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Small mammal seed consumption in the Karoo, South Africa: further evidence for divergence in desert biotic processes

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Summary. Annual seed consumption by a small mammal community in the semi-arid Karoo, South Africa, was calculated using population, biomass and dietary estimates and published estimates of field metabolic rate. The community comprised a macroscelid elephant shrew *Macroscelides proboscideus*, and two rodents *Gerbillurus paebe* and *Desmodillus auricularis*. Only *G. paebe* consumed seed during the study, and then in low amounts (annual mean = 0.4% of diet, insects = 53%, herbage = 47%), with *M. proboscideus* and *D. auricularis* consuming mainly insects (88%) and herbage (90%), respectively. Energy requirements for the *G. paebe* population averaged 568 kJ ha⁻¹ day⁻¹. Total seed consumption was estimated to be ≈ 140 g ha⁻¹, or 155 000 seeds ha⁻¹ which represents ≈ 0.5% of the annual seed production for this site. These levels of granivory by small mammals are significantly lower than those recorded for North American deserts, and raises the question as to why granivory varies between these systems. These findings also refute the hypothesis that as a result of the harshness and similarity of physical conditions in deserts, the properties of desert communities are convergent.

Key words: Granivory – Seed production – Rodents – Divergence between deserts – Diet

Factors which influence the fate of seeds affect the structure of plant communities. For example, granivory, principally by rodents, birds and ants, has been shown to be one of the major avenues of seed loss in desert systems. In North American deserts granivorous rodents are diverse and abundant, and are capable of consuming up to 86% of the annual seed crop (Chew and Chew 1970). Furthermore, manipulative field studies have shown that selective seed predation by this taxon influences the abundance of plants, particularly large-seeded species, and has far-reaching indirect effects on the structure and dynamics of desert communities (Brown et al. 1986).

The Karoo comprises the vast semi-arid dwarf shrublands of southern Africa. Despite the size (650 000 km²) and agricultural importance of this area, little information is available on processes which may influence the structure of the plant community. In contrast with the North American deserts, the Karoo is depauperate in terms of granivorous small mammals, with most representatives of this taxon being relatively omnivorous (Kerley 1989, 1992). This paper reports on an energetically based estimate of seed consumption by small mammals in the Karoo, addressing the hypothesis that owing to the paucity of granivorous small mammals in the Karoo, levels of granivory would be depressed in relation to those in North American desert systems.

Methods

Study site

This study was conducted at the Karoo Biome Research site at Tierberg (33° 10' S, 22° 17' E), 25 km east of Prince Albert, South Africa. Vegetation is dwarf shrubland dominated by *Pteronia pallens* and *Eberlanzia ferox*. Mean annual precipitation is 167 ± 7 mm (mean ± SE; Milton et al. 1991). A total of 260 mm rain was recorded at the study site during this study (S.J. Milton in litt.).

Small mammal populations

Trapping was conducted monthly from November 1987 until November 1988, as close to new moon as possible, using Sherman traps (7.5 × 9 × 23 cm) baited with peanut butter and rolled oats and equipped with a small woolen blanket. For each sampling session 100 traps were set for four nights, 10 m apart, on a permanently marked 10 × 10 grid. Traps were checked at dawn and dusk and rebaited every 48 h. Captured animals were identified, sexed, weighed, uniquely toeclipped and released at the point of capture. Traps in which animals had been caught were replaced with clean traps. Population estimates were derived using the Minimum Number Alive method (Krebs 1966). Densities were calculated using the area of the trapping grid, extended by half the distance between traps (Korn 1987), yielding an effective trapping area of 1 ha.

Diet

Faecal pellets that had been voided in the traps by captured individuals were collected (Churchfield 1985) and analysed microscopically following Hansson (1970), to yield estimates of the consumption (expressed as percentage contribution) of herbage, seeds and insects. In the laboratory there is a good correlation between the contribution of seed to the diet and faecal seed content (Kerley 1990). For individuals captured on more than one occasion in a trapping session, only the sample from the first capture event was used, to avoid faecal samples contaminated with bait.

Seed consumption by small mammals

The seed consumption by small mammals at Tierberg was calculated on a monthly basis (seeds consumed $\text{ha}^{-1} \text{month}^{-1}$), using the population estimates for the small mammals, their body-weights and the proportion of seed in their diets.

Energy requirements were calculated for each individual using field metabolic rates for rodents based on doubly-labelled water studies ($\text{FMR} = 10.5(\text{bodymass})^{0.507}$; Nagy 1987), and summed for the estimated population. The daily energy provided by seed was estimated from the proportion of seed in the diet, assuming a digestive efficiency of 85.0% (Drodz 1975; Soholt 1973). The weight of seed consumed daily was calculated using an energy value of 7.11 kJ/g (mean energy intake for seeds of 11 common Karoo plants after husks, etc. have been discarded; Kerley and Erasmus 1991). The number of seeds consumed daily was calculated on a monthly basis, using the average weight (1.1 mg) of seeds produced at this site (Milton and Dean 1990).

Results

Small mammal community

Trap success during the 5200 trapnights of this study was 4.8%. The small mammal community was dominated by

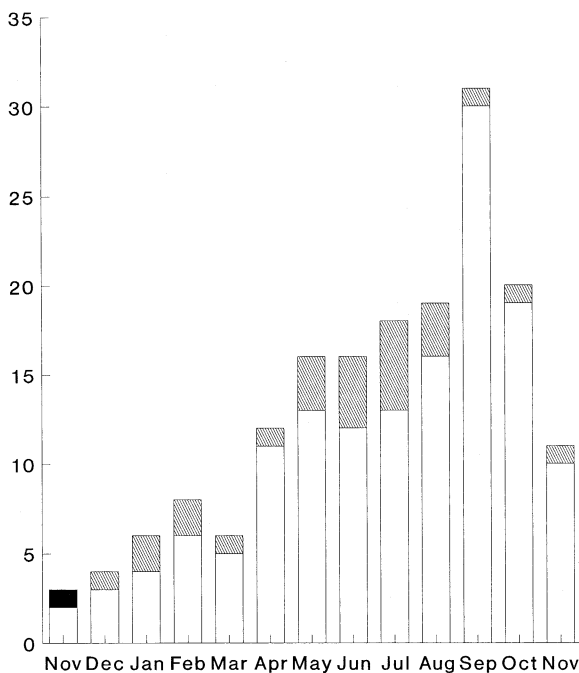


Fig. 1. Monthly density (no ha^{-1}) estimates of small mammals on the trapping grid at the Tierberg study site. Open bars, *Gerbillurus paeba*; hatched bars, *Macroscelides proboscideus*; solid bars, *Desmodillus auricularis*

the hairy-footed gerbil *Gerbillurus paeba*, with low numbers of the round-eared elephant shrew *Macroscelides proboscideus*. A single short-tailed gerbil *Desmodillus auricularis* was recorded in November 1987 (Fig. 1). Numbers were low in spring (November) 1987, but increased during the following autumn and winter (April–July) to peak in spring (September) and declined over the next two months.

Diet

The contribution of seed to the diet of small mammals at the Tierberg study site was limited, seed being recorded only in *G. paeba* samples (Table 1). On an annual basis the diet of this species comprised approximately equal proportions of herbage and insects (Table 1), but the importance of these two dietary categories varied throughout the year (Table 2). During winter herbage predominated in the diet, but during spring and autumn *G. paeba* consumed mainly insects. Seed consumption by *G. paeba* was highest in summer, autumn and early winter. *Macroscelides proboscideus* ate mainly insects throughout the year, while the single *D. auricularis* had eaten mainly herbage (Table 1).

Seed consumption by *G. paeba*

The biomass, energy requirements and seed predation (weight and numbers of seeds) for *G. paeba* are presented

Table 1. Contribution (mean % volume, with SE in parentheses) of seeds, herbage and insects to the diet of small mammals at the Tierberg study site

Species	<i>n</i>	Seed	Herbage	Insects
<i>Gerbillurus paeba</i>	119	0.4 (0.1)	46.9 (3.3)	52.7 (3.3)
<i>Desmodillus auricularis</i>	1	0.0	90.2	9.8
<i>Macroscelides proboscideus</i>	17	0.0	11.8 (2.1)	88.0 (2.4)

Table 2. Monthly contribution (mean % volume, with SE in parentheses) of seeds, herbage and insects to the diet of *Gerbillurus paeba* at the Tierberg study site

Month	<i>n</i>	Seed	Herbage	Insects
November 1987	2	0.0	58.4 (5.4)	41.6 (5.4)
December 1987	2	1.3 (0.9)	40.4 (6.8)	58.3 (7.7)
January 1988	3	1.7 (1.4)	25.1 (6.7)	73.2 (7.4)
February 1988	5	0.2 (0.2)	52.8 (12.6)	47.0 (12.6)
March 1988	5	0.5 (0.3)	39.7 (13.6)	59.7 (13.7)
April 1988	11	0.0	51.7 (8.4)	48.2 (8.4)
May 1988	11	0.9 (0.9)	91.4 (5.9)	7.6 (5.9)
June 1988	9	1.1 (0.7)	78.2 (7.2)	20.7 (6.8)
July 1988	8	0.1 (0.1)	76.2 (8.6)	23.7 (8.6)
August 1988	10	0.0	30.0 (7.9)	70.0 (7.9)
September 1988	25	0.0	12.7 (3.9)	87.3 (3.9)
October 1988	19	0.0	34.7 (6.5)	65.3 (6.5)
November 1988	9	1.0 (0.4)	75.7 (9.3)	23.3 (9.4)

Table 3. Monthly densities, biomass, energy requirements (calculated individually as field metabolic rate: Nagy 1987) and seed consumption for *Gerbillurus paebe* at the Tierberg study site

Month	<i>n</i> no ha ⁻¹	Biomass g ha ⁻¹	Energy requirements kJ ha ⁻¹ day ⁻¹	Seed ¹ consumption	
				g ha ⁻¹ month ⁻¹	seeds ha ⁻¹ month ⁻¹
November 1987	2	50.9	108.4	0	0
December 1987	3	78.0	164.3	13.5	12 300
January 1988	4	102.4	214.6	22.7	20 600
February 1988	6	138.3	307.3	3.6	3 300
March 1988	5	120.9	262.7	8.7	7 900
April 1988	11	258.2	570.7	1.3	1 200
May 1988	13	337.3	710.5	41.4	37 600
June 1988	12	288.9	629.1	43.7	39 700
July 1988	13	325.5	696.9	4.2	3 800
August 1988	16	347.0	788.0	0	0
September 1988	30	617.7	1446.4	0	0
October 1988	19	441.1	978.5	0	0
November 1988	10	230.1	506.1	31.9	29 000

¹ To the nearest 100 seeds

in Table 3. The total annual seed consumption by this species is calculated as ≈ 140 g ha⁻¹ or 155 000 seeds ha⁻¹.

Discussion

Seed predation has long been recognised as one of the key biotic factors influencing seed survival and subsequent seedling establishment (Janzen 1971) with implications for entire biotic communities (Brown et al. 1986). However, there are few published studies quantifying the role of granivores in seed dynamics. Of these, those assessing seed predation indirectly using seed dishes are of limited value (Parmenter et al. 1984). However, the energetics approach can provide a direct realistic assessment of the rates of seed predation by granivores, provided the ecological data upon which the calculations are based are sound (Parmenter et al. 1984). The present study is based upon such robust data, an important feature being the incorporation of time-specific dietary information. The densities, biomass and community structure measured here are typical of those in the Karoo (Kerley and Erasmus in press). A parameter which needs to be further investigated is seed size selection by African rodents. Variation in this value would however not affect the amount of seed consumed, though the number of seeds eaten is sensitive to this parameter.

Diet compositions reported here for these species agree in general with published accounts, although the contribution of seeds is low. Elsewhere *G. paebe* has been shown to be omnivorous (Kerley 1989), insectivorous (Boyer 1987), granivorous (Nel 1978) or herbivorous (Kerley et al. 1990; Kerley 1992). Similarly, both *M. proboscideus* and *D. auricularis* have been shown to consume significant amounts of seeds (Kerley 1989). This dietary variability suggests that resource availability plays a greater role in determining dietary patterns than evolutionary specialization (Kerley 1989). It would

therefore appear that the extent of seed consumption by small mammals depends on the availability of both seeds and alternative food resources.

Seed consumption

At Tierberg, Milton and Dean (1990) estimated the annual seed production to be 30.5×10^6 seeds ha⁻¹ or 33.8 kg ha⁻¹, during this study. The results of this work therefore indicate that the small mammals at the Tierberg site are consuming about 0.5% of the annual seed production by weight. Thus, it can be seen that the impact of rodents as granivores at this site is negligible in terms of seed production. These findings concur with results of seed dish experiments which indicate that small mammals are not important seed harvesters in the Karoo (Kerley 1991).

How does this compare to the levels of seed consumption estimated for North American deserts? Unfortunately, the results of two of these studies (Nelson and Chew 1977; Parmenter et al. 1984) are biased by unrealistically high assumed levels of granivory in their communities (Kerley 1990).

Chew and Chew (1970) and Soholt (1973) estimated the energy requirements and diets of *Dipodomys merriami* populations in California and Arizona, respectively. They found mean population energy budgets of 664 and 953 kJ ha⁻¹ day⁻¹, respectively, which is slightly higher than (but within the range of) the values found in this study. This difference may be ascribed to the higher densities and biomasses observed in their studies. Chew and Chew (1970) concluded that their small mammal community consumed 86.5% of the annual seed production. Soholt (1973) calculated that kangaroo rats consumed 85% of the seed produced by *Erodium*, the primary food species at his Mojave desert site. These differences indicate strong divergence between the impact of small mammals as seed consumers in the North Amer-

ican and southern African semi-arid systems, despite the comparability of the resource base.

Two questions arise from these findings: can the role of small mammals as granivores be ignored in the Karoo and why do the deserts differ in the levels of granivory by small mammals?

Is granivory by small mammals in the Karoo inconsequential?

It would be premature to assume that granivory by Karoo small mammals has no impact on the plant community. Rodents are highly selective in their consumption of seeds (Nelson and Chew 1977; Kerley and Erasmus 1991), and Brown et al. (1986) showed that it was primarily through the selective removal of larger seeds that rodents influenced the plant community. Therefore, although the gerbils in the present study did not consume that much seed, they could possibly have influenced the survival of seeds of a few selected plant species. Furthermore, these animals' diets are highly variable (Kerley 1989; 1992) and during drought when both insect and herbage availability may be limited, gerbils may concentrate more on granivory and thereby increase their impact on seed fluxes. For example, if the diet of *G. paeba* of 36% seed found elsewhere in the Karoo (Kerley 1989), is applied to the above model, then the annual seed consumption is calculated as 16.4 kg ha⁻¹, considerably higher than the previous values and approaching some of the estimates for desert seed reserves. The extreme assumption that the gerbil population was exclusively granivorous results in a calculated annual seed consumption of 45 kg ha⁻¹, more than the total annual production for this site. This example illustrates the sensitivity of these calculations to variation in dietary values, and emphasizes the importance of reliable dietary information.

Variation in rodent granivory between deserts

Differences in the levels of granivory between different desert systems have been measured in terms of seed harvesting rates using seed dish techniques (Morton 1985; Kerley 1991). These studies indicate that small mammals are the dominant seed removers in relation to ants and birds in North American and Israeli deserts. However, small mammals play a lesser role in South American, Australian and southern African deserts. This study is the first confirmation that levels of seed consumption by small mammals do differ between the different deserts. These divergences, in what has up to now been seen as a fundamental process in desert systems, are particularly surprising in view of the apparent similarity of the physical environments of these deserts. Orians and Solbrig's (1977) hypothesis that the structure and functioning of desert biotic communities are convergent is refuted by the present study.

What has led to these differences in levels of granivory? Morton (1985) discussed a number of hypotheses which may account for depressed levels of granivory by

desert small mammals. One of these suggests that low soil nutrients result in reduced seed production, and hence limited small mammal granivory (Morton 1985). Karoo soil nutrients are low (Ellis and Lambrecht 1986). However, Karoo seed banks (mean = 185 × 10⁶, range = 50–410 × 10⁶ seeds ha⁻¹; Van Rooyen and Grobbelaar 1982) and annual seed production (30.5 × 10⁶ seeds ha⁻¹ or 33.8 kg ha⁻¹; Milton and Dean 1990) do not appear to be lower than North American desert seed banks (2.8 – 3700 × 10⁶ seeds ha⁻¹ and 5.6 – 84.3 kg ha⁻¹; Reichman 1975 and references therein) or annual seed production (mean = 57.8 kg ha⁻¹, range = 5.3 – 109.7 kg ha⁻¹; French et al. 1974). Thus seed resources are of the same order of magnitude in the different deserts, falsifying Morton's (1985) hypothesis.

Implications of reduced small mammal granivory in the Karoo

Small mammal granivory is depressed, while seed production in the Karoo is similar in relation to North American deserts. Also, granivory by birds and ants in the Karoo (Kerley 1991), as well as Karoo seed banks, are not elevated to account for an apparent excess of seed availability. What processes are operating to increase seed fluxes in the Karoo?

Brown and Ojeda (1987) suggested that granivory is an important selective pressure on plants, with plants evolving mechanisms to limit seed predation. According to this hypothesis, Karoo plants should show few adaptations to limit granivory by small mammals. I am not aware of any data that are available to test this hypothesis, but it would be useful to explore this aspect of the evolutionary consequences of granivory.

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References

- Boyer DC (1987) Effect of rodents on plant recruitment and production in the dune area of the Namib Desert. M.Sc. thesis, Univ. Natal, Pietermaritzburg, S.Africa
- Brown JH, Ojeda RA (1987) Granivory: patterns and processes, and consequences of seed consumption on two continents. *Rev Chil Hist Nat* 60: 337–349
- Brown JH, Davidson DW, Munger JC, Inouye RS (1986) Experimental community ecology: the desert granivore system. In: Diamond J, Case TJ (eds) *Community Ecology*. Harper and Rowe, New York, pp 41–61
- Chew RM, Chew AE (1970) Energy relationships of the mammals of a desert shrub (*Larrea tridentata*) community. *Ecol Monogr* 40: 1–21
- Churchfield S (1985) Diets of two syntopic small mammals in the Inyanga National Park, Zimbabwe. *S Afr J Zool*, 20: 65–67
- Drodz A (1975) Feeding and nutrition. In: Grodzinski W (ed) *Methods of ecological bio-energetics*. (IBP Handbook no. 24) pp 325–357
- Ellis F, Lambrecht JJN (1986) Soils. In: Cowling RM, Roux PW, Pieterse AJH (eds) *The Karoo Biome: a preliminary synthesis*.

- Part 1 – Physical Environments. S Afr Natl Sci Progm Rep 124:18–38
- French NR, Maza BG, Hill HO, Aschwanden AP, Kaaz HW (1974) A population study of irradiated desert rodents. Zool Monogr 44:45–72
- Hansson L (1970) Methods of morphological diet micro-analysis in rodents. Oikos 21:255–266
- Janzen DH (1971) Seed predation by animals. Annu Rev Ecol Syst 2:465–492
- Kerley GIH (1989) Diet of small mammals from the Karoo, South Africa. S Afr J Wildl Res 19:67–72
- Kerley GIH (1990) Small mammals as granivores in the Karoo. Ph.D. thesis, Univ Port Elizabeth, S Africa
- Kerley GIH (1991) Seed removal by rodents, birds and ants in the semi-arid Karoo, South Africa. J Arid Environ 20:63–69
- Kerley GIH (1992) Trophic status of small mammals in the semi-arid Karoo, South Africa. J Zool, Lond 226 (in press)
- Kerley GIH, Erasmus T (1991) What do mice select for in seeds? Oecologia 86:261–267
- Kerley GIH, Erasmus T (in press) Small mammal communities in the semi-arid Karoo, South Africa: biomass and energy requirements. J Arid Environ
- Kerley GIH, Knight MH, Erasmus T (1990) Small mammal micro-habitat use and diet in the southern Kalahari, South Africa. S Afr J Wildl Res 20:123–126
- Korn H (1987) Densities and biomasses of non-fossorial southern African rodents during the dry season. Oecologia 72:410–413
- Krebs CJ (1966) Demographic changes in fluctuating populations of *Microtus californicus*. Ecol Monogr 36:239–273
- Milton SJ, Dean WRJ (1990) Seed production in rangelands of the Karoo. S Afr J Sci 86:231–233
- Milton SJ, Dean WRJ, Kerley GIH (1991) Tierberg Karoo Research Centre: history, physical environment, flora and fauna. Trans Roy Soc S Afr 48:in press
- Morton SR (1985) Granivory in arid regions: comparison of Australia with north and south America. Ecology 66:1859–1866
- Nagy KA (1987) Field metabolic rate and food requirement scaling in mammals and birds. Ecol Monogr 57:111–128
- Nel JAJ (1978) Habitat heterogeneity and changes in small mammal community structure and resource utilization in the southern Kalahari. Bull Carnegie Mus Nat Hist 6:118–132
- Nelson JF, Chew RM (1977) Factors affecting seed reserves in the soil of a Mojave desert ecosystem, Rock Valley, Nye County, Nevada. Am Midl Nat 97:300–320
- Orians GH, Solbrig OT (1977) An evolutionary approach to ecosystems. In: Orians GH, Solbrig OT (eds) Convergent evolution in warm deserts. US/IBP Series 3, pp 1–12
- Parmenter RR, MacMahon JA, Vander Wall SB (1984) The measurement of granivory by desert rodents, birds and ants: a comparison of an energetics approach and a seed dish technique. J Arid Environ 7:75–92
- Reichman OJ (1975) Relation of desert rodent diets to available resources. J Mammal 56:731–751
- Soholt LF (1973) Consumption of primary production by a population of Kangaroo rats (*Dipodomys merriami*) in the Mojave desert. Ecol Monogr 43:357–376
- Van Rooyen MW, Grobbelaar N (1982) Saadbevolkings in die grond van die Hester Malan-natuurreservaat in die Namakwalandse Gebroke Veld. S Afr J Bot 1:41–50