HOARDING IN FOUR SOUTHERN AFRICAN RODENT SPECIES

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ABSTRACT

The comparative hoarding behaviour of four rodent species, *Saccostomus campestris, Desmodillus auricularis, Tatera brantsii* and *T. leucogaster* was studied under semi-natural conditions after prior determination of the seed preferences of each species.

The results are consistent with all available ecological data. *Desmodillus* and *Saccostomus* are true larder-hoarders, although *Desmodillus* also scatter-hoards on occasion. The *Tatera* spp. did not hoard, but frequently covered seeds, a possible primitive form of scatter-hoarding.

INTRODUCTION

Hoarding, i.e. the transport and subsequent storing of food, may be an essential survival pattern for animals living in environments where food is not abundant throughout the year. Lyman (1954) stressed the importance of hoarding in certain hibernators, although it is reasonable to assume that hoarding may be of even greater importance to animals that do not hibernate or aestivate during times of food shortage.

The term "larder-hoarding" is commonly used where food is stored in the nest or burrow of the animal (Ewer 1968) with "scatter-hoarding" being used if food is stored elsewhere. The latter form of hoarding was first described by Morris (1962) who referred to scatter-hoarding as the storing of each individual load separately within the animal's home range, but for the purpose of this study this term will be extended to cover any form of hoarding other than larder-hoarding.

Although hoarding behaviour has been noted for a number of animals, most experimental investigation has been conducted on laboratory rats, e.g. Morgan *et al.* (1943) and Bindra (1948, 1949). A few accounts of hoarding under more natural conditions are available, e.g. Morris (1962) and Ewer (1965, 1967).

This paper reports on the hoarding behaviour of the following muroid species: the pouched mouse *Saccostomus campestris* (Murinae), the Namaqua gerbil *Desmodillus auricularis,* the highveld gerbil *Tatera brantsii* and the bushveld gerbil *Tatera leucogaster* (Gerbillinae). In order to induce maximum hoarding the preference for ten seed types was

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first determined for each species and the animals then tested for hoarding, using the most preferred seed types.

MATERIAL AND METHODS

For every species five males and five females were tested. All the animals were trapped in Sherman aluminium live-traps and transferred to the Zoology Department, University of Pretoria, where they were housed in 43,2 x 27,9 x 22,9 cm plastic cages with wire-mesh lids. Two male and three female *Saccostomus* and all the *Tatera leucogaster* were trapped in the vicinity of Pretoria; the remaining *Saccostomus* were trapped in the Derdepoort area. All the *Desmodillus* and two *Tatera brantsii* males were trapped in the Kalahari Gemsbok National Park. The remaining *T. brantsii* were trapped in the Balfour district.

The test animals had been in captivity for varying lengths of time (two weeks to 10 months) before being tested. Prior to testing for seed preference, the animals were fed on small amounts of each seed type for ten days, forcing them to "try out" the different seed types. For the seed preference tests a glass aquarium subdivided into two 1 x 0,5 m compartments was used with the floor covered with sand to a depth of 4 cm. One animal was placed in a compartment at a time. Twenty grams of each seed type were placed in separate glass bowls mounted on glass discs and distributed at random throughout the compartments. Water was provided *ad lib.* The seeds left over in each glass bowl were weighed daily at 08h00 and subtracted from the original 20 g. The bowls were then refilled to 20 g of seed and redistributed in the compartments. This procedure was repeated on six successive days for each pair of animals. Any signs of hoarding were noted.

To see if any correlation exists between a seed's colour and size, and an animal's preference for it, 10 seed types showing a variety of colours and sizes were used in this experiment.

The seed types used, in descending order of size, were:

Arachis hypogaea	(peanuts - shelled)
Helianthus annuus	(sunflower - unshelled)
Hordeum vulgare	(barley)
Triticum aestivum	(wheat)
Fagopyrum esculentum	(buckwheat)
Sorghum vulgare	(sorghum)
Setaria sp.	(millet)
Medicago sativa	(lucern)
Eragrostis curvula	(weeping love grass)
Urochloa bulbodes	

To study the hoarding behaviour of each species, a large hardboard cage subdivided into four 1 x 0,5 m compartments was used, each equipped with a 20 x 20 x 15 cm nestbox, nesting material, and a permanent supply of water. Fine sand covered the floor to a depth of 6 cm.

Two weeks prior to each experiment the test animals were placed under a reversed light cycle (16:8) at 30° C. One week's acclimatization to the experimental cage was allowed, with one individual per compartment provided with a minimum amount of food per day (5 g). Eight animals of each species were starved for 24 hours prior to being tested, the remaining two animals being starved for 48 hours. Half an hour before the start of the dark cycle 50 g of each of the two most preferred seed types were placed in two separate piles into each compartment. During eight hours of continuous observation for every set of four animals, the hoarding behaviour and other related activities were recorded.

RESULTS

In every species a high degree of individual preference for particular seed types occurred so that no one seed type was preferred by all the individuals of a given species.

From Figure 1 it appeared that all species had a high selection for peanuts and sunflower. The Chi-square test was applied against the total mass of the ten seed types removed from the glass bowls by the ten individuals of each species under the assumption that should there be no preference for any one of the seed types (nul hypothesis), the expected mass of each seed type removed would be one tenth of the total. All four rodent species showed a significant preference for peanuts and sunflower ($p>0{,}01$; $n = 10$).

Saccostomus x^2 (peanuts) $= 473{,}79$; x^2 (sunflower) $= 225{,}25$
Desmodillus x^2 (peanuts) $= 166{,}12$; x^2 (sunflower) $= 181{,}78$
T. brantsii x^2 (peanuts) $= 183{,}82$; x^2 (sunflower) $= 24{,}65$
T. leucogaster x^2 (peanuts) $= 249{,}62$; x^2 (sunflower) $= 398{,}83$
(x^2 values are high due to individual variation)

No significant differences in seed selection were found between the sexes of any species tested, nor were there any correlations between body mass and seed size as found by Brown & Lieberman (1973). All the species appeared, however, to prefer the larger seed types except for millet which is relatively small (Figure 1). Millet was never hoarded. On the strength of these results the animals were tested for hoarding using 50 g of peanuts and 50 g of sunflower seeds in each test.

Saccostomus and *Desmodillus* proved to be true larder-hoarders. *Desmodillus* was seen to scatter-hoard on two occasions. This process consisted of the transport and subsequent caching of seeds in a corner of the experiment cage. In both cases the seeds were later retrieved from the caches and stored in the nestboxes. In all the tests all the available seeds were hoarded except in the case of one *Desmodillus* female and one *Saccostomus* male. Figure 2 shows the number of hoarding trips for each individual *Desmodillus* and *Saccostomus*. *T. brantsii* and *T. leucogaster* were never observed to larder- or scatter-hoard. Occasionally a seed was carried into the nestbox when the animals were disturbed while feeding. These seeds were often half eaten when abandoned in the nesting material, a behavioural trait which might be confused with hoarding.

The hoarding behaviour appeared to be very stereotyped for a specific species. *Desmodil-*

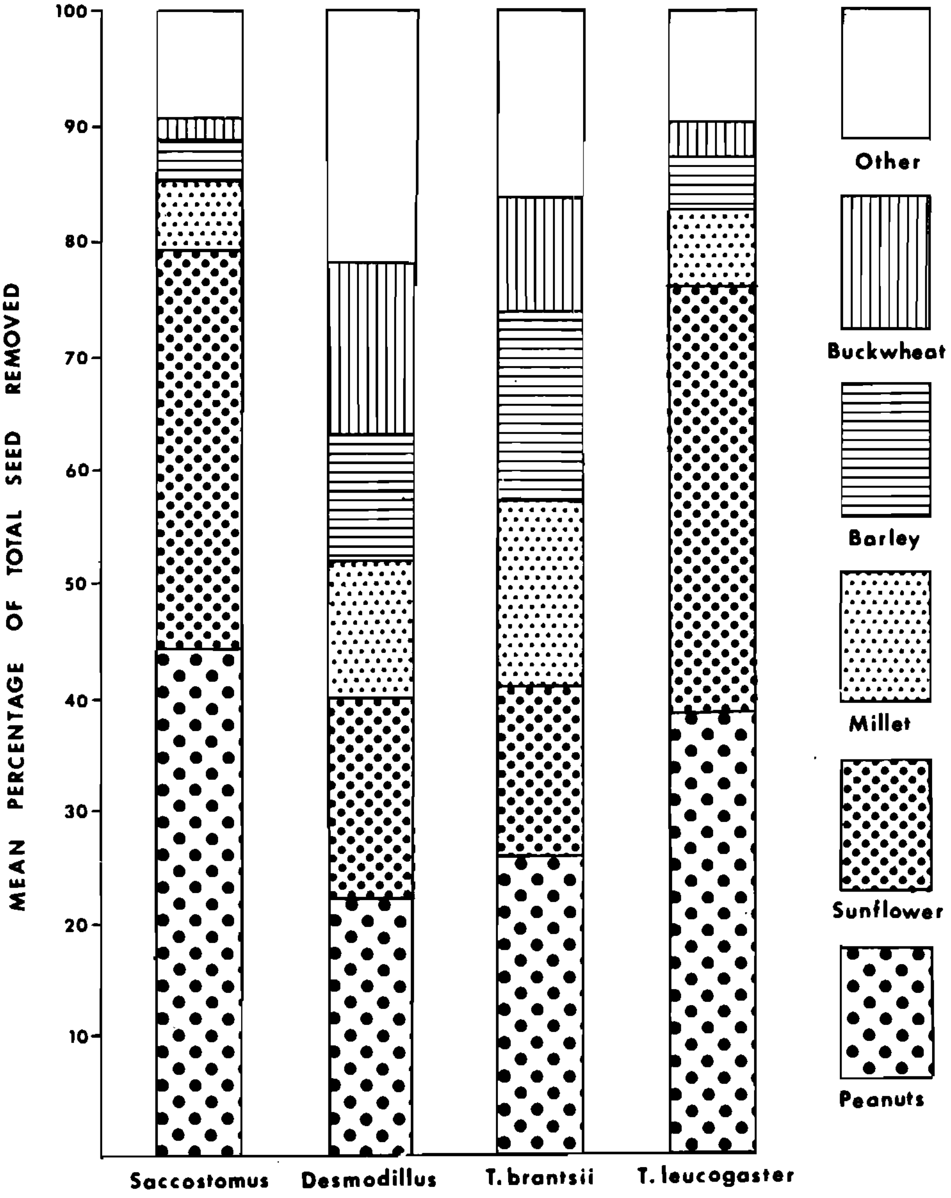

FIGURE 1
Seed preference of four rodent species shown by the mean percentage contribution of each seed type to the total removed, based on 10 individuals of each species.

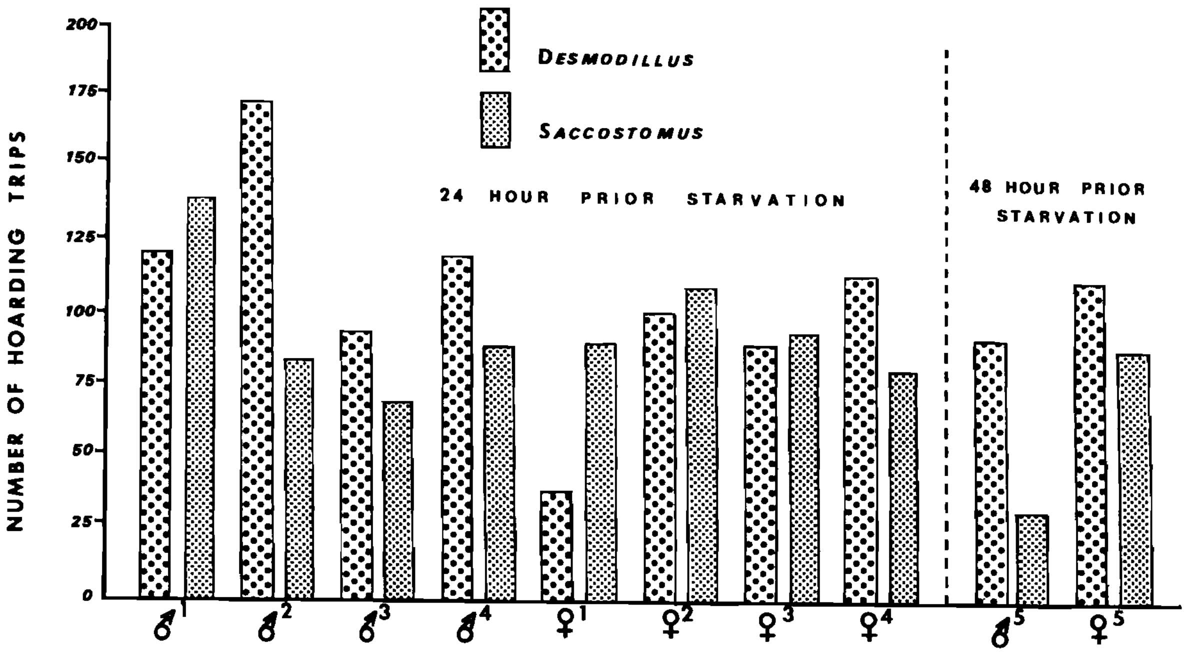

FIGURE 2

The number of hoarding trips undertaken by 10 individuals of two species of rodents.

lus was generally active just before the dark cycle began. In all cases the animals would investigate both piles of seed before commencing to hoard. Initially the hoarding trips followed on each other in very rapid succession, but tended to slow down after the first half-hour of hoarding. Females were not found to hoard faster than males or vice versa.

Hoarding consisted of running to a seed pile, loading up, returning to the nestbox and unloading. The run to the seed pile was usually rapid, with the head slightly lowered. *Desmodillus* would almost invariably use the forefeet to scoop seeds towards the mouth, but would only on occasion actually use them to shovel seeds into the mouth. On the average seven sunflower seeds or five peanuts were loaded at a time, although *Desmodillus* is quite capable of carrying three times this amount, as was occasionally shown. A mixed load of peanuts and sunflower seeds was rare, but sometimes loads were alternated. The return to the nestbox was always fast and normally followed the outward route. A remarkably short period was spent unloading in the nestbox and on the two occasions when *Desmodillus* scatter-hoarded the unloading was clearly observed as simply spitting out the seeds.

Saccostomus is a rather sluggish animal and would not make an appearance until approximately one hour after the onset of the dark cycle. Stretching and short hurried scuttles around the cage normally followed, until the seeds attracted the animal on what appeared to be olfactory grounds. A small number (3-5) of seeds would then be loaded and carried into the nestbox. A period of approximately ten minutes would then be spent within the nestbox, possibly attributed to the animal eating its first load, as *Saccostomus* was not seen to eat outside the nestbox except on one occasion after extensive (48 hour) starvation (Table 1).

Subsequent trips consisted of fairly rapid runs to the seed piles, loading up, hurried return trips and unloading. The first few runs to the seed piles were done in the head-down posture, but the head was progressively raised as the trips continued. Loading up was normally aided with the forefeet which were also often used to push seeds into the cheek pouches by drawing them across the cheeks towards the shoulder. Approximately 6-7 peanuts or 9-10 sunflower seeds were loaded per trip. Mixed loads occurred more frequently than in the case of *Desmodillus*, but were not the rule. The return trips were hurried and along the outward route, but the animals took much longer to reappear for another load than did *Desmodillus*. This is due to *Saccostomus* having to aid unloading with the forefeet. In both *Saccostomus* and *Desmodillus* any disturbance while busy hoarding resulted in an incomplete load being hurriedly transported to the nestbox and a delay of several minutes before hoarding was resumed.

The final sequence to hoarding is the actual storing of seeds once all the seed is inside the nestbox. *Desmodillus* covered the seeds with sand by drawing sand under the belly with the forefeet, then kicking the mound of sand so formed over the seeds with the hind feet. An untidy pile of mixed seed and sand is formed, on top of which the nesting material is placed. *Saccostomus* would shovel all the seeds into a neat pile with the snout and place the nesting material on top. In nearly all cases *T. brantsii* and *T. leucogaster* were observed to kick sand over any seed piles after or during feeding. This was also observed, but to a far lesser degree, in *Desmodillus* and on one occasion in *Saccostomus*. Once again sand was scooped under the belly with the forefeet, then kicked over the seeds with the hind feet with the animal's back to the seeds. In *T. brantsii* and *T. leucogaster* this continued, on most occasions, until all the seeds were completely covered. *T. leucogaster* usually achieved this far faster than *T. brantsii*, hence the higher frequency of this behaviour in *T. brantsii* (Table 1). It is difficult to conclude whether this seed-covering behaviour is a form of hoarding or not, as the animals survived eight days without any additional food, indicating that they must have obtained food from these covered seed piles. Ewer (pers. comm.) believes that this is a primitive form of hoarding, but for comparative purposes we have treated it separately (Table 1). *T. brantsii* and *T. leucogaster* spent most of their active time exploring, digging and scratching in a manner that suggests searching for food, in comparison to *Desmodillus* and *Saccostomus* which spent most of their active time hoarding food.

Animals starved for 48 hours were generally very nervous and inactive. In the case of *Saccostomus* and *Desmodillus* hoarding began later and with *T. brantsii* and *T. leucogaster* seed-covering bouts were considerably less, or absent.

All the species tested blocked off the nestbox entrances with sand. This was achieved by kicking sand over the entrance from the outside in the sand-kicking manner already

TABLE 1

The number of seed-covering, eating and drinking bouts in four rodent species.
(♂^{5} and ♀^{5} pre-starved for 48 hours, all others for 24 hours.)

	Individual											
Species	♂^{1}	♂^{2}	♂^{3}	♂^{4}	♀^{1}	♀^{2}	♀^{3}	♀^{4}	♂^{5}	♀^{5}	$\bar{X}$	
Saccostomus	1	1	0	0	0	0	2	0	0	1	0,5	SEED-COVERING
Desmodillus	0	1	4	0	8	0	3	0	0	2	1,8	
T. brantsii	5	11	20	11	9	30	1	4	6	0	9,7	
T. Leucogaster	0	5	4	5	5	4	16	7	1	0	4,7	
Saccostomus	0	0	0	0	0	0	0	0	3	0	0,3	EATING
Desmodillus	6	3	3	4	32	0	0	1	7	2	5,8	
T. brantsii	35	21	12	10	19	16	9	2	8	8	14,0	
T. leucogaster	5	13	11	9	17	8	10	8	8	5	9,4	
Saccostomus	1	1	1	4	8	2	5	4	2	5	3,3	DRINKING
Desmodillus	1	1	2	0	6	1	0	2	0	1	1,4	
T. brantsii	4	3	3	3	4	8	3	1	2	3	3,4	
T. leucogaster	1	6	7	9	8	1	3	5	2	2	4,4	

described, then creeping through a small opening left and filling the hole up from the inside. *Saccostomus* would invariably aid this by shovelling sand with the snout.

Desmodillus drank water considerably less often than the other species (Table 1). *T. brantsii* and *Saccostomus* had approximately equal water requirements, whereas *T. leucogaster* had a comparatively high water consumption (Table 1).

DISCUSSION

Although the seed-preference results were adequate for the purposes of this study (i.e. which seeds to use for the hoarding experiments), they are by no means conclusive. Better control tests, for example breaking the larger seeds up into a similar size and shape as the smallest seeds, are suggested in order to obtain more valid results.

The two largest seed types, namely peanuts and sunflower, were preferred in all the species. From a hoarding point of view this can be expected as larger seeds have a better 'keeping quality', are easier to transport, as well as having more mass and therefore more calorific content per unit. The *Tatera* spp. always held the food in the forefeet when eating. They probably chose larger seed types as these are easier to handle. According to Smithers (1971) *Desmodillus* would very rarely be attracted to peanuts as bait. This is confirmed by the comparatively low level of peanut retrieval of this animal in the seed preference test (Figure 1).

Lockhard & Lockhard (1971) found that the desert kangaroo rat preferred seeds with a high carbohydrate content to those high in protein. They also state that the dependence of these rodents on metabolic water derived from the oxidation of carbohydrates could suggest preference for seeds high in carbohydrate. From Table 1 it is clear that *Desmodillus* must depend on metabolic water to some degree because of the low frequency of drinking and tthe low water content of the seeds provided. Of interest is the greater preference of all the species for seeds high in lipids, which give off even more metabolic water than carbohydrates during oxidation, and which would therefore be advantageous to desert-living rodents. Even those species (e.g. *Tatera* and *Saccostomus*) showing a higher number of drinking bouts (Table 1) would benefit from selecting seeds high in metabolic water, especially under arid conditions; the high incidence of drinking in *Tatera* probably reflects on its normal food (e.g. bulbs, rhizomes and insects) which has a high water content.

In all cases the data obtained from the hoarding experiments are consistent with the known ecological data on the species tested. According to Smithers (1971) *Desmodillus* is graminivorous, living off seeds of grasses and annuals. Roberts (1951) states that remains of locusts are often found near their burrow entrances, but that the diet consists mainly of seeds and pips of melons. *Desmodillus* occurs in dry areas where seed production is seasonal and erratic. That these animals hoard is thus not surprising, as they are compelled to provide food for periods of low or no seed production; in the wild extensive larder-hoarding occurs (Nel 1967).

Saccostomus wanders far from the burrow to feed, filling the cheek-pouches as it moves.

The diet includes grass seeds, seeds of *Acacia* sp., *Grewia* sp. and *Combretum* sp. (Smithers 1971), although Roberts (1951) reports having occasionally found termites in the cheek pouches. Hoarding would be advantageous to such a forager, and the development of cheek-pouches is clearly to facilitate this mode of living.

Tatera brantsii has a more versatile habitat and diet, living on bulblets, seeds and other vegetable matter (Roberts 1951; Smithers 1971). De Beer (1972) found a high percentage of insect material in the stomach contents. Hoarding is thus not essential for survival.

Tatera leucogaster is very similar to *T. brantsii* in diet and habitat, although it cannot tolerate conditions as dry as those in which *T. brantsii* occurs (Smithers 1971). If we assume that the seed-covering behaviour of these two species is a form of hoarding as suggested by Ewer (pers. comm.) we are faced with two possibilities. It can be considered as the starting point in the evolution of scatter-hoarding behaviour, or it may be regarded as a retrograde step in the evolution of hoarding. Either way, it fits in well with Ewer's (1965) belief that scatter-hoarding evolved separately from larder-hoarding. Miller & Viek's (1944) security hypothesis (supported by Bindra 1948) in which an animal carries food to its home because that is where it feels safest, appears to be sufficient explanation for the origin of larder-hoarding.

One would not expect hunger to be a prerequisite for hoarding in natural hoarders. *Desmodillus* and *Saccostomus* were persistent hoarders even when caged awaiting experimentation. Similar observations were reported by Ewer (1967) in *Cricetomys,* although Lockner (1972) found that hoarding trips in the red-tailed chipmunk were significantly faster after 23 hours of food deprivation than in sated animals. In the present study animals that had been starved for 48 hours became extremely nervous, and hoarding, if it occurred, always started later than in animals that had been starved for only 24 hours. Furthermore, seed-covering behaviour in the *Tatera* spp. either did not occur, or was at a very low frequency. From this study and others (Morris 1962; Ewer 1967; Lockner 1972) it seems clear that hunger is not a prerequisite for hoarding; on the contrary excessive starvation had an inhibiting effect. Morgan *et al.* (1943) showed experimentally that in hungry animals hoarding is in competition with eating. It is reasonable to believe that an excessively starved animal would have to restore its strength before becoming fully active again, which is possibly in this case a reasonable explanation as the animals were extremely inactive throughout the test period.

It is not clear why *Desmodillus,* on the two ocasions that it scatter-hoarded, subsequently retrieved the seeds from these caches and stored them in the nestboxes.

The sand-kicking behaviour involved in seed-covering and blocking off the nestbox entrance is stereotyped in all the species. One can assume that this behaviour evolved early in the phylogenetic history of desert rodents and as it is a highly effective manner of covering up an object, has been effectively selected for.

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