



## **Seed reserves in the central Monte Desert, Argentina: implications for granivory**

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It has been suggested that lower rates of granivory in South American warm deserts compared to their North American counterparts arose from a reduction of seed reserves in the former owing to the extinction of argyrolagid marsupials. We measured seed reserves in two habitats of the central Monte Desert in an attempt to detect such seed decline, but to no avail. After moderate rainfall, maximum seed standing crops reached 16,000 and 23,000 seeds  $m^{-2}$  in shrublands and open forests, respectively. Under the canopy of trees and shrubs there were 19,000 and 37,000 seeds  $m^{-2}$ ; whereas in exposed areas there were *c.* 10,000 seeds  $m^{-2}$  in both habitats. Seed banks in other South American semi-arid areas showed similar values. Total grass seeds as well as those presumably preferred by ants also seem to be similar in both continents. Hence, granivory in South America, as has been already reported for Australia, is lower than in North America in spite of the great similarity of seed bank sizes. Moreover, argyrolagids were unlikely seed-hoarding granivores, therefore some other reason than argyrolagid extinction should be sought to explain the lack of specialized seed-eating mammals, and the smaller overall seed consumption rates in South American deserts.

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### **Introduction**

Studies of seed removal show highest intensity of granivory in North American deserts and Israel, intermediate in Australia and the South African Karoo, and lowest in the South American Monte (Mares & Rosenzweig, 1978; Abramsky, 1983; Morton, 1985; Kerley, 1991). Such comparisons have been taken to indicate that granivorous assemblages are 'very poor' (Abramsky, 1983) or 'insignificant' (Morton, 1985) in the Monte Desert. In their pioneering paper, Mares & Rosenzweig (1978) stated that current granivory is 'much depressed' in the Monte as a result of the abrupt seed decline that followed the Pliocene extinction of argyrolagid marsupials, some of which were assumed to be ecological equivalents of the North American heteromyid rodents (Simpson, 1970).

Mares & Rosenzweig (1978) suggested two evolutionary scenarios where marsupial

extinction might have decreased Monte's seed availability. The first explanation considered the argyrolagids involved in indirect mutualism with ants, and assumed that desert plants may need to specialize in defending their seeds against different taxa of granivores (Pulliam & Brand, 1975). Prior to argyrolagid extinction, some of Monte's plants may have evolutionarily 'opted' for avoidance of mammalian predators, and in so doing rendered their seeds more harvestable by ants. When these marsupials become extinct, ant-avoiding plants would have been producing seeds which faced few predators. These plants would be expected to outcompete mammal-avoiding plants because of the sudden preponderance of successful seeds. Consequently, seeds consumed by ants, i.e. small seeds (Davidson, 1977; Medel & Vásquez, 1994), would have declined thus leading to a reduction in the richness and diversity of granivorous ants in the Monte.

The second explanation of Mares & Rosenzweig (1978) considered the argyrolagids as mutualistic with the plants whose seeds they were consuming, and assumed that extinct marsupial granivores, like extant heteromyid rodents, stored some of the seeds in surface caches, thus affording many seeds an ideal site for germination. After marsupial extinction, seeds should have suffered a high failure rate that would have led to an overall decreased production of the seeds aided by the marsupials.

Although originally proposed as a historical explanation (Peters, 1991; Morton, 1993) for the lower rate of seed consumption and the paucity of granivorous ant assemblages in the Monte, argyrolagid extinction should have consequences on current seed reserves. For example, seeds nowadays consumed by ants as well as those aided by marsupials in the past should be lower in the Monte than in North American deserts. Though the debate on desert granivory has moved beyond such an hypothesis (Mares, 1993; Kerley & Whitford, 1994), its predictions have not been explicitly tested in spite of their key importance for comparative research on desert granivory. In this paper we test whether seed reserves for current granivores are lower in South American than in North American arid zones. In so doing, we report our own data on seed reserves in the central Monte Desert, and compare them with published seed bank data of several South and North American warm deserts. Finally we briefly discuss South American granivory in a worldwide perspective.

## Methods

### *Study site*

We surveyed seed standing crops in an open forest and a shrubland of the Biosphere Reserve of Ñacuñán (34°02' S, 67°58' W), central Monte Desert, Argentina during 1993 and 1994. The floristic composition of both habitats is very similar, but the relative cover of plant layers varies widely between them (Table 1). *Prosopis flexuosa* and *Geoffroea decorticans* trees, together with tall shrubs (> 1 m) of the genera *Larrea*, *Capparis* and *Condalia* are major woody plants. The main low shrubs (< 1 m) are *Lycium*, *Verbena*, *Accantolippia*, and *Larrea* sprouts. The grass layer is composed of perennial grasses like *Pappophorum*, *Trichloris*, *Setaria*, *Sporobolus*, *Digitaria*, *Aristida* and *Diplachne*. Grass cover is high under the canopy of trees and shrubs as well as in the open among them. In contrast, forb cover is usually low, though highly variable from year to year (Marone, 1991).

Climate in the central Monte is dry and temperate, with cold winters. On average 84% (271 mm,  $N = 23$  years) of the annual rainfall occurs in spring and summer (September–March), and nearly all plants produce seeds in summer. Consequently, seed standing crops are maximum in winter (L. Marone, unpublished data). Rainfall in the previous growing season is the key factor limiting the replenishment of seed reserves in deserts (Brown *et al.*, 1979). Since 299 mm fell from September 1992 to

**Table 1.** Relative cover (%) of the six environmental strata defined for soil seed bank samplings over two habitats of the central Monte Desert. The number of replications allocated to each stratum is indicated in parentheses. Natural depressions had too low coverage to be considered as a true stratum at the habitat and mesohabitat scales (see text)

Strata	Open forest	Shrubland
Trees	15.3 (11)	3.6 (4)
Tall shrubs	34.4 (25)	53.2 (37)
Low shrubs	13.4 (9)	6.8 (5)
Grasses	15.5 (12)	24.4 (17)
Bare soil	20.2 (16)	11.7 (10)
Natural depressions	1.2	0.3
Total	100.0 (73)	100.0 (73)

March 1993, we assume that our data on seed banks correspond to an average year in the central Monte Desert.

#### *Estimating seed abundance*

We sampled seed standing crops on three 2 ha plots (200 × 100 m) in both the open forest and the shrubland. In each habitat, we took soil samples ( $N = 73$ ) in the winter of 1993 (2 August), and the summer of 1994 (12 February), which corresponded to the annual maximum and minimum soil seed accumulation, respectively. Roughly one-third of the sampling effort was allocated to each plot. We were careful not to resample previously cored points. A stratified random design was used, with five microhabitats and two mesohabitats. The first two microhabitats were located beneath trees and tall shrubs, and jointly formed the 'under canopy mesohabitat' (see Table 1). Samples were taken from a randomly chosen quadrant generated by the projection of the canopy. The sampler (see below) was placed midway between the trunk and the perimeter of the plant canopy. Three other microhabitats were located in the open area between trees and tall shrubs. They included low shrubs, grassy areas, and bare soil which jointly formed the 'exposed mesohabitat'. We proportionally allocated the number of replications according to the cover of each microhabitat in the open forest and the shrubland (Table 1).

Owing to their likely importance for granivore foraging, we counted seeds in small-soil depressions located in the exposed mesohabitat. The cover of these depressions was very low over the general habitat (Table 1), therefore we did not include them in analyses at the habitat and mesohabitat scales. Samples were taken in winter ( $N = 16$ ), and summer ( $N = 18$ ).

We used a cylindrical sampler, 3.2 cm diameter and 2 cm deep (80% of soil seed reserves are found in the upper 2 cm; L. Marone *et al.*, unpublished data). The cylinder was pushed into the soil, and then a metal scoop was pushed carefully just under the bottom edge of the cylinder to isolate the soil within. Sampler contents were placed in 250 ml plastic vials, air-dried for at least 7 days in the laboratory, and then sifted through a sieve (0.27 mm mesh). The finer fraction was discarded (trial inspections showed that none of the discards contained seeds), and the coarser fraction was washed on the same sieve under water pressure for 8–12 min. The residue on the mesh was dried, and then searched for seeds under a stereoscopic microscope. Seed scans under the microscope were repeated twice by different observers. Numbers of apparently viable seeds (those that did not crumble when probed with forceps) were

recorded and identified using a reference collection. The residue was treated with gibberelic acid ( $20 \text{ mg l}^{-1}$ ), then placed in a growth chamber (14 h light at  $30^\circ\text{C}$ ; 10 h darkness at  $15^\circ\text{C}$ ), and seedlings were recorded during the next 15 days.

Both the number and mass of seeds were used to compare seed reserves in South and North American deserts. We estimated seed masses by multiplying each species' abundance by its mean per-seed mass, obtained from husked seeds (i.e. without any investing structures). We do not know whether seed masses in North American studies (e.g. Pulliam & Parker, 1979; Price & Reichman, 1987; Pulliam & Dunning, 1987) were calculated on husked or whole seeds, therefore intercontinental mass comparisons should be made cautiously. As we lack raw data on seed reserves in North America, we were unable to use statistics. Instead, we compared ranges of seed abundance from several South and North American arid zones with ours in the Monte. The lower limit of Monte's range corresponds to summer samplings and the upper one to winter samplings.

## Results and discussion

### *Seed reserves in South and North American warm deserts*

Seed reserves in the central Monte Desert do not appear to be smaller than those in several North American deserts. Kemp (1989) has suggested that all North American warm deserts can achieve similar maximum seed bank sizes of  $8000\text{--}30,000 \text{ seeds m}^{-2}$  at the habitat scale, a range that may also be appropriate for the central Monte and other South American deserts (Table 2). The great similarity or the even larger seed reserves in some South American deserts also become apparent at both the microhabitat and mesohabitat scales (Table 2).

Some authors have inferred seed reserves at the habitat scale by measuring seed production instead of standing crops. Under moderate rainfall conditions, Pulliam & Dunning (1987) found an average grass + forb seed production of  $21.6 \text{ kg ha}^{-1}$  in the Chihuahuan Desert. Data on seed production in South American warm deserts are lacking. Nevertheless, during the moderately rainy 1994–95 growing season we measured a total grass + forb seed production of roughly  $18 \text{ kg ha}^{-1}$  in the open forest (L. Marone *et al.*, unpublished data). Further, the maximum grass + forb seed standing crop in 1993 was *c.*  $51.8$  and  $32.0 \text{ kg ha}^{-1}$  in the open forest and the shrubland, respectively (see Appendix).

The major granivorous animals in the Monte Desert are ants and birds, while seed consumption by rodents seems to be much depressed (Mares & Rosenzweig, 1978; Marone, 1992; J. Lopez de Casenave *et al.*, unpublished data). Grass seeds predominate in the diets of granivorous birds everywhere (Schluter & Repasky, 1991; Diaz, 1996), and are also avidly consumed by ants in the central Monte (J. Lopez de Casenave *et al.*, pers. obs.). Therefore intercontinental comparisons of grass seed reserves may be a suitable way to assess the likely impact of argyrolagid extinction on seed availability for current South American granivores. In Arizona, Pulliam & Parker (1979) measured an average grass seed production of *c.*  $13.0 \text{ kg ha}^{-1}$  (this value was recalculated from their Table 1 considering only the moderately rainy seasons of 1972–73, 1973–74 and 1975–76, over 3–4 sites). Several years later Pulliam & Dunning (1987) found an average of  $15.8 \text{ kg ha}^{-1}$  ( $N = 2$  years, six sites) in similar locations. In the Monte, grass seed production approached  $12.5 \text{ kg ha}^{-1}$  in the 1994–95 growing season (L. Marone *et al.*, unpublished data), and the maximum grass seed standing crops in 1993 were  $13.8$  and  $16.4 \text{ kg ha}^{-1}$  in the open forest and shrubland, respectively (see Appendix).

Likewise, the proportion of small seeds (i.e. those presumably preferred by ants; Davidson, 1977; Medel & Vásquez, 1994) would not be lower in the central Monte

**Table 2.** Mean total seed number and mean total seed mass per m in soil banks of several American warm deserts. Only one value usually reflects an average calculated over several seasons, years or sites, during moderately rainy periods. Two values, on the other hand, indicate a range. The habitat type and nature of the range (seasonal, year-to-year) are indicated when such information was available. (UC: beneath the canopies of trees and shrubs; EX: interspaces among the canopies of trees and shrubs.) In the Monte Desert, ranges correspond to the annual minimum (summer) and maximum (winter) seed accumulation during 1993–1994 (see text)

Reference	Desert	General description	Seeds m <sup>-2</sup>	Seed mass (g m <sup>-2</sup> )
<b>Microhabitat scale</b>				
Reichman, 1984	Sonora	UC, Larrea shrubs	13,400	
		UC, Ambrosia shrubs	12,400	
Price & Reichman, 1987	Sonora	EX, open area	5600	1.2
		EX, dry washes	4000	2.1
		EX, soil depression & accumulations	50,000	0.5
		UC, trees	6800	0.8
		UC, large shrubs	8300	10.6–14.6
This study*	Monte	EX, large opens	5600	4.0–6.3
		EX, small opens	7800	1.0–2.2
		UC, trees	40,300–57,300	1.1–1.9
		UC, tall shrubs	17,000–23,200	0.3–1.7
		EX, among low shrubs	4600–9100	3.5–8.8
		EX, among grasses	5700–9500	
		EX, bare soil	2200–10,000	
EX, soil depressions	5700–35,000			
<b>Mesohabitat scale</b>				
Reichman, 1984	Sonora	UC, shrubland	12,500	
		EX, shrubland	4500	
Nelson & Chew, 1977	Mojave	UC, dry-rainy year	3600–37,000	
		EX, dry-rainy year	300–6200	
This study	Monte	UC, open forest	27,400–37,100	6.8–10.5
		EX, open forest	2700–9000	0.4–1.7
		UC, shrubland	12,300–19,400	2.9–4.5
		EX, shrubland	5600–10,600	1.0–2.1

Table 2. (Continued)

Reference	Desert	General description	Seeds m <sup>-2</sup>	Seed mass (g m <sup>-2</sup> )
<b>Habitat scale</b>				
Kemp, 1989	Sonora	dry-rainy year	400-7700	
Childs & Goodall, 1973	Mojave	shrublands, dry year	430	0.5
Nelson & Chew, 1977	Mojave	shrublands, dry-rainy year	800-12,100	0.5-5.2
Dye, 1969	Chihuahua	shrublands	13,000-22,000	
Kemp, 1989	Chihuahua	shrubland, fine soils	8800-24,500	
		shrubland, coarse soils	1300-6000	
Capurro & Bucher, 1982	Arid Chaco	open forest	>20,000	
Meserve, 1982	Central Chile	thorn scrub site, seasonal	10,700-23,900	8.3-24.9
Lopez-Calleja, 1995	Central Chile	matorral, seasonal	13,100-20,500	
This study	Monte	open forest	14,900-22,900	3.6-6.0
		shrubland	9300-15,600	2.1-3.5

\*Values for each microhabitat are averages between shrubland and open forest samples.

Desert than in those North American deserts where data are available. For example, seeds weighing  $< 0.25$  mg constituted *c.* 80% of total seed number in both the Sonoran (Price & Reichman, 1987) and Monte Desert (see Appendix). On the other hand, 30% of grass seed mass produced in 1981–82 in the Chihuahuan Desert weighed  $< 0.25$  mg (Pulliam & Dunning, 1987), whereas in the Monte such seeds comprised *c.* 70% of total grass seed mass in winter. Further, in either case the absolute abundance of small seeds was higher in the Monte than in its North American counterparts.

In sum, seed reserves in the central Monte Desert, measured as total seed numbers or seed masses, do not appear to be lower than those in several North American warm deserts at several spatial scales. Seed reserves in the semi-arid Chaco (Capurro & Bucher, 1982) and central Chile (Meserve, 1981; López-Calleja, 1995) would not be lower either (Table 2). These results do not support the suggested seed decline that would have occurred in some South American deserts after argyrolagid extinction (Mares & Rosenzweig, 1978), and therefore some other reasons should be sought to explain the paucity of granivorous rodents, and the relatively lower seed consumption rates in South America (Vásquez *et al.*, 1995).

#### *Granivory in the Monte Desert revisited*

The background assumption in the historical explanations of Mares & Rosenzweig (1978), i.e. granivory by argyrolagids, meets with criticism. Based on Simpson's conclusions (1970) about argyrolagid diet, Morton (1993) asserted that 'it takes a leap of faith to conclude that they were specialized seed-eaters'. Mares (1993) recently pointed out that such marsupials seemed to fill an herbivorous niche, possibly similar to the niche of the Old World rodent genera of jerboas, which widely forage on roots and tubers. Therefore, if argyrolagids cannot be proven as major seed eaters, coevolutionary explanations about the paucity of granivory in the Monte (e.g. Mares & Rosenzweig, 1978; Brown & Ojeda, 1987) would be unsuitable. Mares (1993) also stated that some previous generalizations about how mammalian species adapt to desert conditions worldwide (i.e. bipedality and seed-hoarding) may be too simplistic because such features are idiosyncratic of North American heteromyids. Thus, seed hoarding by argyrolagids arises as a non-parsimonious assumption, and the hypothesized mutualism between plants and marsupials seems unfit.

As previously said, Mares & Rosenzweig (1978) stated that argyrolagid extinction led to a decline of granivorous ants, via a reduction in the availability of ant-preferred seeds. Data discussed above do not support any reduction in seed reserves in South America compared to North America. In addition, the similar composition of the seed-eating ant fauna of deserts in both continents have recently been emphasized (Medel & Vásquez, 1994; Medel, 1995).

The lower seed consumption rates as well as the impoverished granivorous assemblages (e.g. the lack of specialized seed-eating rodents) of South American deserts have been broadly debated (Mares, 1993; Morton, 1993; Kerley & Whitford, 1994; Medel & Vásquez, 1994; Medel, 1995). Our suggestion that both lower seed removal and poorer seed-eating assemblages are independent from the abundance and composition of seed reserves in the Monte Desert appears to be true for Australian deserts also (*cf.* Wiens, 1991, p. 296), as well as for the South African Karoo (Kerley, 1992). All three southern hemisphere deserts support less diverse mammal granivorous assemblages than North American deserts, but have very similar seed reserves.

The question of why deserts with similar seed availability support different granivorous assemblages is an important issue in desert ecology. Careful assessment of the unique historical circumstances (e.g. paleoclimate), and of the current differences in the physical environments of every continent (Kerley, 1991; Kerley & Whitford,

1994) should provide insights for comparative research on desert granivory. Such effort, however, will not be entirely successful unless studies of the impact on seed reserves of some underrated granivores like birds, bacteria and fungi, and of germination losses are increased, involving deserts throughout the world.

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**Appendix**

*Number of species-specific seeds m<sup>-2</sup> in the summer (minimum total seed accumulation) and the winter (maximum total seed accumulation) over shrublands and open forests of the central Monte Desert. Individual per seed masses are also indicated*

Species	Mass (mg)	Open forest		Shrubland	
		Summer	Winter	Summer	Winter
number/m <sup>2</sup>					
<b>Trees &amp; shrubs</b>					
<i>Condalia microphylla</i>	33.00	0	17	0	0
<i>Larrea spp.</i>	2.30	0	34	34	68
<i>Atriplex lampa</i>	0.62	0	0	0	102
<i>Lycium spp.</i>	0.42	119	290	102	153
<i>Verbena aspera</i>	0.60	34	188	0	0
<i>Acantholippia seriphioides</i>	0.25	34	0	0	0
<b>Grasses</b>					
<i>Sporobolus cryptandrus</i>	0.06	1755	2521	3441	4942
<i>Pappophorum spp.</i>	0.24	358	2419	715	2351
<i>Trichloris crinita</i>	0.18	137	699	221	664
<i>Aristida spp.</i>	0.46	51	34	17	0
<i>Digitaria californica</i>	0.38	221	733	51	137
<i>Setaria leucopila</i>	0.60	511	239	374	647
<i>Diplachne dubia</i>	0.24	51	324	239	613
<i>Neobouteloua lophostachya</i>	0.08	0	17	51	17
<i>Stipa spp.</i>	0.10	0	102	17	0
<i>Bouteloua spp.</i>	0.14	0	0	0	494
<b>Forbs</b>					
<i>Chenopodium papulosum</i>	0.24	9218	13,341	699	2096
<i>Heliotropium mendocinum</i>	0.63	51	17	0	51
<i>Parthenium hysterophorus</i>	0.45	0	17	0	0
<i>Conyza spp.</i>	0.04	85	272	0	34
<i>Phacelia artemisioides</i>	0.36	1414	1244	1516	1585
<i>Glandularia mendocina</i>	0.40	119	34	341	392
<i>Sphaeralcea miniata</i>	0.20	68	153	443	290
<i>Descurainia sp.</i>	0.08	562	68	443	392
<i>Lappula redowskii</i>	0.40	85	102	255	272
<i>Plantago patagonica</i>	0.38	0	0	392	272
Total number/m <sup>2</sup>		14,893	22,865	9351	15,572
Total mass (g m <sup>-2</sup> )		3.618	6.028	2.078	3.487