

Granivory in Southern South American Deserts: Conceptual Issues and Current Evidence

LUIS MARONE, JAVIER LOPEZ DE CASENAVE, AND VÍCTOR R. CUETO

Ecolologists have abandoned attempts to develop a simple, unifying theory to account for community patterns (Lawton 1999). Instead, to explain such patterns, they rely on local ecological processes as well as on more contingent historical processes acting at large temporal and spatial scales (e.g., unique historical events controlling speciation and biogeographic interchanges). This mixed approach should lead to a more realistic idea of the real world, but it deserves careful epistemological consideration. Although historical hypotheses may account for a substantial part of community patterns, they impose limits to theory development because they deal with contingent events that may often be theoretically intractable. An ecological system may be unique, but this does not necessarily imply that it is lawless in the ontological sense. Consequently, the methodological problem remains of distinguishing its general properties from its idiosyncratic properties (Mahner and Bunge 1997). Historical explanations also impose limits to hypothesis testing because they often do not make predictions and can be elucidated solely by historical reconstruction (Schluter and Ricklefs 1993).

Because theory development is a prerequisite for ecological understanding, researchers should continue to develop general theories, even as they recognize the importance of history (Pickett et al. 1994, Mahner and Bunge 1997). Theory development can be fostered by testing the predictions of the "community convergence" hypothesis through comparative studies (Schluter and Ricklefs 1993). This hypothesis specifies that independently assembled communities in similar but geographically distant habitats converge in composition and functioning if they face similar environmental pressures (i.e., if they are molded by the same local ecological processes).

Ecologists have long searched for matching patterns in the biota of arid lands because similar harsh pressures are thought to prevail in deserts (e.g., Orians and Solbrig 1977, Mares 1993a). An example of such an analysis is the set of experimental tests for convergence in seed harvesting by granivorous mammals, ants, and birds in deserts worldwide (Mares and Rosenzweig 1978, Abramsky 1983, Morton 1985, Kerley 1991, Vásquez et al. 1995, Lopez de Casenave et al. 1998). The initial conclusions of such experiments indicated that seed removal by mammals was

GRANIVORY MAY HAVE A SIGNIFICANT COMMUNITY ROLE IN THE MONTE AND OTHER SOUTH AMERICAN DESERTS, DESPITE THE PROBABLE LACK OF HIGHLY SPECIALIZED SEEDEATERS

higher in deserts of the northern continents than of the southern continents, that ants are the main seed harvesters in southern deserts, and that seed removal by birds is low in deserts around the world (Mares and Rosenzweig 1978, Abramsky 1983, Morton 1985, Kerley 1991, Kerley and Whitford 1994).

These studies seem to suggest a lack of convergence in seed harvesting. However, comparative studies depend strongly on the robustness of established patterns, and the above generalization was not tested for robustness but inferred by using one research approach alone (i.e., bait removal experiments). Furthermore, this generalization was supported, in some cases, by only one experiment carried out in one location within a particular desert. Therefore, some of the purported patterns of granivory at the continental scale might be artifacts of the limited basis of

Luis Marone (e-mail: lmarone@anet.com.ar) is a scientist researcher for Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) of Argentina. Javier Lopez de Casenave is a scientist researcher and teaching assistant in the Department of Biology, Universidad de Buenos Aires, 1428 Buenos Aires, Argentina. Víctor R. Cueto is a scientist researcher at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," 1405 Buenos Aires, Argentina. Marone is a desert biologist interested in community ecology and epistemology, and Lopez de Casenave and Cueto are biologists studying the ecology, distribution, and biogeography of Argentine birds. All three authors are members of the Desert Community Ecology Research Team (Ecodes), Argentine Institute for Arid Zones Research (IADIZA), Casilla de Correo 507, 5500 Mendoza, Argentina. © 2000 American Institute of Biological Sciences.

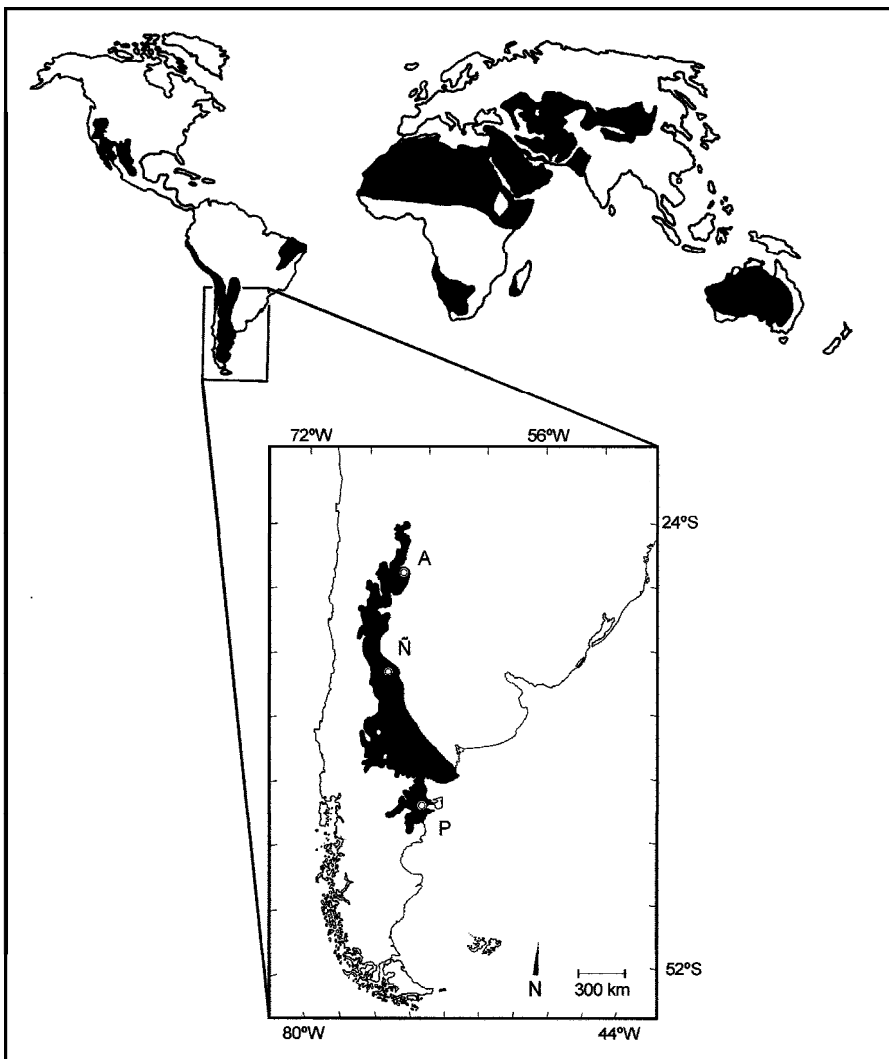


Figure 1. The Monte Desert in perspective. (top) The world's desert regions, including some semi-arid areas that are not generally considered true deserts, are indicated by shading. (inset) The Monte Desert in southern South America is a relatively narrow north-south belt that is oriented along the eastern slopes of the Andes Mountains. It broadens to the south and extends to the Atlantic coast in northern Patagonia. Seed removal rates by granivorous animals have been assessed in three localities, all in Argentina: A, Andalgala, Catamarca Province; N, Nacuñan, Mendoza Province; P, Puerto Madryn, Chubut Province.

empirical information (Mares 1993a). For example, Mares and Rosenzweig (1978), Abramsky (1983), and Morton (1985) all asserted that total granivory in the extensive Monte Desert of Argentina is depressed, and granivorous assemblages depauperate, in comparison with other warm temperate deserts. However, this conclusion was derived from a single experiment carried out near Andalgala, in the far northern reaches of the Monte Desert (Figure 1; Mares and Rosenzweig 1978). Despite the narrow domain of this study, many scientists have tacitly extended its conclusions to arid South America as a whole (Abramsky 1983, Morton 1985, 1993, Brown and Ojeda 1987, Kerley 1991, Wurm 1998; but see Vásquez et al. 1995, Lopez de Casenave et al. 1998).

In this article, we summarize current evidence about the resource base of granivorous animals, the pressures these animals impose on seed reserves, and the main ecological features of the assemblages of seed-eating ants, mammals, and birds in the Monte Desert and other southern South American deserts. We examine the general validity of the commonly accepted patterns of granivory by using multiple research approaches to verify pattern robustness. If the

patterns are robust, they should be the basis for more reliable tests of the community convergence hypothesis of granivorous assemblages in deserts from different continents. Such tests could provide a more informed assessment of the relative roles of local ecological processes and unique historical circumstances in organizing desert communities.

The resource base

Mares and Rosenzweig (1978) observed that "total granivory is much depressed in the Monte Desert, where granivorous mammals are rare and ill-adapted, ants are depauperate and not usually granivorous, and birds are unimportant seed consumers," and they suggested that low granivory would be the consequence of a seed decline in South American deserts caused by the relatively recent extinction of the marsupial family Argyrolagidae in South America. Mares and Rosenzweig (1978) assumed that argyrolagids were ecological equivalents of the rodents of the North American family Heteromyidae (Sánchez-Villagra and Kay 1997), and they outlined two alternative evolutionary scenarios whereby marsupial extinction might have led to a decline in granivorous assemblages (particularly of ants) via a decrease in their resource base (i.e., seeds). In the first alternative, argyrolagids were indirect evolutionary mutualists with ants, consuming seeds not preferred by ants. Thus, when the argyrolagids became extinct, ant-preferred plants, whose seeds were still consumed, would have been outcompeted by predator-free, ant-avoided plants. The decreased availability of seeds from ant-preferred plants would have led, in turn, to a decline in the granivorous ant assemblages themselves. In the second scenario, argyro-

Table 1.^a Average total seed number and seed mass in soil seed banks in different habitats from several South and North American warm deserts.^b

Desert	General description ^c	Seed number (per m ²)	Seed mass (g/m ²)	Reference
North America				
Sonora	Shrubland dry-rainy year	400–7,700		Kemp 1989
Mojave	Shrubland; dry year	430	0.5	Childs and Goodall 1973
Mojave	Shrubland; dry-rainy year	800–12,100	0.5–5.2	Nelson and Chew 1977
Mojave	Shrubland	106,000	38.0	Price and Joyner 1997
Chihuahua	Shrubland	13,000–22,000		Dye 1969
Chihuahua	Shrubland; fine soils	8,800–24,500		Kemp 1989
Chihuahua	Shrubland; coarse soils	1,300–6,000		Kemp 1989
South America				
Arid Chaco	Open forest	>20,000		Capurro and Bucher 1982
Central Chile	Thorn scrub; seasonal	10,700–23,900	8.3–24.9	Meserve 1981b
Central Chile	Matorral; seasonal	13,100–20,500		López-Calleja 1995
Central Monte	Open forest; seasonal	14,900–22,900	3.6–6.0	Marone and Horno 1997
Central Monte	Shrubland; seasonal	9,300–15,600	2.1–3.5	Marone and Horno 1997

^aReprinted, in modified form, from Marone and Horno (1997), with permission of Academic Press.
^bA single value for seed number or mass signifies an average calculated over several seasons or years. Two numbers signify the extreme values of a range.
^cThe habitat type and the contrasting conditions when the measurements were made are indicated where available. These conditions account for the extreme values of each range (e.g., different seasons, years, or soil types).

lagids were mutualists with food plants shared with ants, perhaps storing some of the seeds of these plants in surface caches and thereby enhancing germination, as has been shown among North American heteromyid rodents (Mares and Rosenzweig 1978). After the extinction of argyrolagids, those plants would have suffered a decrease in their populations, and the ant assemblages would also have declined in abundance and richness.

Although these historical explanations about the role of extinct argyrolagids cannot be tested directly, they do lead to testable predictions about the status of present-day seed reserves in the Monte Desert (Mares and Rosenzweig 1978, Brown and Ojeda 1987). For example, the seeds consumed by present-day ants, as well as those presumably involved with marsupials in the past, are predicted to be less abundant in seed banks of South American than North American deserts (Marone and Horno 1997). We tested this assertion by comparing seed reserves in woodland and shrubland of the central Monte Desert with those in several other South and North American deserts (Marone and Horno 1997). Densities of seeds in soil banks were similar in arid North and South America at the habitat scale (Table 1). Regardless of continent, most reports fall within the range of 8,000–30,000 seeds/m² proposed by Kemp (1989), with the exception of one extraordinarily high value in the eastern Mojave Desert of California (Price and Joyner 1997).

Moreover, with respect to production of seeds in South America, the few available data suggest seed production rates similar to those in North America. By using seed traps to catch the seed rain during primary dispersal, we estimated grass seed production in years of moderate rainfall in the central Monte Desert to be 12.5 kg/ha (Marone et al. 1998a). Using similar methods, Pulliam and Parker

(1979) and Pulliam and Dunning (1987) reported average grass seed production of 13.0–15.8 kg/ha in moderately rainy years in grasslands of the North American Chihuahuan Desert of southeastern Arizona. Finally, seed numbers at the microhabitat scale as well as the proportion of small seeds (i.e., those presumably preferred by ants) also appear to be similar in deserts of North and South America (Marone and Horno 1997). Overall, these findings fail to support the hypothesis of a seed decline in the South American sites. Therefore, differences in the resource base should not be invoked to account for differences in granivorous assemblages (Mares and Rosenzweig 1978) or in the foraging behavior of particular species (Medel and Vásquez 1994) between South and North American deserts. Morton (1985, 1993) also ruled out differences in the resource base as an explanation for differences in granivorous assemblages between Australia and North America.

Bait removal experiments

The results of Mares and Rosenzweig (1978) on present-day consumption of seeds in the northern Monte Desert by different granivorous taxa in bait removal experiments are still often extrapolated to the entire Monte Desert (e.g., Wurm 1998). To assess the applicability of those results to the central Monte Desert (Figure 2), we therefore used the same kinds of experiments, in which seed consumption is estimated by comparing the amounts of seeds taken by different taxa from feeding stations (dishes) placed in the desert (Figure 3). There can be problems, however, in comparing results from bait removal experiments because such experiments often lack standardized procedures. For instance, different authors have offered a variable assortment of seeds to granivores and have placed seed dishes



Figure 2. *The open Prosopis flexuosa woodland in the Biosphere Reserve of Ñacuñán, in the central Monte Desert, Argentina. We carried out fieldwork in open woodlands and in Larrea cuneifolia shrublands of the reserve between 1993 and 1998. Ñacuñán's climate is dry and temperate, with cold winters, and most annual rainfall occurs in spring–summer (October–March). Perennial C₄ grasses, mainly of the genera Trichloris, Pappophorum, Setaria, Sporobolus, Digitaria, and Aristida, are abundant in both open woodland and shrubland. Grass seed production and dispersal are mostly restricted to late summer and early autumn (Marone et al. 1998a).*

among microhabitats in unspecified ways, even though the rate of seed consumption by mammals, birds, and ants may differ with the type of seed (Kelrick et al. 1986) or the microhabitat (Lopez de Casenave et al. 1998). Consequently, researchers need to use caution when comparing seed removal rates quantitatively (Parmenter et al. 1984, Kelrick et al. 1986, Vásquez et al. 1995).

Even when we used the most conservative measure of seed consumption (i.e., the average seed removal rate in exposed microhabitats, in which seed consumption by birds and ants in the summer was significantly lower than in microhabitats located under the canopy of shrubs and trees), we found that the total rate of seed consumption in the central Monte (Lopez de Casenave et al. 1998) was more than five times greater than in the northern Monte (Mares and Rosenzweig 1978). Indeed, if data from the central Monte Desert are incorporated into global comparisons of the impact of desert granivores on seed resources, the most logical conclusion appears to be that total granivory in the Monte is not abnormally depressed (Lopez de Casenave et al. 1998); rather, total seed removal as well as seed removal by mammals and ants is exceptionally high in North American deserts (see Morton 1985).

To avoid troublesome quantitative contrasts, Vásquez et al. (1995) compared rankings of the relative importance of mammals, birds, and ants among bait removal experiments worldwide. We summarize their findings in Table 2, adding our own results from the central Monte Desert as

well as an independent data set from the southern Monte Desert near Puerto Madryn, Chubut, Argentina (Figure 1; Sergio L. Saba, Centro Nacional Patagónico, Puerto Madryn, Chubut, Argentina, personal communication). Although these rankings show only the relative impacts of every taxa in every study site (i.e., they tell us nothing about absolute granivory rates), they corroborate previous generalizations that the relative impact of mammals is greater in northern continents and that the relative impact of ants is greater in southern continents. The rankings also reveal a novel finding: granivorous birds are major seed consumers in several South American locations.

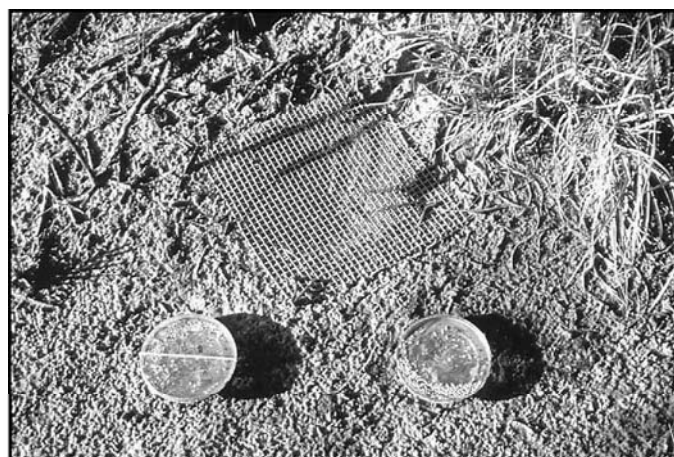
The likely importance of seed-eating birds calls attention to some underappreciated mechanisms of seed loss. To assess the similarities of the impact of granivores on seed resources in deserts around the world, it is necessary to simultaneously evaluate both seed availability and all plausible mechanisms of seed loss (which may vary among deserts, even when total seed loss remains constant). Some mechanisms that have received far less attention than mammal and ant consumption include avian granivory, seed germination and burial, and seed mortality caused by fungi and bacteria. These and other possible sources of seed output should be carefully quantified before conjecturing whether historical or ecological causes are more likely to explain the organization of the seed–granivore system at regional and intercontinental scales (Kerley and Whitford 1994, Marone and Horno 1997).

Granivorous ant assemblages

Researchers have often assumed that assemblages of granivorous ants are substantially less diverse in arid South America than in similar habitats of North America (e.g., Mares et al. 1977, Mares and Rosenzweig 1978, Brown and Ojeda 1987, Holldobler and Wilson 1990). For example, James Hunt (in Mares et al. 1977) compared ant communities of a Sonoran Desert site near Silver Bell, Arizona, and the northern Monte Desert site near Andalgalá. He recorded a higher species richness of ants in total, but fewer granivorous species, at Andalgalá. The granivore status of ants, however, was grounded not on direct foraging observations but on assumptions based on taxonomy.

When the granivore status of ants was defined according to foraging records, however, the conclusions changed. Medel (1995) compared seed-harvester ant assemblages of North America, Australia, and South America by using seed removal experiments, following the methods of Morton and Davidson (1988). He sampled ants in 11 locations in the central and northern Monte Desert, including Andalgalá, and found that these assemblages were, in fact, more diverse and abundant than their North American counterparts (Medel and Vásquez 1994, Medel 1995). Using the same method, we assessed the composition of seed-harvester ant assemblages in the central Monte Desert (Javier Lopez de Casenave, Silvia Claver, Víctor R. Cueto, Luis Marone, unpublished data). In December

Figure 3. A feeding station used in bait removal experiments (Lopez de Casenave et al. 1998). A known amount of seeds is offered in each station at the start of the trial. Every station consists of three plastic Petri dishes (9 cm in diameter): a “mammal” tray, a “bird” tray, and an “ant” tray. Vertebrate trays are glued to the top of long plastic cylinders and set 2–3 cm above the ground to prevent access by ants. Seeds for birds are available only during the day, and seeds for mammals are available only at night. Ant trays are buried with the rim of the Petri dish level with the soil surface and covered with mesh hardware cloth to prevent access by vertebrates (these trays remain active 24 hours a day). The stations are periodically replenished with known amounts of seeds to avoid total depletion (total duration of the experiment is 48 hours).



1995, we recorded 12 and 14 species removing seeds from two nearby sites. This species richness exceeded the mean of 9.8 ($n = 11$ sites) and 2.8 ($n = 5$ sites) reported for the northern Monte Desert and central Chile, respectively (Medel and Vásquez 1994), as well as the mean of 5.2 ($n = 10$ sites) and 8.5 ($n = 16$ sites) reported for North American and Australian deserts, respectively (Morton and Davidson 1988). In summary, direct foraging observation of ants is not in agreement with previous assertions that granivorous ants are depauperate in the Monte Desert.

The bait removal method employed in all these studies is sensitive to the definition of “harvester ant” used. If ant species are considered to be seed harvesters simply because they are seen at seed stations, then the number of harvester ant species may be overestimated. By contrast, we counted only ants that effectively loaded seeds from seed stations. Consequently, we conclude that assemblages of potentially seed-harvesting ants are not depauperate, at least in the central Monte Desert.

The South American ant assemblages, however, include several species with more generalist diets than those of the

obligate seed-harvester ants of the genus *Pogonomyrmex*, which make up the bulk of ant assemblages in North American deserts. Although Mares and Rosenzweig (1978), Medel (1995), and Medel and Vásquez (1994) all hypothesized that omnivory of the ant species in South American deserts results from a lower seed availability in these deserts than in North American deserts, the figures in Table 1 do not support this explanation. Indeed, *Pogonomyrmex* species exist in South America as well. The three *Pogonomyrmex* species (*P. rastratus*, *P. pronotalis*, and *P. inermis*) that occur in the central Monte Desert (Claver and Fowler 1993) appear to be highly specialized granivores (Javier Lopez de Casenave, Silvia Claver, Víctor R. Cueto, Luis Marone, unpublished data). However, given that the South American species of this genus seem to display smaller colonies and lower population densities than those in North America (Holldobler and Wilson 1990), the hypothesis of a lower impact of South American *Pogonomyrmex* species on seeds (naturally available as well as offered in baits) is a plausible although still unexplored hypothesis.

Table 2.^a Rankings of the relative importance of the three main granivore taxa (A, ants; B, birds; M, small mammals) as suggested by bait removal experiments carried out in different arid regions of the world.^b

Region	Granivore ranking	Reference
North America (Sonora Desert)	M > A > B	Mares and Rosenzweig 1978
Israel (Negev Desert)	M > A ^c	Abramsky 1983
South Africa (Karoo Desert)	A > M > B	Kerley 1991
Australia (Simpson Desert)	A > B > M	Morton 1985
Chile (dense matorral)	A > B > M	Vásquez et al. 1995
Chile (sparse matorral)	B = A > M	Vásquez et al. 1995
Argentina (central Monte Desert)		
Under-canopy sites	A > B > M	Lopez de Casenave et al. 1998
Open sites	B = A = M	Lopez de Casenave et al. 1998
Argentina (Southern Monte Desert)	B > M = A	Sergio L. Saba, personal communication
Argentina (Northern Monte Desert)	A > B = M	Mares and Rosenzweig 1978

^aExpanded from Vásquez et al. (1995).

^bAccording to Vásquez et al. (1995), we considered two taxa to have different granivory intensities when the average seed removal rate of one was at least twice that of the other.

^cThis study was carried out only during spring–summer; birds were thought to have a negligible influence and were therefore not studied.

Low population densities of *Pogonomyrmex* ants and generalized food habits among some other ant species might explain why the Monte Desert's granivorous ants appear to remove fewer seeds from experimental baits than do North American ants. But it does not follow that the ants of the Monte Desert "are depauperate and not usually granivorous" (Mares and Rosenzweig 1978). To understand whether differences in seed removal from artificial baits reflect intercontinental differences in ant granivory, it will be necessary to examine more closely the foraging behavior of the Monte Desert's ants. For example, preliminary observations indicate that some *Pogonomyrmex* species of the Monte Desert harvest the majority of their seeds directly from plant stalks. At the same time, the frequency of individuals of these highly specialized seed-eating species was very low at experimental seed stations located on the soil (Javier Lopez de Casenave, Silvia Claver, Víctor R. Cueto, Luis Marone, unpublished data). Subtle differences in ant foraging behavior among continents might reduce the comparability of results from this kind of experiment, thus affecting the conclusions about the importance of granivorous ants as seed harvesters.

Studies of seed removal from bait stations and of food habits of putative granivorous animals are necessary but not sufficient to make inferences about the community role of granivores. One straightforward approach to determine the community role of those animals is to directly assess the extent to which the dynamics of the resource (i.e., seeds) is affected by the activity of the consumer (i.e., birds, ants, or mammals). That is, the importance of granivory can be better addressed through mechanistic studies of the effects of seed consumption on the fate of naturally dispersed seeds (Price and Joyner 1997, Marone et al. 1998b).

Granivorous mammal assemblages

The absence of functional analogues of North America's heteromyid rodents and the low diversity and abundance of other mammalian granivores in South American deserts have been blamed for the "insignificant" mammalian seed consumption recorded in the northern Monte Desert (Mares et al. 1977, Mares and Rosenzweig 1978, Brown and Ojeda 1987). Recent studies, however, suggest that this rate of seed consumption does not apply to the entire Monte Desert: rodents remove almost an order of magnitude more seeds in the central Monte Desert than in the northern Monte Desert (Lopez de Casenave et al. 1998). Mammalian seed removal is also markedly higher in the southern Monte than in Andalgala (Sergio L. Saba, personal communication). Thus, even if South America truly lacks analogues of heteromyids, the premise that rodent granivory is insignificant in the Monte Desert overall deserves scrutiny, for at least two reasons.

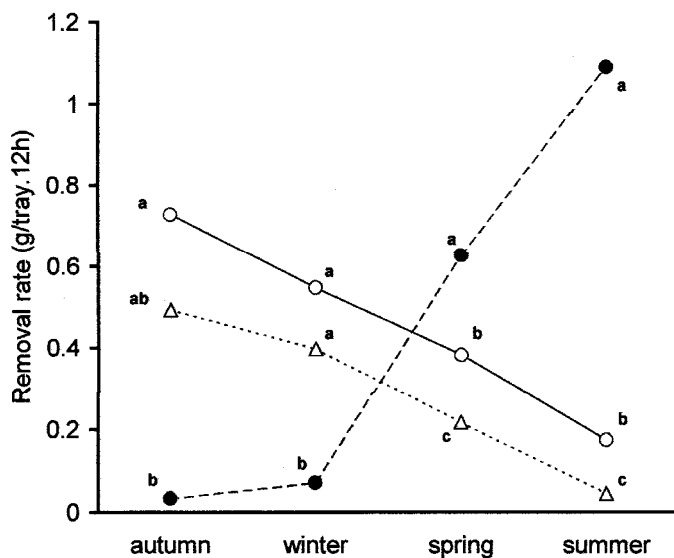
First, the spacious cheek pouches of heteromyids enhance their fabled proficiency at gathering and hoarding seeds. In a study of several heteromyid species, indi-

viduals on average filled their cheek pouches to more than 90% of pouch capacity during a single feeding bout in the field (Vander Wall et al. 1997). On a daily basis, therefore, these rodents may harvest far more seeds than they need to fulfill their immediate energy requirements. Although some South American rodents have been shown to hoard some seeds, at least under laboratory conditions (Vásquez 1996), these species lack cheek pouches (Nowak and Paradiso 1983). It follows that, on average, South American rodents would be expected to harvest fewer seeds from baits than do heteromyids. Some indirect evidence seems to corroborate this assertion: Predavec's (1997) estimates of seed consumption by Australian desert rodents (which, like South American rodents, lack cheek pouches) were dramatically higher when based on calculations of energetics than when based on bait removal experiments.

Another reason for caution with previous generalizations about mammal granivory in South America is that basic dietary information is still lacking for South American desert rodents, and desert ecologists often disagree about their food habits. Although this discrepancy sometimes simply reflects the fact that the proportion of seeds in animals' diets varies widely in time and space, disagreement is also fostered by the lack of dietary information. This lack of information is a major problem because some calculations of seed consumption (e.g., those based on energetics) are sensitive to subtle variations in dietary values (Kerley 1992). Hence, terms such as "granivore" are not always used in a consistent way. Strictly speaking, a selective consumer (e.g., a granivorous mammal) is an animal that takes some or all food items in different proportions than the proportions at which they are present in the patches where the animal feeds, within the size limits imposed by the perceptive, handling, and swallowing capabilities of the consumer (Jaksic 1989).

Because this definition is difficult to apply in nature, other, more rudimentary ones could be used, provided that they are used only as a basis of comparative assessments. For example, Kerley and Whitford (1994) suggested that mammals can be designated as granivores, folivores, or insectivores when their diets are dominated by the respective dietary category (i.e., more than 50% of the diet consists of the category), whereas those of more mixed diets can be termed omnivores. Using this criterion, Meserve (1981a) showed that two rodent species in the southern fringe of the Atacama Desert of Chile, *Oligoryzomys longicaudatus* and *Phyllotis darwini*, were granivorous, especially in the dry season, when 73% and 59%, respectively, of their identified diets consisted of seeds; *Abrothrix (Akodon) olivaceus* almost achieved granivore status, with 45% of its diet consisting of seeds. Similarly, Pizzimenti and De Salle (1980) found that in several localities of the Andes of southern Perú, more than 50% of the diet of some rodent species consisted of seeds (e.g., *Phyllotis darwini*, 53%; *P. pictus*, 60%). Given that some heteromyid rodents that are usually considered specialized seedeaters also consume sig-

Figure 4. Seasonal rates of seed removal by granivores in the central Monte Desert. Birds, open circles; ants, solid circles; mammals, open triangles. Mean rates of removal for the 23–25 trays available only to the respective taxon are shown. Within a season, means with the same letter are not significantly different according to Tukey's test ($P < 0.05$). Figure redrawn from Lopez de Casenave et al. (1998) and used with permission from Blackwell Science.



nificant amounts of insects and green vegetation during some seasons (Mares 1993a), it appears that some of the above-mentioned Atacama and Altiplano rodent species should also be considered granivores.

In the Monte Desert, Mares et al. (1977) and Mares (1993b) reported finding no granivorous small mammals. In some localities of the central Monte Desert, however, *Calomys musculinus* may be the most abundant rodent species (Ojeda 1989), and data from other semi-arid habitats of Argentina show that the dry-season diet of *C. musculinus* consists of approximately 90% seeds (Dellafiore and Polop 1994). In a recent study in the central Monte Desert, Campos (1997) found that during the dry season, *C. musculinus* appeared to consume a relatively high proportion of seeds (50%) and that the diets of other small mammals included few seeds (less than 5% in the diets of *Graomys griseoflavus*, *Eligmodontia typus*, *Thylamys pusillus*, and *Akodon molinae*). However, these low values may severely underestimate the proportion of seeds in the diet of *C. musculinus* and the other small mammals. First, Campos (1997) indicated that the microhistological technique that she had employed underestimates food items other than leaves—in particular, seeds. Second, Campos (1997) tallied seeds in stomach contents by counting only the glume remains of grass diaspores; however, rodents often dehusk grass diaspores and discard the glume before consumption (Martha J. Piantanida, División Mastozoología, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina, personal communication). Finally, rodents consume forb seeds as well as grass seeds. For instance, 43% of the diet of *C. musculinus* in west-central Argentina consists of *Chenopodium* seeds, and 22% of it consists of *Amaranthus* seeds (Dellafiore and Polop 1994).

North American species of the heteromyid genera *Microdipodops* and *Dipodomys* are usually labeled as specialized granivores (e.g., Kelt et al. 1996). Nevertheless, they also consume insects and green vegetation (Mares 1993a, Kerley and Whitford 1994). Moreover, Kerley et al. (1997) have proposed that the keystone status of kangaroo rats in the Chihuahuan Desert might be due to graminivory (i.e., herbivory) rather than to granivory. By contrast, those South American rodents (e.g., several *Oligoryzomys*, *Calomys*, and *Phyllotis* species) that appear to display similar seasonal changes in diet (granivorous at some times, herbivorous/insectivorous at others) are almost never labeled “granivores” in the literature.

This semantic inconsistency, which has implications for the conclusions of comparative studies, may reflect an unfortunate attribute of research practice that deserves the scrutiny of the sociologists of science: when basic empirical information on a particular subject is lacking or fragmentary, unproven assertions may gain credence as facts even though such assertions are only, at best, plausible assumptions. This problem, however, should fade away when these basic assumptions (e.g., that the ability of rodents to harvest clumped seeds is similar in North and South America, or that the incidence of seeds in the diet of South American rodents is negligible) are carefully tested before deciding about the suitability of the specific hypothesis under scrutiny (e.g., that seed-eating mammals in the Monte Desert and other South American deserts have a significant impact on seed reserves). This research strategy is essential to preventing “naive refutationism” (Lakatos 1978), in which a specific hypothesis is considered false simply by the refutation of just one of its predictions (e.g., that South American small mammals remove similar amounts of seeds offered in bait experiments as their North American counterparts).

Granivorous bird assemblages

The low rates of seed removal by birds observed in bait removal experiments seemed to suggest that birds are either unimportant seedeaters in deserts or that they fail to detect the experimentally proffered trays. For example, birds ate few of the test seeds in the South African Karoo (Kerley 1991), the Chihuahuan Desert (Parmenter et al. 1984), and the Australian Desert (Morton 1985). Given the diverse and abundant avian granivores of Australian deserts, Morton (1985, 1993) conjectured that these birds should have a major community role in Australian deserts, even though they did not visit any of his seed stations. Several authors have suggested that the short time span of bait removal experiments (2–3 days) may be inadequate for

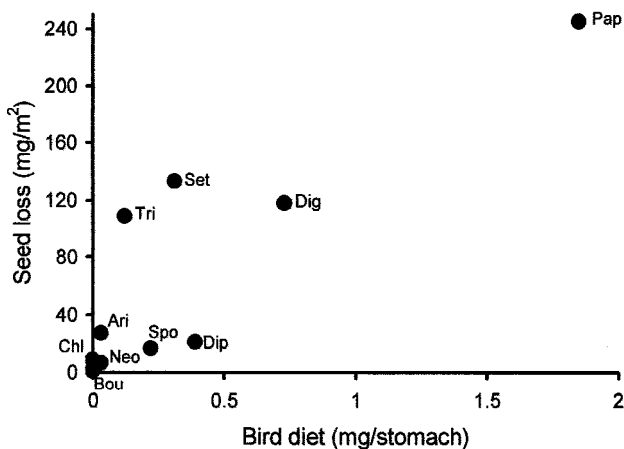


Figure 5. Relationship between the mass of seeds from perennial grasses in the autumn and winter diets (in 1993–1995) of four granivorous bird species in the central Monte Desert and the loss of seeds of each species during the autumn and winter of 1995. The bird species are *Zonotrichia capensis*, *Phrygilus carbonarius*, *Diuca diuca*, and *Saltatricula multicolor*. The overall correlation was significant ($r = 0.87$, $n = 11$, $P < 0.001$). Grass species are as follows: *Pap*, *Pappophorum* spp.; *Set*, *Setaria leucopila*; *Dig*, *Digitaria californica*; *Tri*, *Trichloris crinita*; *Dip*, *Diplachne dubia*; *Spo*, *Sporobolus cryptandrus*; *Ari*, *Aristida* spp.; *Neo*, *Neobouteloua lophostachya*; *Chl*, *Chloris castilloniana*; *Bou*, *Bouteloua* spp. The point for *Stipa* spp. is not shown on the figure but overlaps with that for *Bouteloua* spp.

measuring seed consumption by desert birds (Mares and Rosenzweig 1978, Morton 1985).

In most bait experiments carried out in South American deserts, however, avian granivores quickly discovered baits and consumed seeds. Indeed, birds often consumed more seeds than did the other granivore taxa (Table 2). We know of no idiosyncratic characteristic of South American birds that may explain this pattern. Thus, to control for any propensity of the Monte avifauna to detect seed trays with unusual skills, we used an approach that did not rely on artificial baits to assess whether birds are important seedeaters in the central Monte Desert (Marone et al. 1998b).

Bait experiments have shown that bird granivores are the main autumn–winter seed consumers in the central Monte Desert (Figure 4; see Lopez de Casenave et al. 1998). To assess the impact of seed-eating birds on the autumn–winter soil seed reserves, we compared the soil seed bank in the late summer of 1995 (12 February) with that present the following early spring (25 October), also taking into account the total number of seeds that entered the soil from late summer to early spring (i.e., we measured seed rain; Marone et al. 1998b). In late summer, before consumption by birds, the mean seed density of grass seed banks was 2400 seeds/m², or 0.36 g/m². The next spring—following the input of approximately 3000 grass seeds/m², or 0.71 g/m², as well as the period of bird consumption in autumn and winter—the density of grass seeds was 2700 seeds/m², or 0.39 g/m². Medium and large grass seeds suffered higher postdispersal losses than did small seeds. Likewise, densities of forb seeds in the seed bank were statistically indistinguishable between late summer (5500 seeds/m², or 1.34 g/m²) and spring (6500 seeds/m², or 1.53 g/m²), although forb seed production during the study period had been relatively low (400 seeds/m², or 0.12 g/m²). These results suggest that autumn–winter seed predators in the central Monte Desert favor grass seeds over forb seeds.

Several lines of evidence confirm that postdispersal grass seed loss during autumn–winter in the central Monte Desert is due mainly to vertebrate consumption. First, granivorous ants are active almost exclusively during

the spring and summer (Figure 4; Lopez de Casenave et al. 1998). Furthermore, C₄ grasses germinate mostly in late spring and summer, and total grass seed germination, which usually does not surpass 0.5% of previous soil seed reserves (Marone et al. 1998b), reached only 5% of previous reserves during the exceptionally wet summer of 1998, which was associated with a strong El Niño/Southern Oscillation event (Luis Marone, Manuel E. Horno, Rafael González del Solar, unpublished data). Finally, given the composition of the seed bank at different depths (0–2 cm, 2–4 cm, and 4–6 cm), Marone et al. (1998a) concluded that grass seeds, especially the medium and large seeds, would suffer negligible loss by deep burial.

Therefore, it was not surprising that the pattern of seed losses coincided with the pattern of seed consumption by granivorous birds in the autumns and winters of 1993 through 1995. Nearly 93% of the seed mass in bird stomachs came from grass seeds, and only 7% came from forb seeds. Furthermore, medium and large grass seeds suffered the highest losses from the soil seed bank and were also the main target of foraging by granivores. Moreover, a significant positive correlation existed across grass species between the mass decrease of seed species from the soil toward spring and the mass of those seed species in bird diets in autumn–winter (Figure 5; Marone et al. 1998b). This positive correlation suggests that bird consumption could explain a great deal of the autumn–winter grass seed loss observed in soils of the central Monte Desert.

These lines of evidence indicate that vertebrate granivores (particularly birds) have a major impact on the abundance, floristic composition, and size distribution of seed reserves in the Monte Desert, where vertebrate granivory in general, and avian granivory in particular, had previously been considered unimportant. Moreover, newly produced seeds from perennial grasses constitute a major fraction of autumn–winter bird diet. This finding supports the proposal (Marone 1992) that the timing and amount of rainfall in the central Monte Desert may greatly influence the abundance and migrations of granivorous birds via the opportunistic response of seed production by grasses to variations in rainfall. Population interactions

between seeds and avian granivores in this South American desert may therefore be more important than hitherto appreciated.

Concluding remarks

The relative importance of seed consumption or granivorous assemblages in deserts around the world cannot be assessed through one research approach alone (e.g., bait removal experiments, energetics approaches, descriptions of the species composition of granivorous assemblages, or quantification of individuals' diets). Instead, research programs that include multiple approaches involving redundancy and cross-checks of hypotheses and methods may lead to the most robust conclusions and, therefore, to synthesis and integration (Pickett et al. 1994). Furthermore, any such program should involve long-term studies that take into account the spatial and temporal variability of natural communities.

Partly as a consequence of such a lack of integration, natural rates of seed consumption and the abundance and diversity of granivorous assemblages in some South American deserts may have been underestimated in the past. The evidence we have discussed in this article comes from various desert locations of southern South America and was obtained by using different research approaches. This evidence suggests that birds and ants are important seedeaters during the colder and warmer months, respectively, and that the role of small mammals as granivores in the central Monte Desert of Argentina deserves more detailed assessment. These results should be readily incorporated into comparative studies to distinguish between idiosyncratic and general processes molding desert communities worldwide. Although ecological "laws" are by no means universal, ecological understanding will continue to depend on theory development (Pickett et al. 1994, Mahner and Bunge 1997). To develop ecological theory, researchers need good observations combined with rigorous and realistic experiments carried out in the context of research programs that are focused, whenever possible, on testing mechanisms to account for ecological phenomena (Werner 1998).

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