

## **Desert-dwelling Small Mammals as Granivores: Intercontinental Variations**

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### *Abstract*

Deserts are, by definition, environmentally similar, and this has led to hypotheses of convergence in the properties of desert biotic communities as well as the components of these communities. There is considerable evidence for convergence in some characteristics of desert biota, ranging from plant growth forms to the well-known bipedal, nocturnal rodents. One area that has received considerable attention has been granivory by desert rodents, largely because of the effort focused on the North American desert heteromyids, and also because the process of granivory has far-reaching ramifications for desert plant communities. Specific tests for convergence in the impact of rodents as granivores, by means of bait-removal experiments, however, have shown that the high levels of seed removal by rodents in the North American deserts differs from that of rodents in the South American, Australian and South African deserts, where ants are the most important seed harvesters. The only studies to measure the impact of rodents on desert seed fluxes confirm these patterns, with rodents consuming up to 86% of seed production in North American deserts, but less than 1% of seed production in South African deserts. A review of dietary data for desert rodents confirms these trends, with little evidence for the presence of granivores in deserts besides those of North America. A variety of hypotheses have attempted to explain these variations in desert rodent granivory. These include recent extinctions of granivores, that seed burial, low soil nutrients and/or limiting seed production prevented the radiation of granivorous small mammals, and that particular deserts are too young or too recently colonised by rodents for granivorous rodents to have evolved. However, none of these hypotheses are supported by available evidence. Alternative hypotheses suggesting that climate variability may have precluded the development of specialised granivores need to be tested. In particular, more data are needed to confirm these patterns of granivory, and gain an understanding of the effects of Pleistocene and recent desert climate variability on seed production. An alternative perspective suggests that the presence of the heteromyid rodents may explain the high levels of granivory by small mammals in North American deserts. The variability in granivory by small mammals between deserts suggests that deserts will also differ in terms of anti-granivore adaptations of plants, seed fluxes and the mechanisms whereby small mammals coexist.

### **Introduction**

Deserts are extreme environments where the shortage of moisture is the major limiting factor. This scarcity of water is further compounded by extremes of temperature, which may increase water requirements of animals and plants, or further reduce its availability. Considering the physical environment as the driving force of adaptations by organisms, it may be expected that, given sufficient time, desert biota should show convergence in their adaptations to their habitat (Orlans and Solbrig 1977). This convergence would, however,

be mediated by constraints inherent in the organisms, as well as the nature and extent of biological interactions. The degree of convergence may therefore differ between the individual species level (mainly affected by the environment and species characteristics) and the community level (with the additional variable of biotic interactions). However, Noy-Meir's (1979) Autecological Hypothesis that, as a result of the harsh environments of deserts, community processes will be largely mediated by abiotic processes, suggests that convergence in deserts should occur at the community level.

There are numerous examples of convergence in some characteristics of desert biota, particularly of plant growth form and leaf shape (Orians and Solbrig 1977). Well-known examples include the morphologically similar North American *Agave* (Agavaceae), South American *Dyckia* (Bromeliaceae) and African *Aloe* (Liliaceae). The bipedal, large-eyed, nocturnal rodents of North American (e.g. *Dipodomys*), North African (e.g. *Jerboa*) and South African deserts (e.g. *Tatera*) are text-book examples of convergence.

Prominent among the properties of desert communities that are assumed to have been shaped by the peculiar features of deserts is the presence of a guild of mammalian granivores (Mares and Rosenzweig 1978). Interest in these mammals has largely been stimulated by the extensive research on the North American heteromyids, the best-studied desert rodents, whose diversity and abundance has led them to be considered the epitome of desert small mammals (Reichman and Brown 1983). The heteromyids are largely granivorous, and seeds are thought to represent an abundant and predictable resource (Mares and Rosenzweig 1978). This has led to granivory being considered one of the key adaptations of small mammals to desert environments (e.g. Smith 1980). A further stimulus for research on granivory by desert small mammals has been the demonstration that the process of granivory has major impacts on desert plant communities. Seeds, besides being important for reproduction and dispersal, are one of the major strategies by which desert plants survive periods of drought. Thus, the consumption of seeds, which represents mortality of individual plants, can influence the composition and distribution of plant communities. This has been elegantly demonstrated by Brown and his coworkers (e.g. Brown and Munger 1985; Brown and Heske 1990), who through the manipulation of granivore assemblages have induced major changes in desert plant communities.

This paper reviews evidence for convergence in patterns and levels of granivory by desert small mammals, evaluates hypotheses that attempt to explain these patterns, and discusses some of their implications.

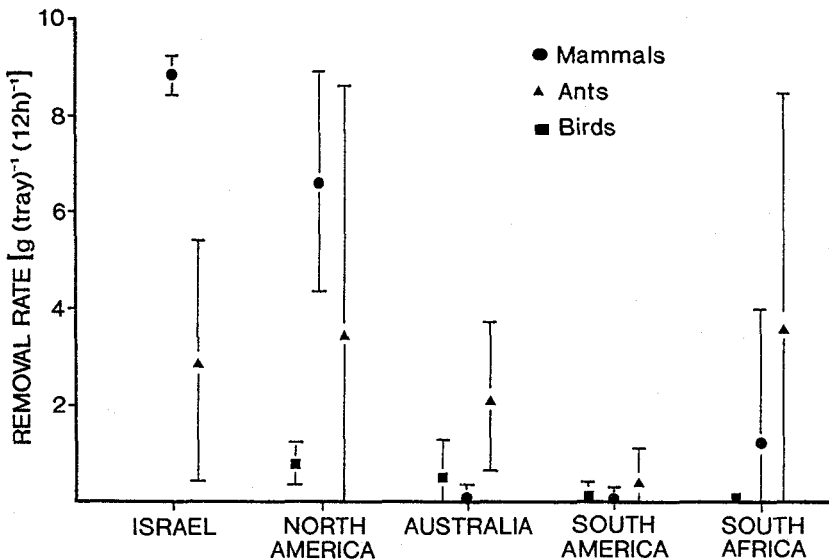
### Seed-harvesting Experiments

A common approach to measuring granivory by desert small mammals (primarily rodents) has been the use of experimental seed baits that are offered to the animals and the removal of seeds then recorded. Such experiments are normally run with baits selectively available to the major granivorous taxa found in deserts (small mammals, birds and ants), which also allows an evaluation of the relative importance of the different classes of granivores in seed removal (Brown *et al.* 1975; Mares and Rosenzweig 1978).

Interpretation of the results of these experiments should, however, be undertaken with caution, because the technique has some limitations. The removal of seeds by small mammals and ants does not reflect the time-specific seed requirements of these taxa, as both taxa cache seeds for later consumption, and caching is a common response to an abundance of seed (Parmenter *et al.* 1984). Furthermore, birds can take a long time to start using the experimental baits, apparently because birds rely on predictable, high-quality food patches, and spend little time locating new resources (Mares and Rosenzweig 1978). Thus, when interpreting seed-removal experiments, it should be borne in mind that this technique does not measure granivory *per se*, but rather measures a component of granivory: the ability to locate and harvest seeds. Within these constraints, studies of this type permit comparisons of seed-harvesting rates of the different taxa at differing localities and times.

Furthermore, the fact that these experiments are easily repeatable has resulted in a number of comparable experiments being conducted in different deserts.

The first such comparison of seed harvesting between deserts was Mares and Rosenzweig's (1978) comparison of the North American Sonoran Desert with the South American Monte Desert, with the specific aim of testing for convergence in the patterns of granivory. The results, however, failed to support the original hypothesis, with high levels of granivory by small mammals in the Sonoran Desert not being duplicated by those in the Monte Desert (Fig. 1). Subsequently, these experiments have been repeated in Israeli (Abramsky 1983), Australian (Morton 1985) and South African deserts (Kerley 1991). The results, summarised in Fig. 1, indicate that seed harvesting operates at two levels, with high (absolute and relative to ants) seed harvesting by small mammals in North American and Israeli deserts. This contrasts with the low seed harvesting by small mammals (absolute and relative to ants) in the South American, Australian and South African deserts (Morton 1985; Kerley 1991). Unfortunately, the Israeli data set is incomplete, comprising only a single season (Abramsky 1983), and significant seasonal variations in these patterns of granivory have been observed (Morton 1985). Furthermore, there are no comparable data for the Asian, North African or South American Atacama deserts.



**Fig. 1.** Mean seed removal (vertical bars are standard deviations) of experimental seed baits in Israeli (Abramsky 1983), North and South American (Mares and Rosenzweig 1978), Australian (Morton 1985) and the South African Karoo deserts (Kerley 1991). Data for the first four localities redrawn from Morton (1985).

It may be concluded that levels of seed harvesting by small mammals do differ between deserts, refuting the hypothesis of convergence in this supposedly fundamental trait of desert communities. The present evidence actually suggests convergence in patterns of seed removal between the Southern Hemisphere deserts, with the North American deserts being distinctly different.

### Seed Fluxes

Parmenter *et al.* (1984) demonstrated that seed-removal experiments were limited in that they did not measure actual levels of seed removal. In order to estimate consumption

of naturally occurring seed production by small mammals, it is necessary to adopt an indirect, energetics approach (Parmenter *et al.* 1984). Here, the energy requirements of the community of small mammals under consideration are estimated, and the contribution of seeds to this energy budget is calculated. Knowledge of the calorific yield of the seeds then allows an estimate of seed consumption. Studies of this nature have been largely confined to the North American deserts (Chew and Chew 1970; Soholt 1973; Pulliam and Brand 1975; Nelson and Chew 1977; Parmenter *et al.* 1984) (see Table 1) with a single study in the South African Karoo (Kerley 1993). Of these, only Soholt (1973), Pulliam and Brand (1975) and Kerley (1993) incorporated realistic dietary data into their models.

**Table 1. Summary of study sites, communities, dietary assumptions and levels of impact of seed-consumption studies of desert small mammals**

Authors	Study area	Principal species	Dietary assumption	Level of impact
Chew and Chew (1970)	Shrublands, Chihuahuan Desert	<i>Dipodomys merriami</i>	Constant 82% seed	86% of seed production
Nelson and Chew (1977)	Shrublands, Mojave Desert	<i>Perognathus formosus</i>	Constant 100% seed	50% of seed reserves
Soholt (1973)	Shrublands, Mojave Desert	<i>Dipodomys merriami</i>	Diets monitored from stomach contents	37% of seed production
Pulliam and Brand (1975)	Grasslands, Chihuahuan Desert	<i>Perognathus hispidus</i>	Diets monitored from fecal samples	0.8% of seed production
Kerley (1993)	Shrublands, Karoo, South Africa	Entire community	Diets monitored from fecal samples	0.5% of seed production

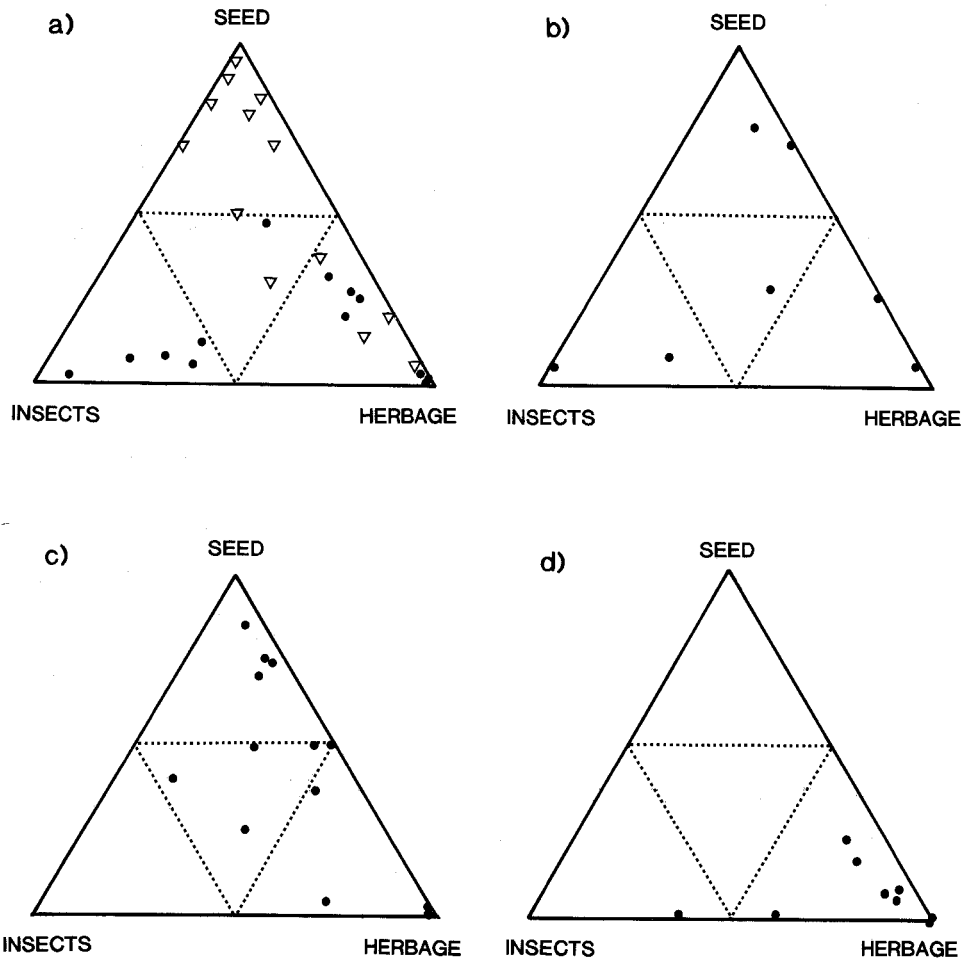
The levels of seed consumption estimated for North American desert shrublands have been high (Table 1), ranging from 37–86% of seed production. Surprisingly, the single study of seed consumption in North American desert grasslands showed seed consumption at orders of magnitude lower than the levels in desert shrublands. This suggests high variability in seed consumption among arid habitats, presumably as a function of variation in abundance and community structure of small mammals. The low level of granivory recorded in the South African desert shrublands (0.5%) is similar to that in the North American desert grasslands, and mirrors the low removal of experimental seed baits by small mammals in this desert (Kerley 1991). Furthermore, the relative levels of seed consumption by ants (24.8% of production) and birds (4.8%) in the South African Karoo (Milton and Dean 1990) show the same patterns as seed-removal experiments. These measures of seed flux therefore confirm the lack of convergence in granivory between North American and the South African Karoo desert shrublands.

### Granivory as a Trophic Strategy

Another approach to evaluating the importance of granivory by desert small mammals is from the diet of the animals. Thus, Mares (1983) predicted that communities of desert small mammals should include a guild of granivores. This hypothesis is based on the situation in the North American deserts. Surprisingly, there are actually few data sets on the diet of desert small mammals, and the term 'granivore' tends to be used loosely. The terms 'granivore', 'insectivore' and 'herbivore' should refer to animals whose diet is

dominated (>50%) by one of these dietary categories, while 'omnivore' should refer to those species whose diets are not dominated by any particular category.

A review of the diet of small mammals of North American deserts (Fig. 2a) indicates that there is indeed a well-developed guild of granivores, although no species feeds exclusively on seeds. Of the 13 heteromyids for which dietary data are available, seven species have a diet comprising more than 50% seed (Fig. 2a), although one of these, *Perognathus parvus* (seed = 50%), can only marginally be considered to be granivorous according to the above definition. None of the non-heteromyid rodents recorded in North American deserts average more than 50% seed in their diet. Of the 27 species recorded in Fig. 2a, 30% ( $n = 8$ ) are granivorous, 44% ( $n = 12$ ) herbivorous, 19% ( $n = 4$ )



**Fig. 2.** Diets of desert small mammals for (a) North American deserts (triangles, heteromyid rodents; circles, non-heteromyid rodents; see References marked with \* for sources), (b) South American Atacama Desert (Meserve 1981), (c) Australian deserts (from Morton and Baynes 1985) and (d) a community in the South African Karoo desert (Kerley 1992a). Points within the triangles represent species' diets, with proximity to the apex indicating the importance of the food component at that apex. Dotted lines indicate the 50% value for each component.

insectivorous, and the remainder omnivorous (7%,  $n = 2$ ). Thus, herbivory is the most common trophic strategy in these North American desert rodents. Clearly, the high levels of seed removal recorded in North American deserts can be attributed to the granivorous heteromyids.

Although the Sahara is the largest desert in the world (Cloudsley-Thompson 1975), there is little information regarding the diets of Saharan rodents. Happold (1975), in his review of the food requirements of rodents of the Sudan, indicated that none of these species could maintain bodyweight on a diet consisting purely of seed. This suggests that these rodents do not rely extensively on seed in their diet.

The gerbilline rodents of the deserts of the Middle East have been shown to be largely granivorous during spring and summer, but consume mainly foliage in the winter (Bar *et al.* 1984). Of the four species (*Gerbillus pyramidium*, *G. allenbyi*, *G. gerbillus* and *Meriones sacramenti*) studied by Bar *et al.* (1984), the diet of two species averaged less than 50% seed. Other components of these communities such as the fat sand rat, *Psammomys obesus*, are, however, exclusively herbivorous (Daly and Daly 1973).

Naumov and Lobachev (1975) summarised the limited available information on the desert rodents of the Soviet Union. Of the 24 species they dealt with, three (*Meriones libycus*, *M. meridianus* and *Cardiocranius paradoxus*) appeared to be largely granivorous, although these species were recorded eating significant amounts of foliage, roots and arthropods. Naumov and Lobachev (1975) also identified three species that were almost exclusively herbivorous (*Alactagulus pygmaeus*, *Pygeretmus platyurus* and *Rhombomys opimus*), and frequently commented on the seasonal variability in the diets of these rodents, which suggests that their diets may be more opportunistic than specialised.

In the Rajasthan desert, the two most abundant rodent species, *Tatera indica* and *Meriones hurrianae*, had highly variable diets, but were on average herbivorous (Prakash 1975). Prakash (1975) stressed the herbivorous nature of the rodents in this desert.

Mares *et al.* (1977) recorded no granivorous small mammals in the South American Monte Desert. In the southern Atacama Desert in Chile, Meserve (1981) showed that two of seven small mammals he studied were largely granivorous, the remaining species being largely herbivorous, with a single insectivore (Fig. 2b).

The situation in the Australian deserts has been largely obscured by extensive post-European extinctions of small mammals, which Morton and Baynes (1985) suggested was biased against species that were dietary or habitat specialists. However, Morton (1979) showed that the diversity of insectivorous small mammals was high, while that of granivores was low, and Morton and Baynes (1985) concluded that few Australian rodents are granivores (Fig. 2c). More recent work suggests that the levels of granivory presented here may be an overestimate (S. R. Morton, personal communication). The dasyurid marsupials appear to be primarily insectivores, although they will also eat other small mammals (Morton and Baynes 1985).

In the Namib, Kalahari and Karoo deserts of southern Africa, the small mammal fauna is dominated by omnivores, insectivores or herbivores, with no species recorded as consistent granivores (Boyer 1987; Kerley 1989, 1992a; Kerley *et al.* 1990). The most common species in these different deserts, *Gerbillurus paeba*, is a generalist, but prefers insects when available (Boyer 1987; Kerley 1989). An example of the dietary status of a community of small mammals in the Karoo (one year's data; Kerley 1992a) is presented in Fig. 2d. It can clearly be seen that this community consists largely of herbivores, with the single insectivorous species being the round-eared elephant shrew (Macroscelididae; *Macroscelides proboscideus*).

Besides indicating the paucity of quantitative dietary studies of desert small mammals, the above review provides little evidence for the predominance of granivory as a trophic strategy for desert small mammals even in the North American deserts. Although much of the available data are qualitative, there is considerable evidence to suggest that herbivory

is the most common trophic strategy adopted by desert small mammals. It would be interesting to compare trophic strategies of small mammals from other biomes in order to test whether desert small mammals do differ in their trophic strategies.

### **Convergences and Divergences**

An overriding pattern therefore emerges from independent seed-removal, seed-flux and dietary studies. This pattern of high levels of granivory by desert small mammals (in terms of both absolute amounts of seeds harvested or consumed, and removal of seeds in relation to that by ants) in the North American deserts contrasts with low levels of granivory in the South American, Australian and South African deserts. The data from the Israeli desert (Abramsky 1983) is at present inconclusive; the summer pattern of seed removed by rodents and ants is similar to that in North America, but this is only one summer's data, and these rodents switch their diets away from granivory in winter (Bar *et al.* 1984).

From these data it would appear that the deserts having low levels of granivory by small mammals are actually the norm, while the North American deserts have exceptionally high levels of granivory by small mammals, as suggested by Morton and Baynes (1985) in a comparison of Australian and North American deserts.

### **Hypotheses to Explain Patterns in Granivory by Small Mammals**

Subsequent to the initial hypothesis of convergence in granivory by desert small mammals being rejected by Mares and Rosenzweig's (1978) comparison of the Monte and Sonoran deserts, numerous hypotheses have been presented to explain this lack of convergence. However, many of these hypotheses have attempted to explain why granivory by small mammals differs between particular deserts, with no unified theory emerging.

Furthermore, many of these hypotheses have been based on the assumption that the high levels of granivory by small mammals in North American deserts are the norm. Consequently, these hypotheses have attempted to explain low levels of granivory by small mammals in other deserts. This is largely due to the strong influence of North American desert ecologists in this field.

### *Extinction*

Mares and Rosenzweig (1978) suggested that differences in patterns of granivory between the North American Sonoran Desert and the South American Monte Desert may have been caused by the extinction of a marsupial family, the Argyrolagidae, which they suggested were ecological analogues of the granivorous heteromyids, on the basis of morphological similarities [a poor predictor of small mammal diets (Fig. 2a) (Mares 1983)]. A similar situation may have prevailed in the Australian deserts, which have also experienced a recent loss of small marsupial species (Morton and Baynes 1985). However, this loss of a class of granivores does not explain the patterns of granivory in the Karoo, where granivorous small mammals are absent and there is no evidence for recent extinctions (Kerley 1991).

### *Seed Burial*

North American soils are generally coarse and sandy, whereas those of Australia are fine and crusty. This led Westoby *et al.* (1982) to suggest that seeds in Australia are less available to granivores, as a large proportion are rapidly buried. Morton (1985) postulated that this could have in part given rise to the differences in the levels and patterns of granivory between North American and Australian deserts. However, although buried seeds are not available to ants, rodents are capable of detecting and excavating seeds at depths of up to 15 cm (Abramsky 1983). This hypothesis does not, therefore, explain the depressed levels of granivory by small mammals in Australia. A further prediction of this hypothesis is that ant granivory should be depressed in Australia, a prediction not supported by Morton's (1985) findings. In addition, like North American deserts, South African Karoo

soils tend to be coarse (Ellis and Lambrechts 1986), but the level of granivory by small mammals is low.

#### *Low Soil Nutrients and Seed Production*

Soil nutrients, another edaphic feature, tend to be lower in Australian deserts than in North American deserts, presumably limiting seed production and therefore granivory (Morton 1985). However, South African Karoo soil nutrients are also low (Ellis and Lambrechts 1986), but levels of seed production in the Karoo are not depressed (Milton and Dean 1990; Kerley 1990). This does not support the hypothesis that low nutrients result in low seed production, or lead to depressed granivory by small mammals. Long-term data series on seed production and the factors influencing this are needed to further evaluate this hypothesis.

#### *Age of Deserts*

One of the crucial requirements for convergence in the biota of different deserts to occur is that sufficient time must have elapsed for adaptations to the desert environment to evolve (Orians and Solbrig 1977). Thus, if granivory by small mammals is a result of selective pressures in deserts (as suggested by the original hypothesis of convergence), it may be argued that deserts lacking granivorous small mammals are simply too young for this guild to have evolved. However, the Namib desert, one of the oldest deserts (Ward and Corbet 1990) is depauperate in terms of granivorous small mammals (Boyer 1987).

Another time factor is the period since a desert was colonised by a taxon of small mammals, and whether this has been long enough for a granivorous guild to evolve. Both the South American Monte and Australian deserts have been colonised by rodents relatively recently (Mares and Rosenzweig 1978; Morton and Baynes 1985). This recent colonisation may provide a partial, special-case explanation for the paucity of granivores in these deserts (although they are by no means absent; Morton and Baynes 1985), but does not hold for the African or Asian deserts.

#### *Uncertainty of Climate*

When comparing North American and Australian deserts, Morton (1985) hypothesised that these two regions may differ in their intensity of granivory as a result of differences in climatic factors, Australian deserts possibly being less predictable climatically. Westoby (1980) suggested that, in desert and semi-deserts, the predictability of rainfall influences plant life-history strategies, including the patterns of seed production. A relatively predictable, seasonal rainfall favours the development of an annual flora, which relies on the production of large numbers of seeds to survive unfavourable periods (Westoby 1980). This reliable, annual production of seed may favour the granivorous guild, and in particular sedentary homeotherms (e.g. rodents), while uncertain seed production may depress the levels of granivory, and favour poikilothermic or highly mobile homeothermic granivores (e.g. ants and birds, respectively; Morton 1985). Furthermore, with increasing climatic unpredictability larger numbers of smaller seeds are produced by perennials (Westoby 1980), to the detriment of granivorous rodents, which select seeds from the larger-seeded shrubs (Brown and Munger 1985).

Our knowledge of the predictability of climates, as experienced by granivores, is limited and the problem is further compounded by the need to consider palaeoclimatic uncertainty to understand the evolutionary basis of this guild.

The mechanisms of these putative differences in climatic variability are not clear, but may range from regional to global processes. As an example, Morton (1979) and Morton and Baynes (1985) speculated that the low overall relief of continental Australia leads to relatively mild winters and year-round insect availability, favouring omnivory/insectivory by Australian small mammals. On a larger scale, Kerley (1990) pointed out that differences



in patterns of granivory are apparent between the Northern and Southern hemispheres. He suggested that this could be due to the effect of the differing proportions of land masses in the two hemispheres. The large land masses of the Northern Hemisphere result in more extreme continental type climates (e.g. Vuillemeier 1971), and this may have affected the Pleistocene climatic extremes. In this scenario, a more severe winter climate in the Northern Hemisphere may have limited the availability of insects and herbage, and desert small mammals may have been forced to rely on seeds (produced mainly by annuals). However this hypothesis requires a large component of granivorous small mammals in the Asian deserts, a prediction not supported by the available data.

An alternative large-scale influence on climatic variability may be the El Niño Southern Oscillation (ENSO) phenomenon, which results in major drought in southern Africa, Australia and south-eastern South America, but may cause high rains on the west coast of North and South America (Canby 1984; Allan 1991). Recent ENSO-induced drought in the southern African Karoo caused a collapse of the community of small mammals (Kerley 1992b). The full implications and periodicity of ENSO events have yet to be worked out on local and global scales, and it would be useful to quantify the impacts of this phenomenon on desert seed/granivore systems.

#### **North American Deserts: High Levels of Granivory due to the Heteromyids?**

As argued above, the available information on seed removal, seed fluxes and diets of small mammals indicates that the North American deserts may in fact be divergent from the remaining deserts in terms of granivory by small mammals. This suggests that explanations for elevated levels of granivory by small mammals should be sought in terms of unique features of the North American deserts.

Probably the most prominent feature of the North American deserts relevant to granivory by small mammals is the diversity and abundance of the heteromyid rodents. The high levels of granivory by small mammals can be attributed largely to the activities of the members of this family (Mares and Rosenzweig 1978).

Is there any particular feature of these deserts that has led to the diversity and abundance of the heteromyids? A possible palaeoclimatic factor is the impact of Pleistocene climate extremes on radiation. Thus, Mares (1983) suggested that the Pleistocene climate shifts would have generated a series of isolated habitat refuges in the basin-and-range landscapes of the North American deserts. He speculated that this may have encouraged radiation of the heteromyids through allopatric speciation. It is important to note that this hypothesis relies more on the geomorphology of the North American landscape to explain the radiation of the heteromyids than any characteristic of deserts.

Eisenberg (1975) and Brown *et al.* (1979) have commented on the fact that most of the North American deserts actually enjoy elevated rainfall compared with other deserts. Consequently, the abundance of rodents may in fact be due to the high productivity of these areas (Mares 1983). This observation suggests confusion regarding definitions of deserts or looseness of the use of these terms. Furthermore, the variability in rainfall decreases with increasing rainfall (Hoffman and Cowling 1987), and this may be relevant to Morton's (1985) climatic predictability hypothesis. Obviously a review of desert climates (and definitions) is needed in order to clarify this point. Also, care should be taken in selecting study sites for comparisons of desert ecology.

Even if elevated productivity does explain the abundance of rodents in North American deserts, this does not explain why it is invariably the heteromyids (e.g. Brown 1973) that dominate these communities. Many other desert small mammals possess some of the features of the heteromyids (including cheekpouches, nocturnalism, bipedalism, seed consumption, caching etc.) but not the total combination of these features. This argument leads to the conclusion that the high levels of granivory observed in North American deserts is a result of the outstanding success of the suite of adaptations (including granivory)

of the heteromyids to the desert environment. The fact that none of the non-heteromyid North American desert rodents are granivorous supports the argument that granivory by the heteromyids is not a response to some unique feature of the North American deserts, but a feature of the heteromyids.

In opting for a historical/biotic determinant (the evolution and radiation of the heteromyids) for elevated levels of granivory in North American deserts, we do not exclude the important role of the physical factors discussed in the above hypotheses.

### Implications for Desert Ecology

The above review of the variation in granivory by desert small mammals and possible determinants of this variation will provide, we hope, an incentive for desert ecologists to review the current paradigms of desert ecology. So much of how we think about desert structure and functioning is influenced by the preponderance in the literature of research in the North American deserts (Morton and Baynes 1985). The impacts of granivory by small mammals on desert communities have been shown to be profound and far-reaching (Brown and Munger 1985; Brown and Heske 1990). Thus, limited granivory by small mammals observed in other deserts suggests that we can expect other differences in the structure and function of these desert communities.

Mares and Rosenzweig (1978) and Brown and Ojeda (1987) discussed the importance of coevolution in the desert granivore/seed system. They argued that plants would be under major selective pressure to minimise the impact of seed predators. They further suggested that it was unlikely that plants could specialise in avoiding the attention of all seed predators, but would probably adapt to minimise the impact of a particular taxon (small mammals, birds, ants). This hypothesis suggests major differences between seed characteristics and seeding strategies of North American desert plants and those of plants where granivory by small mammals is limited, and provides an opportunity to evaluate the strength of these coevolutionary pressures (Brown and Ojeda 1987).

Kerley (1993) pointed out that, in the South African Karoo, seed production, seed banks, and levels of seed predation by birds and ants were similar to those of North American deserts. This was despite seed consumption by Karoo small mammals being orders of magnitude lower than that of small mammals of North American deserts. It would therefore appear that seed predation by birds and ants has not increased to take up the apparent increased availability of seeds, and some as-yet-unknown process appears to be operating to control seed fluxes in the Karoo. Seed production and consumption measurements are needed in other deserts with low levels of granivory by small mammals in order to evaluate how these vary, and we need to investigate other avenues of seed loss in the Karoo, and possibly the other deserts.

One of the most exciting areas of research on desert small mammals has addressed the mechanisms of coexistence of these desert species. The current competition-based theories, developed largely within the North American deserts, suggest that coexistence is largely mediated through microhabitat-based resource partitioning of seeds (Reichman 1992). However, in deserts where the small mammals are largely herbivorous or omnivorous, the resource base for which the animals are competing will be different, particularly in terms of microhabitat-specific distributions. There are some data to show differential use of microhabitats by non-granivorous small mammals (Kerley *et al.* 1990), and we need to further investigate the mechanisms whereby species within these communities coexist.

It is now 10 years since Mares (1983) pointed out the exciting potential for research on small mammals in deserts besides those of North America. It is apparent that communities of desert small mammals are useful tools for the investigation of community processes (e.g. Reichman 1992) as well as larger-scale coevolutionary pressures. We hope that this paper and others within this symposium will provide further incentive to expand on the small beginnings of this programme of comparative research on desert small mammals.

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