arid regions of the world (Mares and Rosenzweig 1978, Abramsky 1983, Morton 1985, see also Brown et al. 1979). Usually, seed removal rates have been estimated at one or a few sites, and the results have been considered to reflect the intensity of granivory for a whole region or continent. The assumption behind this extrapolation is that the environment is homogeneous; i.e. what happens at a local scale also oc-

curs at larger geographical scales. Nevertheless, arid regions do present important spatial and temporal heterogeneities (Wiens 1986, Kotler and Brown 1988). Even at a local scale, different habitats can be distinguished within a single ecosystem (Kolasa and Pickett 1991). This variability has seldom been addressed in granivory studies (but see e.g. Brown et al. 1975, Morton 1985, Díaz 1992), and once taken into account, it could challenge current inter-regional or inter-continental comparisons. If distinct habitats of a given arid ecosystem present different patterns of granivory, then the validity of broad scale extrapolations would be weakened. On

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the contrary, if they present similar patterns, then extrapolations and hence current comparative studies would be strengthened.

For South American arid regions, Mares and Rosenzweig's (1978) pioneering work is the only experimental evidence on year round granivory intensity. Through seed removal experiments in the Monte desert, Argentina, they found that overall granivory intensity was low compared to the Sonoran desert, North America. That difference was attributed to the absence of specialist granivores in the Monte desert. Seed removal rates by taxa (hereafter granivore ranking) were, in decreasing order: ants > birds = rodents. The results of Mares and Rosenzweig's (1978) work, carried out at one site near Andalgalá, Catamarca, Argentina, have been tacitly assumed to be general for arid ecosystems of South America (e.g. Abramsky 1983, Morton 1985, Brown and Ojeda 1987, Kerley 1991, Wiens 1991), despite the evident lack of research in other habitats of the same region and in other arid or semi-arid regions of the continent. In this paper, we study the supposed generality of the granivory pattern for South America in the semi-arid Chilean matorral. We address the problem of local and regional heterogeneity, the former through experimental analysis of seed removal rates by different taxa in two contrasting habitats of the matorral, and the later by comparison with the work of Mares and Rosenzweig (1978).

Material and methods

Study site

The study was carried out during 1990 at Fundo El Pangué, 90 km north-west of Santiago (coastal range, 33°18'S, 71°11'W, 500 m a.s.l.). The site is located in the mediterranean Chilean matorral (semi-arid shrubland, Rundel 1981). This region is characterized by warm, dry summers and wet winters (di Castri and Mooney 1973). Annual mean precipitation is variable reaching c. 300 mm, similar to that of Mares and Rosenzweig's (1978) study site (see Mares et al. 1985). In general, the matorral has two conspicuous habitats, a more xeric area with open scrub vegetation (sparse habitat), and a more mesic habitat with more cover of evergreen sclerophyllous shrub species (dense habitat), mostly located in southern exposed slopes (Armesto and Martínez 1978). A portion of the sparse matorral corresponds to degraded shrubland vegetation through past wood-cutting and live-stock grazing (see Fuentes et al. 1984, Simonetti 1989). Physiognomically, the matorral shows some remarkable convergences with other mediterranean-climate areas, such as the North American chaparral and the Mediterranean Basin, and this has been the subject of many comparative studies (e.g. di Castri and Mooney 1973, Mooney 1977, Cody and Mooney 1978). At Fundo El Pangué the dense habitat has a woody/shrub cover of c.

90%, with *Cryptocarya alba*, *Peumus boldus*, and *Lithraea caustica* as the dominant species. Herb cover is c. 15%. The sparse habitat is degraded vegetation and has a shrub and herb cover of 40% and 60%, respectively, and *Baccharis linearis*, *Muehlenbeckia hastulata*, and *Acacia caven* are the most abundant shrub species. The plots of dense and sparse habitat used in this study have c. 20 and 50 ha of extension, respectively. The overall landscape of the area can be characterized as a mosaic comprising patches of dense vegetation embedded in sparse habitat, cultivated areas and/or human settlements.

Seed consumers

Pogonomyrmex spp., and *Solenopsis gayi* are the most conspicuous seed consumer ants. The most important granivorous birds are *Callipepla californica*, *Diuca diuca*, *Elaenia albiceps*, *Nothoprocta perdicaria*, *Phrygilus gayi*, *P. fruticeti*, *P. alaudinus*, *Sicalis luteola*, *Thripophaga humicola*, and *Zonotrichia capensis*, all with diurnal habits (López 1990). Small mammals comprise mainly rodents, though there is one common didelphid marsupial. Important mammalian seed consumers are *Oligoryzomys longicaudatus* and *Phyllotis darwini*. All are nocturnal (Glanz 1977, Meserve 1981a).

Seed removal rate experiments

We evaluated seed removal rate by placing 32 feeding stations located in the sparse and dense habitats of the matorral (16 stations in each). Two trays were placed in each station, one accessible only to birds/mammals and the other only to ants. We set four control trays (all seed consumers excluded) in each habitat to determine possible effects of water gain or loss on seed mass. Trays consisted of plastic Petri dishes. Ant trays were covered with 1 cm² wire netting to exclude vertebrate consumption and they were set at ground level, with small twigs to facilitate access by ants. Bird/mammal trays were glued to the top of large nails and set 2-3 cm off ground surface. Previous trials proved that ants were unable to reach the bird/mammal feeding trays. In both habitats the feeding stations were placed 10-15 m apart, in a linear transect. The trays were filled with seeds of barnyard grass, *Echinochloa crusgalli* (10 g each). Other survey revealed that this species is actively consumed by ants, birds, and small mammals (Vásquez unpubl.). Removal rates were measured over 72 h periods. The bird/mammal trays were emptied and replenished every subsequent dawn and dusk. Ant trays were filled once, except during summer when they were emptied and replenished by the second experimental day owing to high removal. Seed removal rate by tray was determined by weighing the remainder of the samples and correcting for water gain or loss by comparison with the controls. We carried

out the experiments in all four seasons: January (summer), May (autumn), August (winter), and October (spring). All experiments were conducted on moonless nights to avoid reduced activity by small mammals due to predation risk effects via environmental illumination (Simonetti 1989, Vásquez 1994).

For ease of comparison with previous studies, we use removal rate standardized to $\text{grams} \times \text{tray}^{-1} \times 12 \text{ h}^{-1}$. Since our data were obtained with artificial seed aggregates with no depletion (see above), the use of other measures of foraging costs, such as giving-up density (Brown 1988, Kotler et al. 1991) is not justified. We emphasise that to make comparisons with other studies possible, we carried out a similar experimental design to that of previous studies. However, those studies have failed to standardize all procedures across experimental designs, in particular concerning the seed species utilized. Consequently, several criticisms have challenged conclusions derived from comparisons of quantitative measures such as seed removal rates (see Parmenter et al. 1984, Andersen and Ashton 1985, Kelrick et al. 1986, for discussions on the seed dish technique). For this reason, for inter-regional comparisons we will focus on granivore rankings, and not on actual seed removal rates.

Estimation of granivore abundances

To assess if granivory intensities are correlated with granivores' densities, we estimated relative abundances per taxon in the dense and sparse habitats. Ants were estimated placing 20 pitfall traps, 10 m apart, in each habitat during two four-day periods every season. Although this number of traps may be low to assess actual densities, it is adequate to evaluate ant relative abundance between habitats (see Southwood 1978). Point count method was used to assess the relative abundance of birds in each habitat (see Bibby et al. 1992) with a total sampling effort of 1 h^{-1} during five-day periods each season. The minimum number of small mammals alive was evaluated from live-trapping with Sherman traps (grid with 50 traps, 10 m apart each in a 10×5 arrangement). We placed one grid per habitat. Traps were operated during two five-day periods every season, and all animals

were individually marked by fur-clipping. Because two abundance estimations were relative and not actual abundances, comparisons between taxa were not possible.

Data treatment

A three-way balanced analysis of variance was carried out to analyse the effects of taxa, season, and habitat on seed removal rate. Data satisfied the ANOVA assumptions of normal distribution and homogeneity of variances. Tukey tests ($\alpha=0.05$) were used to assess differences between treatments. The relative abundances of granivores are expressed as the percentage of individuals captured (ants and mammals) or observed (birds) in each habitat. We made a survey of studies that measured seed removal rates to compare granivore rankings from other arid regions. Since we could not evaluate this information statistically, we considered two taxa to have different granivory intensities when the average seed removal rate of one is at least twice that of the other.

Results

Seed removal rates

Total seed removal rates (all taxa together) did not differ between habitats (overall annual mean \pm SE: 0.24 ± 0.04 and $0.21 \pm 0.03 \text{ g} \times \text{tray}^{-1} \times 12 \text{ h}^{-1}$ for dense and sparse habitat respectively, Table 1, Fig. 1). There were taxa and seasonal effects (Table 1). Given the significant effect of the interactions between taxa and habitat, and season and habitat (Table 1), we carried out additional within-habitat ANOVAs to evaluate taxa differences. These analyses proved significant differences among taxa in each habitat ($F=12.0$, d.f.= 2, $p<0.001$, in dense habitat; $F=6.8$, d.f.= 2, $p<0.001$, in sparse habitat). On an annual basis, in the dense habitat ants consume significantly more seeds (0.51 ± 0.08) than birds (0.16 ± 0.03) and small mammals (0.05 ± 0.01 ; see Fig. 1; all statistically different, Tukey test). In the sparse habitat, ants and birds consume similar quantities of seeds ($0.29 \pm$

Table 1. Summary of analysis of variance for seed removal rate by three taxa (ants, birds, and small mammals), during the four seasons in two different habitats (dense and sparse) of the matorral.

Source of variation	df	mean square	F	p
Taxa	2	4.11	38.35	<0.001
Season	3	5.71	53.28	<0.001
Habitat	1	0.11	0.98	0.322
Taxa*season	6	6.14	57.26	<0.001
Taxa*habitat	2	1.09	10.14	<0.001
Season*habitat	3	1.04	9.67	<0.001
Taxa*season*habitat	6	0.71	6.61	<0.001
Error	360	0.11		

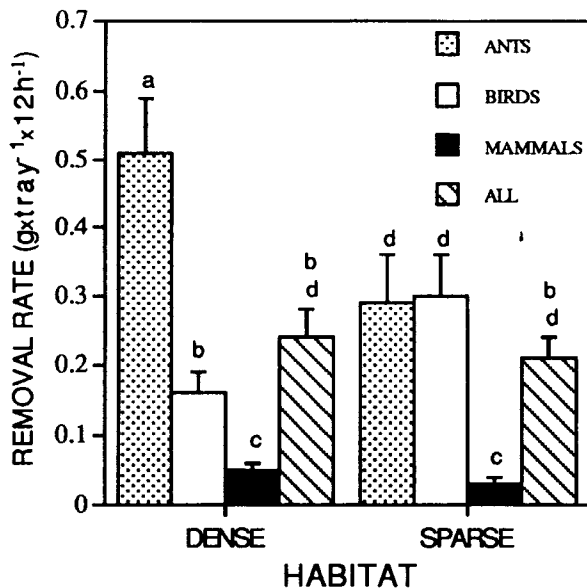


Fig. 1. Annual removal rates (mean \pm SE) by ants, birds, small mammals, and all (average for all taxa grouped) from trays located in dense and sparse habitat. Different letters on top of bars indicate significant differences between means (Tukey test, $\alpha=0.05$).

0.07 and 0.30 ± 0.06 , respectively), whereas mammals have significantly lower removal rates (0.03 ± 0.01 , see Fig. 1, Tukey test).

Seed removal rates vary significantly throughout the year (Table 1, Fig. 2). Total seed removal rate was highest during summer, and lowest during autumn. Overall, ants were the most important seed consumers (0.40 ± 0.07) although their importance varied seasonally (Fig. 2). They are the most important granivores only in summer (Fig. 2). Birds are the second most important seed removers (0.23 ± 0.04), with a lower annual variation (Fig. 2). Small mammals removed the lowest quantities

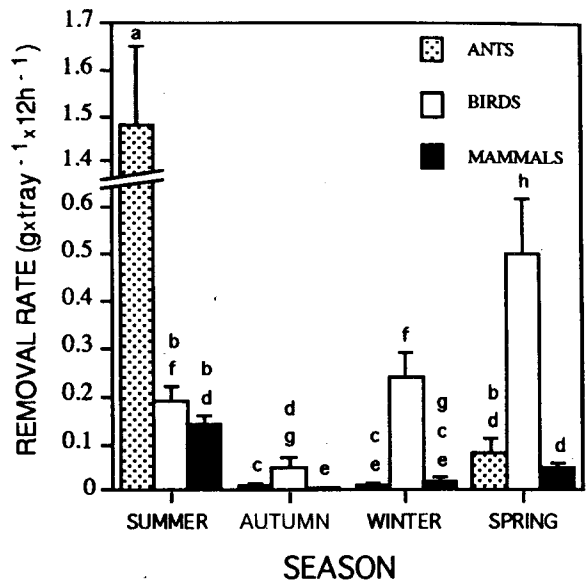


Fig. 2. Seasonal removal rates (mean \pm SE) by ants, birds, and small mammals. Data from dense and sparse habitats has been grouped. Different letters on top of bars indicate significant differences between means (Tukey test, $\alpha=0.05$).

of seeds year round (0.04 ± 0.01). Summarizing, the granivore rankings in each habitat were: (i) ants > birds > mammals, in dense habitat; and (ii) ants = birds > mammals, in sparse habitat.

Granivore abundances

Ant abundance did not differ significantly between dense and sparse habitat (Wilcoxon, $p=0.715$, Table 2). On the other hand, birds tended to be more abundant in sparse habitat, the reverse occurred with small mam-

Table 2. Abundances of seed consumers in the sparse and dense habitat during all seasons. Data is presented as total number of individuals captured (ants and small mammals) and observed (birds). Wilcoxon signed rank tests were carried out to compare abundances between habitats for each taxon separately. The percentage of individuals captured or observed in each habitat are given in parentheses.

Taxa	Habitat	Summer	Autumn	Winter	Spring	p
Ants	Sparse	140 (58.3)	14 (63.6)	7 (33.3)	88 (48.9)	0.715
	Dense	100 (41.7)	8 (36.4)	14 (66.7)	92 (51.1)	
Birds	Sparse	14 (66.7)	21 (72.4)	13 (59.1)	19 (61.3)	0.068
	Dense	7 (33.3)	8 (27.6)	9 (40.9)	12 (38.7)	
Mammals	Sparse	15 (38.5)	4 (12.1)	4 (20.0)	7 (20.0)	0.068
	Dense	24 (61.5)	29 (87.9)	16 (80.0)	28 (80.0)	

imals, although these differences were not significant (Wilcoxon, $p=0.068$, for both birds and small mammals, see Table 2). There is a positive and significant correlation between ant abundance and its respective seasonal seed removal rate (Spearman, $r=0.90$, $p=0.017$). Abundances of birds and small mammals showed lower seasonal variations (Table 2) and they were not significantly correlated with their respective seed removal rates (Spearman, $r=0.24$, $p=0.523$; and $r=0.04$, $p=0.912$, for birds and small mammals, respectively).

Discussion

Comparison within the matorral

Despite the conspicuous physiognomic difference between dense and sparse matorral, total seed removal rates did not vary between these two habitats (Fig. 1). This could be attributable to a compensation effect. That is, while ants removed more seeds in the dense than in the sparse habitat, birds did the reverse. Although not quantified, our observations suggest that in the dense habitat ant activity varies less through the year relative to the sparse habitat, despite their high annual variability. Possibly, the canopy of the dense habitat acts as a buffer from abiotic factors, which favours the activity of ectotherms. This hypothesis is supported by the fact that soil temperature in the matorral varies less in microhabitats with more cover (Del Pozo 1985). The strong dependence between the degree of activity of ectotherm organisms and the seasonal (and daily) variation of soil temperature (Whitford and Ettershank 1975, Bernstein 1979) may also explain the significant correlation between removal rates by ants and their abundance throughout the year.

Several factors such as background resource abundance, trophic specialization, consumer abundance and activity, and/or ability to detect patchy resources among others may explain the observed granivore rankings. In other locality of central Chile, López (1990) found up to six species of strict granivore small birds (over 92% of their total year round diets are seeds). This fact plus the abundance of birds in the Chilean matorral (see Cody 1974), may explain their higher seed consumption as

compared to that of mammals. However, this raises the following question: why don't birds have higher removal rates than ants? It could be argued that the energy requirements are not higher for the bird assemblage. Another answer could rely on bird foraging behavior. Parmenter et al. (1984) have suggested that because birds have different sensory techniques and locomotion modes than ants and mammals, they probably have a lower probability of finding and using seed trays (see also Thompson et al. 1991). Given the seasonal variability in natural seed abundances (Bustamante unpubl.), birds may rely on predictable food sources, and they may not spend much time searching for new food patches (Mares and Rosenzweig 1978, Parmenter et al. 1984, Kerley 1991). The negligible mammalian seed removal may be explained by generalist food habits (Meserve 1981a) and the relative scarcity of small mammals in the matorral compared to other systems (Glanz 1977). Clearly, more studies are needed to explain unequivocally the differences between taxa.

Comparison with other regions

At first sight, a quantitative comparison between Argentina and Chile shows an impressive similarity in total granivory intensity by ants (c. $0.4 \text{ g} \times \text{tray}^{-1} \times 12 \text{ h}^{-1}$ in both regions, see results above, Mares and Rosenzweig 1978; Fig. 2 in Morton 1985). However, this result should be considered cautiously because seed removal rates were measured with different seed species in both studies. When the same seed species are used, ants remove many more seeds in the Monte desert (Medel and Vásquez 1994, Vásquez unpubl.). Ants are also more diverse in Argentina than Chile with more species specialized on seeds in the former region (Medel and Vásquez 1994). The effect of seed species may also apply to birds and mammals (Parmenter et al. 1984, Kelrick et al. 1986). Therefore, we prefer to focus on more qualitative results

Granivore rankings do not match between regions, although there are some similarities. Ants are the most important seed consumers in Argentina and Chile. Although in the Monte desert, birds tend to consume slightly more seeds than mammals do (see Mares and Rosenzweig 1978), there is no statistical test for this pat-

Table 2. Granivore rankings in different arid regions of the world. Symbols: A=ants; B=birds; M=small mammals.

Region	Granivore ranking	Reference
North America (Sonora)	M > A > B	Mares and Rosenzweig (1978)
Israel	M > A > B	Abramsky (1983)*
Australia	A > B > M	Morton (1985)
South Africa (Karoo)	A > M > B	Kerley (1991)
South America: 1. Monte desert	A > B = M	Mares and Rosenzweig (1978)
2a. Dense matorral	A > B > M	This study
2b. Sparse matorral	A = B > M	This study

*That study was carried out only during spring-summer and birds were not evaluated but considered negligible.

tern, and following our criteria for granivore ranking they should be considered not to be different (Table 3). The results of this study support the advanced generalizations that ants are the most important seed harvesters and small mammals the least important seed consumers in arid regions of South America. However, this support is not totally conclusive, since our survey shows that habitat structure may decrease ant importance relative to other taxa. Whether or not birds differ from mammals requires a re-assessment of the data from Argentina.

Seed removal by ants and mammals varies greatly among different arid regions of the world (Table 3). Small mammals, especially rodents, are more important seed consumers than ants in the Sonoran desert of North America (Mares and Rosenzweig 1978) and in Israel (Abramsky 1983), whereas the reverse occurs in Australia (Morton 1985), the South African Karoo (Kerley 1991) and two South American regions (Mares and Rosenzweig 1978, this study). Interestingly, this switch happens between northern and southern hemisphere, and the diversity of granivorous small mammals is lower in southern continents (Glanz 1977, Morton 1979, Meserve 1981a, Kerley 1992). If desert communities are structured to a large degree by inter-specific competition, this pattern suggests a competitive release between ants and mammals (Morton and Davidson 1988). There is no region where birds are the most important granivores, and in four out of six studies, they are the least important seed consumers (Table 3). Because many desert bird species are abundant and specialized in seed resources (Wiens 1991), the reason for very low seed removal rates in several, if not all, studied arid regions may lie in the experimental technique used (Parmenter et al. 1984). Recent research with a different methodology reveals that their importance in North America may be underestimated with traditional seed dish techniques (Thompson et al. 1991).

The different granivore rankings found in nearby habitats of the matorral support the view that large scale extrapolations of previous studies should be considered cautiously. Different granivore rankings were as different between habitats as between some continents (Table 3). Therefore, the contention that phylogenetic or other historical divergences between granivorous taxa may explain different granivore rankings between continents (e.g. Mares and Rosenzweig 1978, Morton 1985) may be unnecessary (see Blondel 1991, Schluter and Ricklefs 1993 for discussions on community-level convergence). More parsimoniously, differences at the ecological time scale in granivore abundances and species composition between sites may explain the observed patterns. On the other hand, the size of the resource base in different regions seems to be quite different, which could affect the occurrence and degree of granivory. In fact, seed abundances in northern Chilean matorral are within the lower ranges found for North American deserts (Meserve 1981b, see also Reichman 1975, Price and Reichman 1987, for North America). This fact could have hindered seed specialization in the matorral, precluding the occur-

rence of inter-taxa competition, which has been shown to be important in several arid regions of the world, and possible a convergence enhancing force (see Brown et al. 1979, 1986). The same situation could apply to other continents. In summary, the assumed homogeneity of conditions across large geographical areas seems equivocal since local heterogeneity can produce granivory rankings as different as between continents. Despite the important contributions provided by studies carried out in arid regions (e.g. Brown et al. 1979, 1986, Davidson et al. 1984, Mares 1993), further studies including different habitats and regions of distinct continents seem still guaranteed. With more information from diverse arid regions, recent developments of analysis (e.g. Armqvist and Wooster 1995) could be used in order to produce a more realistic global picture of granivory in different regions of the world.

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