The Dispersal Paradox:

Can lowland granivorous mice also disperse the seeds they devour?

Fig 1: *Tatera afra* wrestling the flesh from a *Chrysanthemoides monilifera* seed.

Ecology Honours Project
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Abstract

The relationship between two rodent species and the Cape Reed (*Willdenowia incurvata)* were examined. Many studies have focussed on the role of rodents as predators of plant seeds. However, it seems that certain rodents may actually perform a crucial role in the dispersal of plants. Experiments to uncover the dispersal mechanism were carried out. Also examined is the role of the appendages present on the Restio seeds, possibly as energy-rich rewards for dispersal for the rodents. It was found that the Restio may be dependent on seed-dispersing rodents, although this mutualism is not so important in fragmented habitats.

Fig 2: The author up to his shoulder in sand, trying to extract seeds from a *Tatera afra* burrow.

Introduction

not only

Scatterhoarding, a mechanism of seed dispersal by rodents, has been seldom recorded in the Cape, and has not been observed in the lowlands where rodent densities are far higher than in the fynbos (Fraser, 1990). Vlok (1995) suggested that nut-like seeds may be dependent upon rodents for dispersal, not threatened by them. As softer seeds such as sunflower seed (pers. obs.) seems to be purely eaten by rodents such as *Aethomys* and *Acomys*, the most likely candidate for rodent dispersal is a tough-seeded plant such as the Restio, *Willdenowia incurvata*. The morphology of the seed makes it unsuitable for ant dispersal due to the lack of elaiosome, and neither is it well adapted for wind dispersal as it does not present any suitable structure.

Scatterhoarding is the burial of seeds in the open (beyond the nest) where seeds have a chance of escaping predation (Vander Wall, 2001). Buried seeds are thus not only potentially safe from predators, but from the scorching heat of veld fires. Scatterhoarding may represent a third form of fire adaptation and dispersal by plants, being the other two: serotiny –or the retention of fruit on the plant in a protective body- of wind dispersed seeds; and myrmecochory – ant dispersal, both being well documented (Bond & Breytenbach, 1985). Larderhoarding is the burial of seeds below ground within the nest of the rodent. Although relied upon for the survival of many vertebrate granivores, larderhoarding is typically fatal to the seed (Vander Wall, 2001).

The threatened Cape Gerbil (*Tatera afra)* is an endemic rodent from the South-Western Cape strandveld biome (Le Roux *et al.*, 1992). Remarkably little literature exists on the character of this rodent, despite being a potential candidate for scatterhoarding. As mentioned above, scatterhoarding has seldom been recorded in the Cape (Vlok, 1995; Midgley, 2002) and never in the lowlands. *Tatera brandtii,* a closely related species, have been shown to display an intermediate form of hoarding where sand is piled over a cluster of seeds (Pettifer & Nel, 1977). *T. afra* and *T. brandtii* have the same number of and so...

chromosomes and very similar communication patterns (Dempster, 1996). Dempster (1996) questioned whether they were possibly the same species. Based on this similarity, we investigated whether the hoarding behaviour of *Tatera afra* is similar to that of *T. brandtii*. *Tatera afra* and *Gerbirullus paeba* (the hairy-footed Paeba), another co-occuring murid, are tested for scatterhoarding, both in the field and under controlled laboratory conditions.

Scatterhoarding is a greatly beneficial survival strategy ~~as~~ for... it has evolved independently in many different lineages of rodents in vastly disparate areas (Brown *et al.*,1979). In Australia some large fruited tree species are scatterhoarded by musky rat kangaroos (Stocker & Irvine, 1983; in Theimer, 2003). White tailed rats scatterhoard hard-coated seeds, returning later to uncover the seeds and chew through the seed coat, to obtain the nutritious cotyledons within. Theimer (1997) found that all seeds recovered subsequent to caching, were eaten by the rodents. Larger seeds did not prove better at surviving than smaller seeds, nor were they preferred to intermediate seeds. Larger seeds were shown to be dispersed a greater distance in Tree Squirrels, Red Acouchis and Agoutis (Theimer, 2003). Vlok (1995) questioned whether scatterhoarding could effectively safeguard seeds from other rodents. He found that 28 of 30 seeds of *Phylica plumosa* remained uneaten after a night in the same cage as *Acomys subspinosus*. However, many other soft coated seeds were devoured during the night, seemingly in preference to *Phylica plumosa*.

Around 1300 (20%) fynbos plant species are myrmecochorous (Bond & Slingsby, 1983) with appendages (elaiosomes) that attract ants. The west coast region of the South-Western Cape is dominated by strandveld vegetation, of which the Restio, *Willdenowia incurvata* is a major component. From a total of 311 Restios, a family endemic to Cape Floral Kingdom, 43 have seeds with elaiosomes. Because ants take the seeds underground, these are protected form ifre and predators, especially rodents (Bond & Breytenbach, 1985). Once into the ant nest, the ants consume the elaiosome, but leave the intact seed below ground

(Cowling *et al.,* 1987). The majority of Restio species have no elaiosomes, but instead are thought to fall to the ground and be passively dispersed by wind and water (Linder, 2000). Although some Restio seeds are transported by ants, *Willdenowia incurvata is* potentially too big for any ant that occurs in the environ. Midgley *et al.* (2002) thus proposed that the seeds are dispersed by rodents by scatterhoarding, as demonstrated for the Cape Spiny Mouse, *Acomys subspinosus* (Midgley, 2002a).

Willdenowia incurvata is a hard seed without an elaiosome, but with an appendage at the apical end. This appendage is variously known as an apical cap, ornamentation or stylopodium (Linder, 2000). No account has been given for the purpose of this ornamentation (Linder, pers. comm.), but observations suggest that it may be used in either attracting rodents, or providing a nutrient rich treat in exchange for dispersal of the seed. The purpose of the stylopodium was investigated in the laboratory.

Fleming & Nicholson (2002) found that the Cape Spiny Mouse (*Acomys subspinosus*) is an opportunistic species that makes use of nectar from *Protea humiflora* flowers as an seasonal resource. When flowering is in its maximum, reproduction peaks in *A. subspinosus.* Mast seeding of *W. incurvata* may perform an analogous role as *Protea humiflora* in inducing breeding, due to higher availability of food. Mast-seeding is the synchronous production of large seed crops by a population, with long periods of low seed production between fruiting. The predator satiation hypothesis suggests that satiation of consumers occurs due to a rapid and simultaneous dropping of fruit. *Willdenowia incurvata* fulfils all the criteria of mast-seeding. Opportunistic breeding is confirmed for *Acomys subspinosus* by Midgley (2002a). Many of the rodents were found to be pregnant during main seed-fall (late October). These cases demonstrate that not only are mammals timing their reproduction with opportunities provided by plants (flowering and seeding), but that they are sometimes reliant on them for high levels of reproduction. The plants benefit from the rodents by pollination in the case of *Protea humiflora*, and scatterhoarding in the case of *Acomys subspinosus.* These are therefore examples of mutualisms between rodents and plants of the Cape. The case of the present study, *Wildenowia* and scatterhoarding murids, could be a third example of this kind.

The advantages of being dispersed by nut-caching animals are multitudinous. In a summer drought environment like the strandveld, seeds left in the sun are highly susceptible to dessication, with a subsequent loss of viability (Vander Wall, 2001). In the strandveld, light forms of energy-rich rewards such as elaiosomes are plentiful, but water is scarce. Fruit pulp, a reward typically sough after by birds, is a water-expensive product and liable to rapid dessication (Vander Wall, 2001). Although occasional long-distance dispersal is possible through bird dispersal, seeds are often released in low quality sites such as within bushes, or subject to harsh seedling competition under a perch (Vander Wall, 2001).

Wind dispersal has weight constraints and hence little shielding from predation can be placed on a seed. Large wind dispersed seeds can also not be produced, and hence competing in a summer-drought or shady environment is more difficult. Wind dispersal also leads to undirected, low quality dispersal, with many of the seeds ending up clustered in depressions or alongside obstacles (Vander Wall, 2001).

Ant-dispersal is typically extremely short-ranged (<10m) (Cowling *et al.,* 1987). Ants store a high concentration of seeds in underground caches that would thus be subject to severe competition. Underground larders are typically between two and seven cm deep (Cowling *et al.*, 1992) and thus may be deeper than the level through which smaller seeds can germinate (Bond *et al.*, 1999). These seeds are also constrained by weight, as ants cannot haul a massive load. High concentrations of seeds are subject to greater levels of predation by invertebrate predators, as demonstrated by Wilson and Janzen (1972) for a tropical nut. This concentration of seed may be found where seeds are dropped in large numbers under parent plants, and remain undispersed.

Dispersal by scatterhoarding animals is often deliberately spaced out, minimising competition between seedlings (Vander Wall, 2001). Seeds are often deposited singly or in groups of two or three, a tolerable group size. Shallowly buried nuts also experience lower desiccation and predation levels than seeds on the surface, and are in an ideal position for germination and subsequent growth being approximately 2cm below the soil surface. Lastly, nuts have a hard protective coat, that allows them to survive for much longer periods than soft seeded fruit. This makes them ideal candidates for long term seed storage.

Questions and Hypotheses

The following questions were proposed :

1) What rodents occur in the lowlands and how is their diversity affected by landscape transformation?
2) How is *Willdenowia incurvata* dispersed?
3) If *W. incurvata* is dispersed by rodents, is there evidence of scatterhoarding?
4) Is there a relationship between *W. incurvata* abundance and *Tatera afra*?

Materials and Methods

Koeberg Nature Reserve (33^0 54’ S, 18° 21’ W) was chosen as the initial study site as it contained cleared land with a sharp transition to pristine strandveld. This strandveld contains a significant number of *W. incurvata*, with thicket species (*Rhus tomentosum, Putterlickia pyracantha, Euclea tomentosa,* and *Chrysanthemoides monilifera*) making up the majority of the species. This vegetation provides major cover (>80%) for diurnal rodents. The cleared land is a site used as a military parade ground (Craig Hilton pers. comm.). Later, the tar layer was destroyed and the parade ground converted to a sandy grazing pasture for re-introduced Eland (*Taurotragus oryx),* Zebra (*Equus burchellii*) and introduced springbok (*Antidorcus marsupialis).* Vegetation cover is sparse with annual grasses making up the majority of the groundcover with several weedy species (e.g. *Sisymbrium spp.* and *Conyza bonariensis*) making up the rest. This habitat is therefore unsuitable for diurnal rodents, but is severely disturbed by the action of *T. afra*.

Observation of intense tunnelling in the open area, lead to the hypothesis that *T. afra* was inhabiting the open area, but feeding in the pristine strandveld where seed production is higher. Our primary method of testing the dispersal of seeds was to attach dacron strings (flyfishing backing string) with superglue to the seed coat of *W. incurvata*. These strings were adapted to various lengths depending on the usage although 15, 30 and 60 cm lengths were used to establish the dispersal of the seeds, with 1m, 2m and 3m strings used to locate the removed cache. These longer strings were found to be necessary, as many of the strings were taken by the rodents without being found.

laid

To determine where *T. afra* is living and feeding, we lay out 15 piles of ten seeds, each pile spaced 10m apart (Fig 3). The first row was placed in the open/cleared land, the second along the edge of the open and pristine strandveld, and the remaining three rows increasingly deeper into the vegetation. This second row was placed as a control for cover, seeds being dropped from the bushes on the edge, yet little cover being available for the rodents.

This first experiment yielded no trends regarding seed removal and distance into the strandveld, however, several seeds were taken and not relocated. The following experiment was therefore set up to obtain statistical significance for the removal of seeds, and to establish the feeding range of *Tatera afra.* Using the same standard grid pattern, we laid out 25 piles of 10 seeds with marked strings attached.

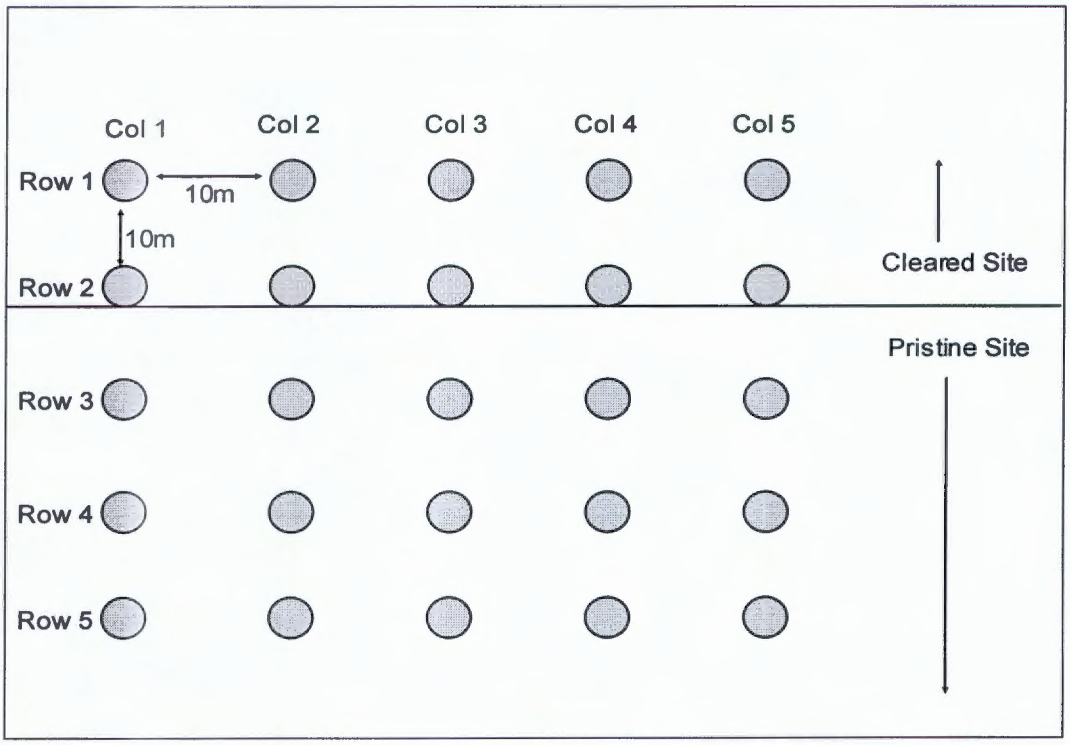

Fig 3: Layout of the grid pattern used in the seed-grid experiments. The arrows on the right highlight the gradients from cleared to pristine, with the solid horizontal line representing the transition zone. Piles on the transition line receive seeds, but little cover.

As few seeds were removed in the field, a question arose as to the fertility of seeds. Restio seeds were found to be infertile until days before dropping (Newton *et al.*, 2000), and rodents have been observed to have a preference for fertile seeds (B. Anderson pers. comm.). Seeds were classified using a float test. In 98% of the cases, the colour of the seed-coat alone could be used to distinguish between fertile seeds (dark brown) or infertile (light brown) (X^2 : df = 199, $p < 0.0001$). Seeds used in the previous experiment were subsequently found to be unripe (milky inside) despite being hard. We therefore replaced infertile seeds in the field experiments, with ripe seeds that were over a year old and chalky inside.

Due to a low level of seed removal attained thus far, and to establish what rodents were present in the site, Sherman traps were used. Trapping took place over six days in late August. Fifty traps, baited with a mixture of peanut butter and oats, were placed at 10 metre intervals in a 50 X 100m grid pattern. To look at the effects of food availability we included an alien infested site with a dominance of Port Jackson (*Acacia saligna)* and Rooikranz (*Acacia Cyclops)*. Although this site is located outside the entrance to Koeberg Nature Reserve, it has similar sands and conditions to the pristine site. Other vegetation in this site was almost entirely absent, due to the allelopathic and competitive nature of these *Acacia* species. To establish the effects of canopy cover and active seedfall on rodents, half of the traps were placed in a recently cleared plot of land adjacent to the alien infested site. This transformed site contained a number of old branches of *Acacia* trees, with numerous indigenous and exotic pioneers occupying the gaps.

Rodents were weighed and hair-clipped, a patch of hair being removed from their hind quarters as a capture-mark. Finally the subjects were released near the point of capture. The status of traps was also noted, traps being recorded as open or closed. The presence/absence of the food inside was also noted. Finally other factors influencing trapping success were also noted such as incorrectly tuned or damaged traps, and the presence of ants. Traps that were strongly exposed to the sun were covered with cardboard which was secured with elastic bands. This was done to minimize the chance of rodent mortality due to excessive heat.

Observations that released rodents typically disappeared down a nearby hole almost immediately subsequent to release, prompted investigation as to hole choice and range size. A long string (3m) was tied to the tail of several *T. afra*, with observations of their hole choice and distance to hole recorded. Where possible, holes were excavated to determine presence, type and status of the seeds underground.

Based upon trapping success and the successful location of active nests, further piles of 10 seeds were placed to determine the fate of seeds. Piles were placed within 2m of active entrances (entrances showing recent digging or footprints and supported by trapping data). Five piles were placed in the *Acacia* dominated plot, and a further five in the open site. The pristine site was ignored in this study due to lack of consistent trapping success of *T. afra*, and due to not having found any active *T. afra* burrows. Piles consisted of eight seeds with 30cm long strings attached. Two extra seeds with extra long strings were included (1m and 3m lengths) to ensure the caches could be found in case of larder hoarding.

The following morning burrows surrounding removed seeds were excavated with a hand shovel. The sand above the tunnel was carefully removed. In this manner, the direction of the tunnel, interleading tunnels, and introduced material at the base of the tunnel could be noted. Both the depth of the seeds in the tunnel, and the distance they were carried in from the entrance were also recorded. Scrapings from the bottom of the tunnels were placed in a 400 micron square mesh sieve, and the number and type of retained seeds recorded.

Fig 4: An excavation of a *Tatera* nest. The entrance is on the right, and strings brought into the hole by the rodent are 30cm long. The tunnel flattens out at about 40cm deep.

As scatterhoarding was not observed, it was decided to try larger cache sizes in an attempt to induce this behaviour. Cache sizes of 50 seeds with strings were placed near active holes. Six of these piles were placed in the open sites (as none of the previous seeds were taken from the alien site), with two 1m strings and one 3m string added. The remaining strings were all 15cm lengths, as scatterhoarding was expected. The piles were checked four days later to ensure that rodents had an opportunity to find the seeds.

A second study site was selected in Rondevlei Nature Reserve. However, *Willdenowia incurvata* does not occur in the reserve (D. Gibbs, pers. comm), but that *Willdenowia teres* does. *W. teres* has an elaiosome on the base of the seed, which is on the opposite side to the stylopodium of *W. incurvata.* This elaiosome was removed by the rodents far more readily than the stylopodium of

Willdenowia incurvata. It was also found that *W. teres* seeds were milky inside, explaining the lack of action experienced thus far by our Rondevlei based colleagues. We thus placed five piles of 50 seed at active sites. These were carefully chosen as having freshly overturned soil leading to the hole.

Lab experiments were also performed on *Tatera afra* (Rondevlei) and *Gerbillurus paeba* to determine the fate of *Willdenowia incurvata* seeds. 50 seeds were placed individually on the soil surface with a minimum spacing of 5 mm. This spacing was done to encourage individual burial of the seeds, such that rodents could choose the seeds to remove. The following day the nest was sieved with the 400 micron sieve. All the seeds were collected from the rest of the detritus. As terminology is tricky regarding the removal of seeds (i.e. removal, taking, eating, etc.), a list of definitions for terms used in the remainder of the paper are provided below. The nest was divided into 3 "compartments" to examine the distribution of the seeds.

1) 'the seed side' - the side where the seeds were placed. This represents the seeds that were eaten or buried in situ;
2) 'the nest' - the nest and its contents – this figure represents the seeds that are larder hoarded;
3) 'the far side' - Seeds carried away from where they were placed. This represents the seeds that were moved before being buried.

The collected seeds of *Willdenowia incurvata* were placed within their compartments into four categories:

1) 'entire' - normal seeds placed in the tank that have remained unmolested;
2) 'intact' - seeds apparently untouched, having both the stylopodium and the base intact;
3) 'trimmed' – seeds with the stylopodium hand-removed before placing in the cage;
4) 'nibbled' - entire seeds, but with the stylopodium removed by the rodents;

5) 'eaten' - seeds that have been eaten by the rodents. Seeds are typically bitten in half, so both the base half and the stylopodium half are recorded separately.

All the entire seeds (with or without the stylopodium or base removed) remaining after a night in the tank were tested for fertility using a float test. This was to determine whether seeds left uneaten were done so because they were infertile (Newton *et al.*, 2000).

In total, 11 field and laboratory experiments were done to test seed recovery, predation and the ease with which buried seeds are discovered. Four independent tests were done to establish stylopodium preference.

Restionaceae nut volumes were determined using the dimensions of nuts (height and width) given in the Restio database (Linder, 2000). The formula used, $V = (4 Pi/3)abc$, is the universal formula for a spheroid, where a is the height, and b & c the width given for the seed. Ornamentation characters were also taken from the database and seeds were coded as either: a) bearing an elaiosome; b) having conspicuous ornamentation (an appendage); or c) having both ornamentation and elaiosome. Seeds were then ranked in ascending order of size, and a scatter -plot produced using Microsoft Excel (Figure 10).

Results

Due to the large number of experiments done and the complexity caused by providing the methods and results separately, a summary of the methods was included to put the results in perspective.

Experiment 1: Do rodents live in the open veld, but feed in the pristine strandveld?

Following a gradient form the pristine vegetation to the open, 25 piles of 10 seeds were placed. Number of seeds removed is shown in Table 1. Number of seeds removed were seeds that mice took form the initial seed pile. Seeds removed, being the string left behind, were included in this number.

Pile	No. seeds placed	No. seeds removed	No. strings in nest
1	11	11	11
2	11	11	11
3	11	10	9
4	11	11	1
5	11	11	1
6	11	11	4*
7	11	11	3*
8-25	**11**	**0**	**0**
	* denotes found at a later stage outside nest		

Table 1: Results of string experiments. Only one pile (pile 5) was found removed from the pristine site. Bold numbers represent piles not taken.

The number of strings in the nest reflects the actual amount that was found, either hanging out of the nest, or through excavation (Table 2). The (*) in table 1 accounts for two piles of seeds that went missing and the seeds were not found. Two weeks later these strings were found just outside the entrance to the hole.

Excavation number	String number	Distance	String number	Distance	String number	Distance	String number	Distance
1	3	60	2	80	2	100	4	105
2	1	60						
3	1	-150	1	-50	2	-10	2	40
4	1	40						

Table 2: Summary of excavations in which strings were found. It documents the location of strings in relation to the entrance of the hole (in centimeters). A negative figure refers to the distance the string was located outside the hole. These strings had the seed removed. A positive figure is the distance the string was founded inside the hole. With the exception of the immediate entrance, most tunnels run about 40cm below the soil surface. Thus any seeds located in the nest would be found at approximately this depth.

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Experiment 2: What rodents occur in the area and how are they distributed in relation to the vegetation?

Three trapping plots were done to examine the relationship of vegetation to murids. Sherman traps were placed 10m apart in a 100 X 50m grid in the open, the pristine veld and in an invasive *Acacia* dominated veld.

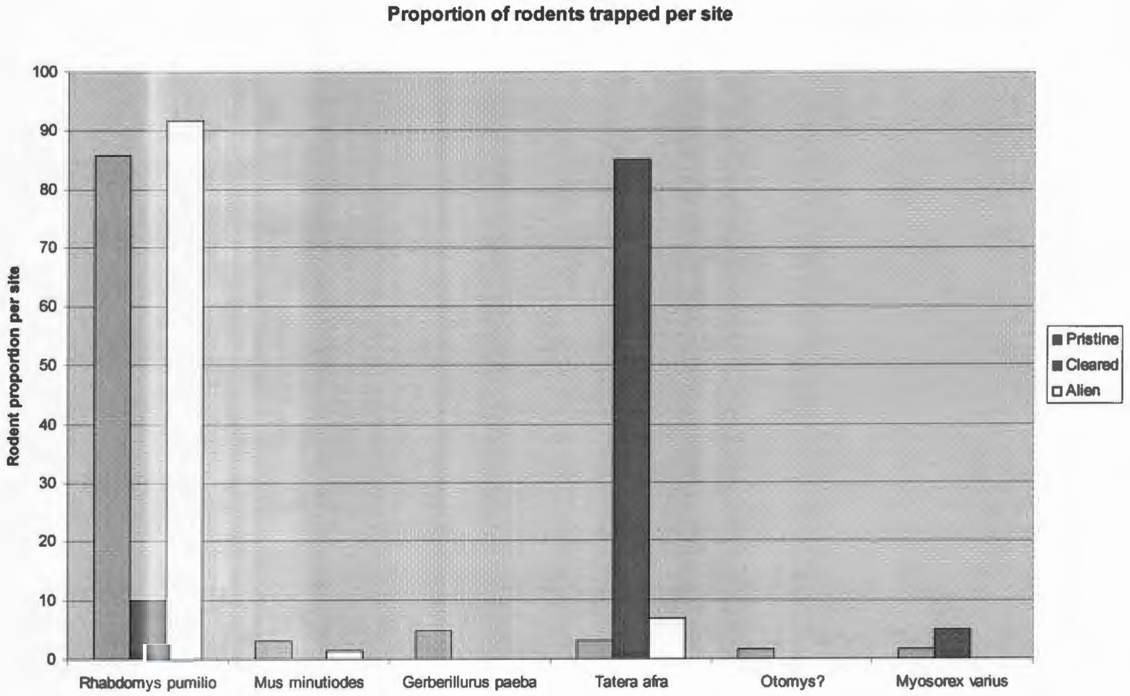

Figure 5: Rodents trapped as a proportion of each site. *Rhabdomys* makes up more than 85% of the rodents trapped at pristine and alien sites (where cover is abundant), but *Tatera* dominates in the cleared land.

Fig 6 shows that the most abundant rodent, both during the day and night, was Rhabdomys pumilio. All other rodents in the strandveld are diurnal, with Tatera afra being the second most frequently trapped nocturnal rodent (Figure 6).

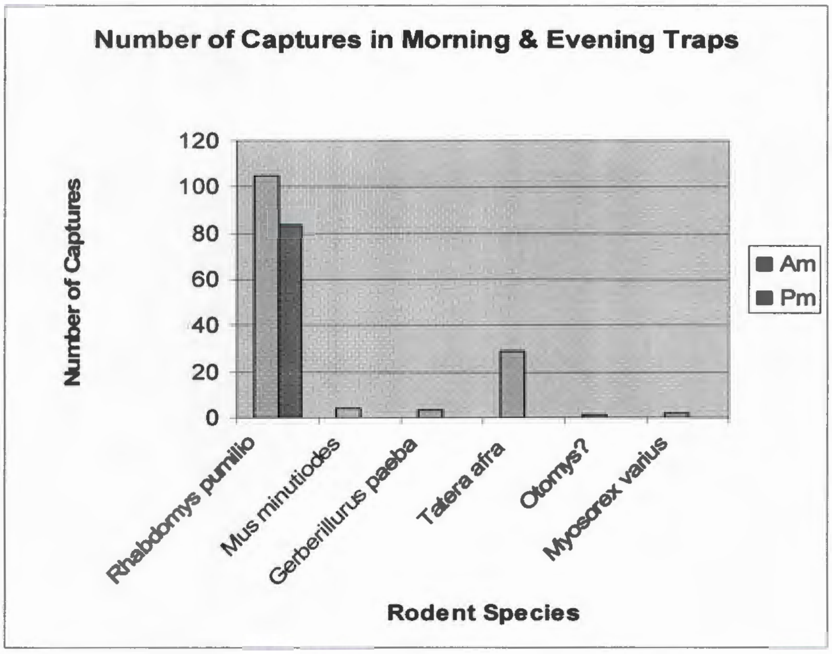

Figure 6: Species of rodents captured in relation with the time of the day.

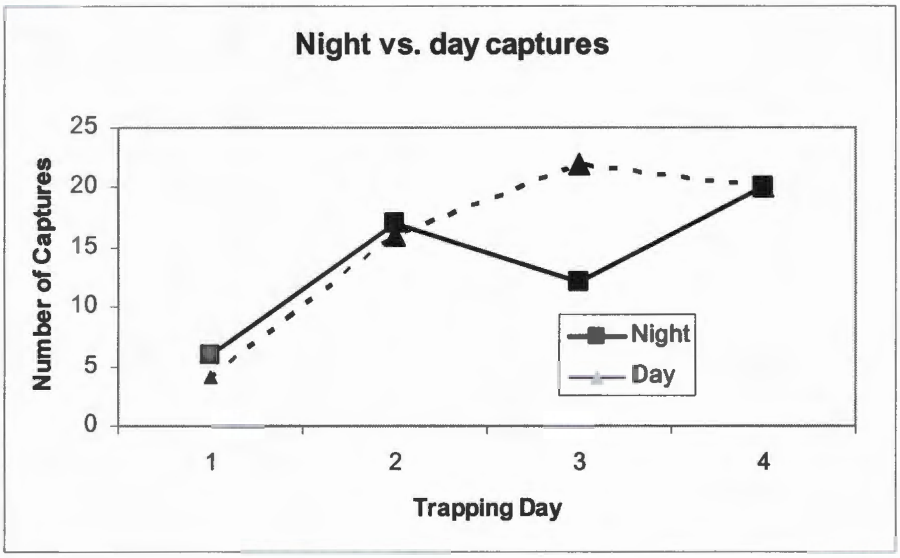

Figure 7: Number of captures of *Rhabdomys pumilio* per day and night. There was no significant difference found.

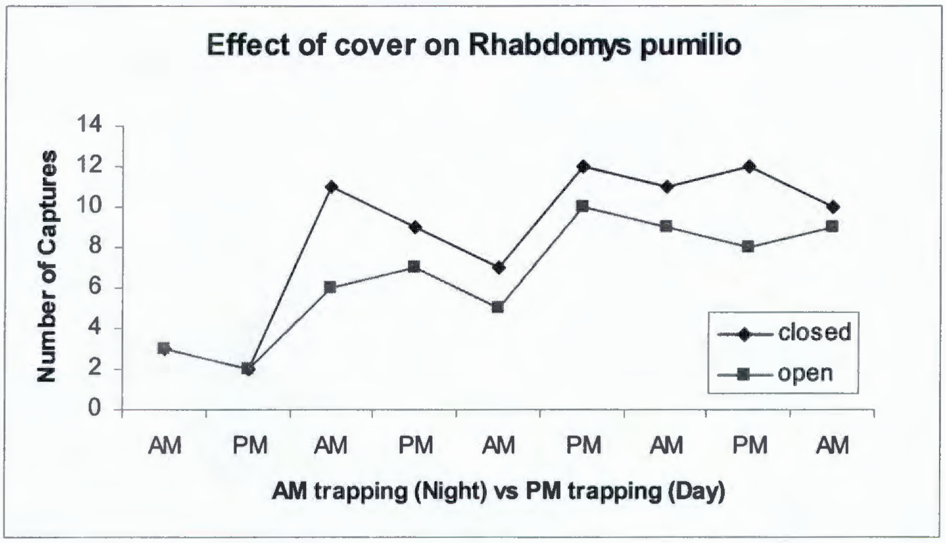

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Figure 8: Significantly more rodents were caught in the closed than the open site.

Figure 5 provides numbers of rodents captured at each site. *Rhabdomys pumilio* was again the dominant species at both the pristine and the alien site. It was more than twice as abundant in the alien site as the pristine site. *R. pumilio* was 13 times as abundant as *Tatera afra* in the alien site. This dominance is reflected in the pristine site as well. All other rodents were of minor consequence in all of the sites.

Although the greatest abundance of rodents was found in the alien site, the pristine site had the greatest diversity of rodents. The alien site and the cleared site both had three species of rodents captured per site.

Experiment 3: What does *Tatera* do with seeds that fall near their nests?

Targeted placement of 10 seeds (10 piles) outside active rodent holes was done, followed by excavation of the nests where seeds were taken to. Six piles of 10 seeds were placed in the alien-dominated site. None were taken. The experiment was repeated in the open site with a further 10 piles of 10 seeds being placed.

This resulted in a total of three piles being removed, with a total of 28 seeds taken.

Seven nests were excavated in Koeberg as far as they could be followed. Most of vegetation matter recovered was grass and roots. One of the nests was excavated till just after the sleeping chamber. It consisted of a bed of grass lining an enlarged room under the ground. Similar nests were constructed by *Tatera* in the laboratory terrarium, with plant material being integrated into the nest.. Sifting resulted in a total of four seeds being found in these nests, being one of them an unknown seed, possibly *Chrysanthemoides monilifera*. This fruit was later found to be a favourite of the rodents in a terrarium cafeteria experiment.

Experiment 4: How does *Tatera* behave when presented an overwhelming quantity of seeds?

To simulate mast seeding of the Restios, targeted placing of 50 seeds (6 piles) was done outside *Tatera* nests in Koeberg Nature Reserve. None of the seeds were removed.

Experiment 5: How does *Tatera* deal with large piles of seed at Rondevlei?

Seeds in five piles of 50 were placed near the entrance to *Tatera* burrows at Rondevlei Nature Reserve. All 250 seeds were recovered from the piles, with only one pile showing any disturbance. Seven seeds from this pile had been covered up with sand to around 1 cm depth, as described by Pettifer & Nel (1977). Many of the seeds had become separated from the strings in the process, implying active burial. It was observed that many of the holes near the seeds were active. Stems of the grass *Lemma* had been ejected from the holes, being the seeds removed from the stalk. Some Daisies were also found in the entrance of the holes.

Experiment 6: What is the Fate of *W. incurvata* seeds in a tank with *Gerbillurus*?

Captive *G. paeba* individuals were presented with a pile of 55 intact seeds of *W. incurvata* to determine whether the species was among its food preferences. The seeds were retrieved the following day. Of the 55 entire seeds placed in the tank, 27 were recovered intact or nibbled, and 51 halves were found. Of these 27 entire seeds, 23 seeds had the stylopodium nibbled, and only four were left intact. All of the stylopodiums had been eaten from the halves, and seven of the bases were still intact from the entire seeds.

Experiment 7: Are stylopodia a meal in themselves? Or are they only an attractant attached to seeds?

Stylopodia trimmings (50) were placed in a tray in the *Gerbillurus* nest, to test for their attractive value. The stylopodia were found to be untouched after a night's activity.

Experiment 8: Is there any significant preference for seeds with a stylopodium, or seeds with the stylopodium trimmed off?

A cafeteria experiment was performed for seeds with stylopodia present vs. seeds with the stylopodia trimmed off. Two dishes were placed in a tank with *Tatera afra*, one containing 25 seeds of *W. incurvata* with stylopodia, another tray with 25 trimmed seeds. A third tray was included to test whether *Chrysanthemoides monilifera* seeds are preferred to *W. incurvata*. A few hours after placing the seeds, 7 *C. monilifera* seeds were eaten. The next morning none of the *C. monilifera* seeds were remaining. None of the *W. incurvata* seeds were eaten, although the seeds with stylopodia were found scattered across the sand.

by Tatera?

Experiment 9: How good is Tatera at locating buried seeds?

Piles of 5 seeds each, with or without stylopodia, were buried in 10 alternative piles. All of the seeds were excavated from their 2cm deep piles beneath the sand. Three ridges of sand along the glass at fixed intervals demonstrated that the seed had actively been targeted and dug out. Exactly 38 of the 50 strings were recovered from the surface of the terrarium. Eight strings were buried on the far side, and four on the seed side. This suggests that either the seeds were buried far away from where they were obtained, suggesting scatterhoarding, or the seeds were inadvertently buried while *T. afra* was foraging. Six of the 25 entire seeds, had the stylopodia remaining by the morning. All six were on the seed side of the cage. This suggests that the majority of seeds were dealt with and that there was not merely chance burial of seeds. Two seeds in total were eaten out of 50.

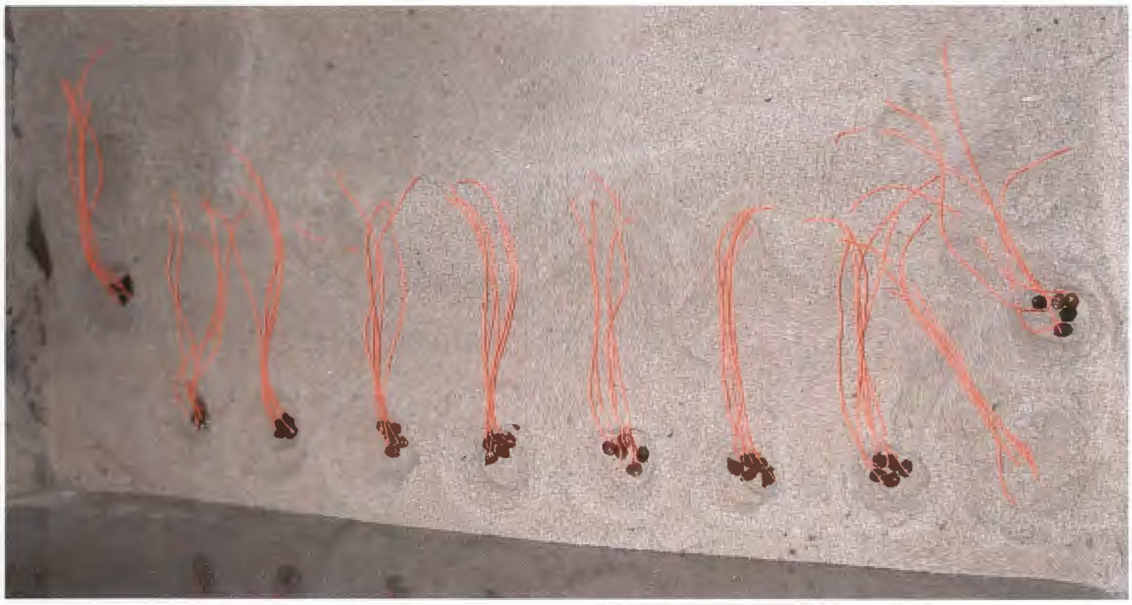

Figure 9: *Willdenowia incurvata* seeds laid out in 2cm deep holes. The holes alternate with entire seeds and seeds with the elaiosomes trimmed off.

Experiment 10: How good is *Tatera* at locating buried seeds, and are seeds more easily found if the stylopodia is attached (does it perform an attractive function)?

In this experiment seeds were randomly placed on the ground within two piles with a small gap (c. 5mm) between the seeds so that seeds with and without stylopodia could be differentiated. Within hours of placing the seeds, these were counted. Five seeds with the stylopodia intact were remaining. Thirteen trimmed seeds were still in the piles. The next morning, a total of 7 seeds remained intact, none of them being still in their piles. Of these, four of the seeds were on the far side, and three on the seed side. In the nest no whole seeds were found, although 50 seed halves were found in it. A further 16 halves were found in the seed half which would suggest that *Tatera* eats a proportion of the seeds out in the open.

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Experiment 11: Does *Gerbillurus* preferentially harvest seeds with a stylopodium or without? What does it do with the stylopodium?

Trimmed and entire seeds were marked separately, 50 of each being alternately placed in a grid fashion in the tank. I employed direct observation to identify *Gerbillurus* feeding preferences.

It proved too difficult for me to identify entire from trimmed seeds in the dim light in which the *Gerbillurus* operates. Harvesting action was not simple, but often characterised by the rodent passing over several seeds, and then selecting two or three that it would take back to the nest. If an entire seed was located, the rodent would often remove the stylopodium, and then grab several other seeds before collecting the nibbled seed. This further complicates matters as in effect the entire seed becomes the equivalent of a trimmed seed. Of the 100 seeds placed (50 trimmed, 50 entire), 17 entire, and 15 nibbled or trimmed seeds remained. 32 halves in total were collected from the sand, with the remaining halves being found in the nest. In this saturation experiment, 68 seeds were eaten by two *Gerbillurus* individuals within one night.

why how

Seed size relationships in Restios

Seed size relationships were analysed for the whole group. If elaisomes are structures produced for ant attraction and stylopodia for rodents, it is expected that there should be some selective pressure on seed size. Seeds which had an elaisome, appendage or both had their volume plotted. It was expected that elaisome bearing nuts would be the smallest, and appendage bearing nuts (rodent dispersed) the biggest nuts. The graph (Fig 10) however shows the reverse, with nuts containing both, appendage and elaisome, in the middle.

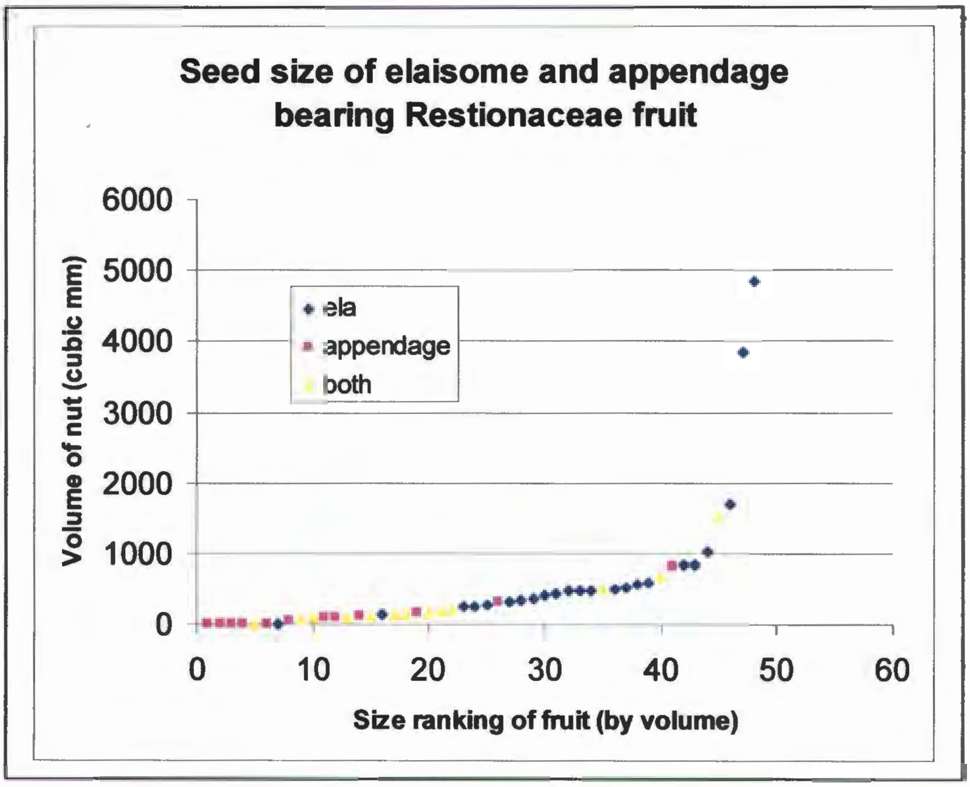

Figure 10: Comparison of volumes of Restio seeds bearing elaiosomes, appendages and both. A trend is clearly discernable, elaiosome bearing seeds being the biggest, seeds with appendages the smallest, and seeds with both appearing in the middle.

Discussion

Hoarding

Hoarding is considered an essential behaviour for survival for those animals dependent upon seasonal food (Pettifer & Nel, 1977), as demonstrated in the excavations of a nest of *Tatera afra* in the pristine strandveld, revealing in excess of 150 seeds (>300 seed halves).

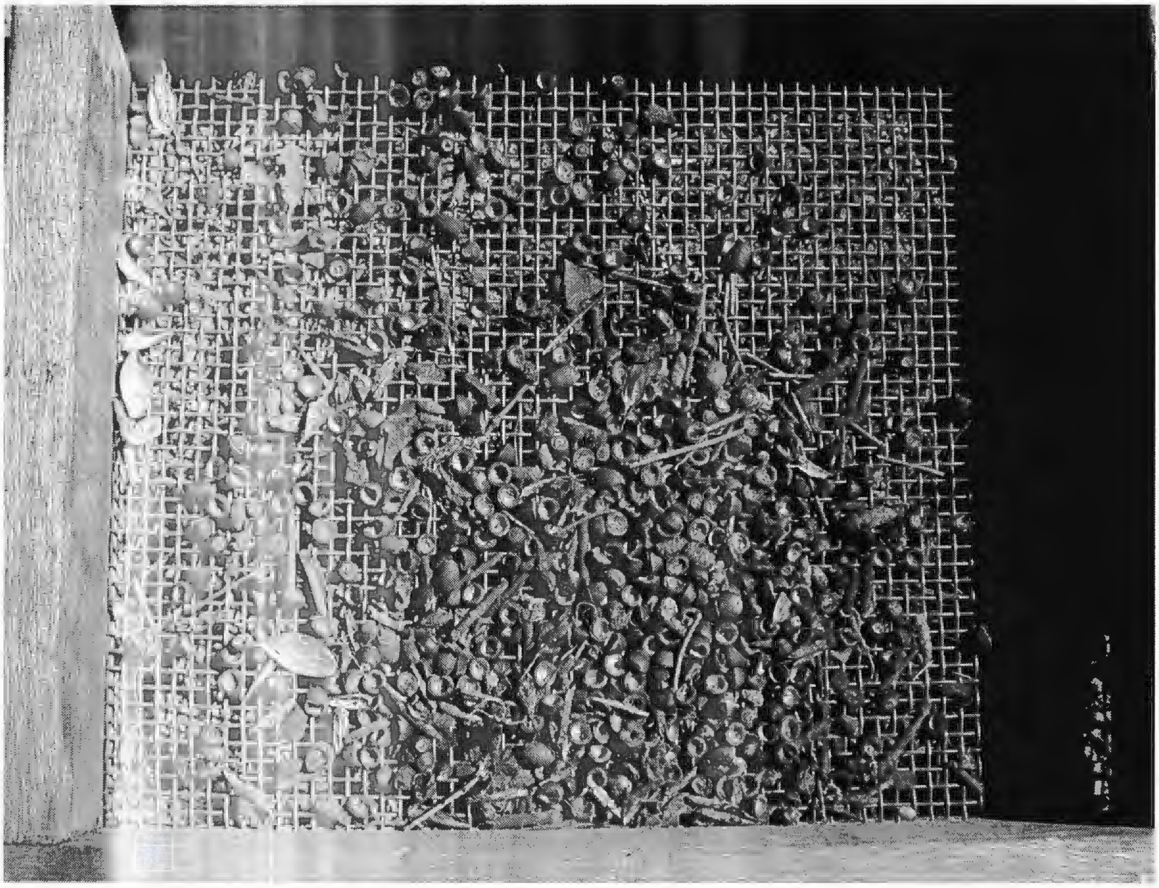

Figure 11: A meal for two? A single nest in the pristine strandveld was located, and around 300 *Wildenowia incurvata* seeds counted. The majority of these seeds were found just beyond the entrance to the nest. Seven seeds are still entire, of which all were hollow. This shows that the rodents can distinguish hollow from fertile seeds.

poor legend

The majority of these seeds were located at the entrance to the nest , which demonstrates that they are eaten in the nest, the unwanted remnants being ejected from it. This suggests larderhoarding, although it does not rule out scatterhoarding as a primary form of storage. At Rondevlei, fresh remains of grass and daisies were found at the entrance to the hole. These were undoubtedly collected during that night, although the material is of the wrong consistency for larderhoarding. Pettifer & Nel (1977) report that in a cage, *Tatera brantsii* & *Tatera leucogaster* never scatter or larderhoard. This was confirmed for *Tatera afra* by personal observations.

Although scatterhoarding by *Tatera afra* has been ruled out for *W. incurvata* seeds at this time of the year, the possibility still exists that at other times of year scatterhoarding may be a standard behaviour for seed storage. *W. incurvata* seems to retain its seeds on the plant and drop them all at once, covering thus two functions: protection from predators; and saturation of seed consumers, causing then scatterhoarding behaviour.

It has demonstrated that even at 15cm depth (Bond & Breytenbach, 1985), most seeds are found within several days. At 2cm depth, all the seeds in the burial experiment were uncovered by *T. afra* within one night. Thus the long-term benefits that *W. incurvata* derive from scatterhoarding are questionable.

In cages, seeds were typically haphazardly buried around the cage through a general process of sand excavation. In the open however, when seeds are removed from a pile, they are typically all taken. Exceptions to this are seeds with long strings (2m or greater) that get caught up in the vegetation.

In the open, when a pile was found, the seeds would be taken. This did not occur in the cages however. This would support the larder hoarding hypothesis, as Pettifer & Nel (1977) found that larder hoarding rodents would load up several nuts before running back to the nest. *T. leucogaster* and *T. brantsii* also did a form of scatterhoarding which involved covering the seeds with soil. This soil-seed mix was raided later to retrieve the seeds. This form of scatterhoarding was not done by *T. afra*, as no piles of buried seeds were found. However, several shallow holes were found in the sand at Koeberg which may have been temporary repositories for seeds before being transferred to the nest. Miller & Viek's (1944) safety hypothesis (in Pettifer & Nel, 1977) seems to fit well with the fate of the seeds. why This hypothesis states that an animal carries food to its home as this is where it feels least threatened. This explains the lack of intact seeds remaining in the nest, as *T. afra* eats all the seeds where it feels safest.

The role of the Stylopodium

relevance?

Pettifer & Nel (1977) found that starvation caused increased agitation in rodents. Rodents moved and retrieved seeds quicker when starved for 48 hours compared with starvation for 24 hours. Hoarding always occurred later in the subjects that had been starved. An excessively starved animal would first fulfil its short term energy requirements (feeding) before satisfying its long term energy requirements (hoarding) (Pettifer & Nel, 1977). Thus it was thought that the function of the stylopodia in *W. incurvata* is to provide short-term energy to the rodents, while trying to collect as many seeds as possible, storing them next to the nest to be eaten in a later stage. In this case there is still an option of the mice not finding the seeds in a later stage, and a chance for the seed to remain intact. However, a seed without a stylopodium would have to be eaten before any energy is gained from the seed. This would not provide quick energy to the ? rodents (they apply several minutes to open the hard outer cover of the seed) and would lead to the death of the seed, with no chance of the seed being spared.

Multiple experiments were undertaken in an attempt to understand the role of the stylopodium for both *W. incurvata* and the rodents *Gerbillurus paeba*, and *Tatera afra*. Nearly 100% of seed halves were found with the stylopodium removed. This suggested (as stated above) that stylopodia are eaten as part of the entire meal. However, most of the whole seeds found in the nest also had the stylopodia removed. This suggested that the stylopodium is eaten prior to storage.

However, observations have shown for *Gerbillurus paeba* that the stylopodium is removed (and not eaten) from the seed shortly before carrying the seed to the nest.. This supports the finding that none of the stylopodia were eaten from the Petri-dish containing stylopodia only. Thus the stylopodium can be excluded as a device for providing the rodents with a snack prior to seed dispersal. No such observations could be carried out with *T. afra,* as it refrains from feeding activity when an observer is present.

The probability thus exists that the stylopodium emits scent and therefore exists as an attractant to rodents. From the terrarium experiments, it can be concluded that there is a preference for seeds that contain the stylopodium, as 21 seeds have the stylopodium remaining vs. 59 with the stylopodium removed (Table 3).

Total seeds taken from ALL Experiments		
Gerbillurus	Stylopodia present	Stylopodia removed
Expt 6	4	23
Expt 9	0	14
	0	3
Expt 11	0	4
	17	15
Total	21	59

Table 3: demonstrates that the stylopodium provides an attractive function under terrarium conditions (Chi-Square = 36.962, $p < 0.0001$, df = 4). Overnight experiments proved of little use in differentiating between seeds with and without elaiosomes, as nearly all of the seeds were eaten.

occur on

Figure 10 demonstrates that elaiosomes are amongst the biggest seeds. This is contrary to expectations that ant dispersed seeds should be small. Seeds with both appendage and elaiosome are in between, and seeds with appendage only are the smallest. A possible reason for this result is that seeds can possibly be buried fairly deep in an ant nest. The bigger a seed is the more chance it has of survival. As many of the seeds that are rodent dispersed are going to be eaten, there is a trade-off between size and wastage of energy and resources through predation.

Predation

Figure 12:This photo illustrates the three stages of ***Willdenowia teres*** after being fed to *T. afra* at Rondevlei Nature Reserve. On the left is seeds with the elaiosome intact, in the middle are nibbled seeds with the elaiosome removed, on the right are the seeds cracked open with the endosperm eaten. Many of the seeds were recovered from beneath the soil surface. Tatera afra clearly makes use of *W. teres,* but does not appear to consume teres as readily as *G. paeba* consumes *W. incurvata.*

Both Gerbillurus and *T. afra* have been shown to be voracious granivores, a pair of *Gerbillurus paeba* capable of consuming around 80 seeds a night (experiment 11). Considering the apparent dependence on Restios, the Restio cover does not seem to considerably alter rodent numbers (Figure 8). This is supported by Bond *et al.* (1980) who consider floristic descriptions "the least useful (factor) in describing or locating rodent habitat". In this study no relationship could be demonstrated between Restio cover and rodent presence.

(1992) hypothesized that the likelihood of a nut being cached by a rodent is influenced by the time taken for the granivore to open the nut. She found that hazelnuts required 30% more time to eat than to cache. As a result, hazelnuts with the husk removed were more likely to be eaten, whereas those with the husk intact were more likely to be cached. Smith & Follmer (1972) found that seed preferences varied with the seasons. In autumn, hard-shelled nuts were preferred, but in winter soft shelled seeds become the primary food source. This may explain the preference of *T. afra* for other seeds such as the fleshy fruited *Chrysanthemoides monilifera* and soft-husked sunflower seeds over the harder coated *W. incurvata*. .

Of particular interest in the potential mutualism between *W. incurvata* and *T. afra* is that scatter hoarding animals often transport nuts from late-successional, closed-canopy forests, to early-successional habitats such as fallow fields (and old parade grounds). Two reasons for this have been suggested by Stapanian and Smith (1986). Firstly, animals can reduce pilfering of caches by moving them out from the more competitive forest, where many nut eating animals live and forange for nuts. This is exemplified by our study site at Koeberg where levels of rodents were found to be 3 times lower in the cleared site than in the adjacent pristine plot. Daytime foraging was found to be 22 times higher in the pristine veld than the open plot. Secondly, Stapanian and Smith (1986) found that hoarding rodents are more likely to move nuts out of their original environment if they were of greater value to the rodent. This is presumably to move them from an area where foraging is likely to be intense. *W. incurvata* nuts, possibly being the most valuable nuts in the area, are likely to get dispersed far from the parent plant into the open habitat according to this hypothesis. From this it can be anticipated that *W. incurvata* would be ideally suited to colonising the cleared patch. Despite much time spent in the environment examining plants, no seedlings were sighted. Several possibilities may explain this pattern. *W. incurvata* seeds are possibly not being scatterhoarded to the cleared patch. Potentially all the seeds are being found and eaten by *T. afra* before they germinate. Finally the seeds may not be ideal for colonizing as they require fire to stimulate them. No fire has been through the area lately.

W. incurvata exemplifies mast seeding. Not only does it hold onto its seeds for most of the year, but these seeds remain infertile until a few days before release. This seed release takes place in only a two week period in November (Linder, 2000). This strategy of rapid seed drop is considered an attempt at predator satiation. As rodents can find seed at depths exceeding burial (Bond & Breytenbach, 1985), it is suggested that fire is a crucial component of the conundrum. Support for the drastic effect of fire on small mammal numbers comes from Tierkop (Midgley & Clayton, 1990) and Swartberg (Bond *et al.*, 1980), where trapping numbers dropped from 10% (pre-fire) to less than 1% success subsequent to the fires. Further support for a decrease in rodent numbers is provided by Breytenbach (1987).

Burial may also play an important role in the success of the seeds, if they are to survive the fire and grow. Timing is thus crucial in ensuring the survival of plants in this habitat, and if no fire arises it is crucial that *W. incurvata* survives till the next year. If the fire comes too late the seeds will all have been excavated and eaten. If the fire comes too early, the seeds will not have ripened and reliance will be placed on a non-existant seed store. The respouting strategy of the plant may be a necessary means to hedge bets in an environment saturated with rodents. If it cannot grow by seeds, then resprouting is the next best survival strategy.

What came first, stylopodia or elaiosome, ants or rodents? It is wasteful to produce seeds with elaiosome and stylopodia, if both are energy rich. Restios would not benefit from having their ant-dispersed seed being taken by rodents, as ants are extremely efficient. However in the west coast, ants are scarce, and do not disperse seeds underground well. It is therefore preferential to be dispersed by rodents in this system as they cover the seeds more effectively. Why are there both syndromes then? Perhaps one is related to an ancestor and it has yet to lose that trait. Linder (2001) found elaiosomes to be paraphyletic in the genus *Ceratocaryum*. Linder found the absence of an elaiosome on the large and conspicuous nuts of *Ceratocaryum pulchrum*, *C. argenteum* and *C. fistulosum* to be unusual within the Restionaceae. This supports our analysis that elaiosome bearing nuts are larger than those without this appendage. No explanations for seed size or dispersal of the none-elaiosome bearing nuts was given in the paper.

Conservation

Where habitats are piecemeal and natural vegetation reduced to islands, rodent numbers may overwhelm seed set. In the case of seed release of serotinous plants subsequent to a fire, neither birds nor small-mammals may occur in high enough densities to consume all the serotinous seeds (Breytenbach, 1987). Serotiny & myrmechochory in fynbos could be adaptive responses to high seed-predation pressures. Fragmented habitats in the fynbos and West coast are less subject to fires. Thus if a combination of scatterhoarding and fire is needed to ensure survival of *W. incurvata*, fragmentation will lead to a slow decline in the number of *W. incurvata* plants. Similarly, fires that occur at the wrong time of the year for *W. incurvata* will either destroy the non-fertile seeds on the plant, or will come too late such that all scatterhoarded seeds have been unearthed and eaten by rodents. Further studies should be conducted in order to clarify the mutualism between *W. incurvata* and scatterhoarding rodents. Focus should also be on the viability of *W. incurvata* in reduced plot sizes.

too vague

Conclusion

Tatera afra and *Gerbillurus paeba* both use *W. incurvata* nuts as a source of food. Although both rodents may have the potential for scatterhoarding, this study found that larderhoarding is more common at this time of year (spring).

Larderhoarding, and the subsequent eating of the seeds, are fatal to seeds and thus these rodents have a purely predatory role during the time of the project.

Seeds with the stylopodium intact were taken significantly more often than those with the stylopodium trimmed off. As these stylopodia are discarded upon discovery, it is suggested that they fulfil an attractive role rather than an energetic role. This finding, if confirmed more conclusively, could radically change our perspective on rodents as merely incidental dispersors. The implications for conservation are that we cannot ignore the role of rodents as friends or foes of the Restios, but must manage them as an integral part of the system. Numbers of rodents in the lowland system have been found to be far in excess from that of the fynbos system, and more emphasis should thus be placed on the role they may have had in shaping the dynamics of the vegetation we see today.

Endnote

As the project is too narrow to encompass all related topics, here are further questions, thoughts and comments by the author regarding rodents and Restios.

Q : The colour of seeds : Why do brown seeds turn a darker brown when mature?

A : Infertile seeds were found to be of a significantly lighter brown than their infertile counterparts. Bruce Anderson (pers. comm.) found that dark seeds deposited into a post-fire environment were better camouflaged and thus less predated than lighter seeds by birds, but there was no difference in rodents. The possibility thus exists that this darker colouring is an adaptation to reduce predation on the ground by unwanted predators. Rodents on the other hand live in an environment governed by smell. If rodents are the main predators, there should be no difference in colour between fertile and infertile seeds. In an environment where fertile seeds are correctly camouflaged, infertile seeds would act as a cheaper decoy than the nutrient rich seeds.

Q : *Is W. incurvata too big for ants to carry? Could the appendage not also be for ant dispersal?*

A : Figure 10 shows that W. incurvata falls in the midrange of elaiosome, and hence ant dispersed seeds. These seeds are thus not too big for ants. However despite weeks of being on the ground, no seeds were removed by ants. There is ? therefore no evidence that producing an appendage is to break free of the constraints of ant dispersal in favour of rodent dispersal.

Q :*Why are seeds elongated and not round. Could elongated seeds be to ensure a crop is harvested.*

A : vander Wall, (2002) stated that a portion of the seeds must go to feeding the animal if the dispersal mutualism is to be successful. Furthermore, the more difficult the seed is to open, the more likely it is to be scatterhoarded. Within these constraints lies the seeds dispersed by rodents. With *Gerbillurus paeba,* all of the seeds were cracked open almost precisely in half, co-inciding with the flattest portion of the elongated seed. A round seed would be far more difficult to find the "sweet spot" in which to open the seed. A *W. incurvata* plant providing round seeds would not be dispersed and would thus be selected against.

Q: *If Acacia is a substitute food for Willdenowia, then is there a significant increase in weight in the Acacia site?*

A : No significant difference could be determined between *T. afra* and *R. pumilio* between the alien, pristine and cleared sites. The rodents are potentially thus all satiated or are below carrying capacity. Numbers increase under the *Acacia* veld and so food per rodent is the same. That the *Tatera afra* in the open are the same weight suggests they are relying on the food from the pristine veld.

by you?

Q: Why are nests buried so deep?

A: It is suggested that nests have to be around 40cm deep to prevent the nest from collapsing if a herbivore walks on top. This makes the nest too deep for seeds to germinate.

Q: Why are seeds elongated and not rounded, surely round seeds are stronger and this better protect seeds for a given thickness of protection? ?

A: Maintenance of elongated seed shape to make rodents eat them. A round inedible seed would be left behind as it is not worth taking when there is an oversaturation of food. This is the same case for seed size, where the bigger the seed the greater the nutrient value. There is therefore a trend towards a medium sized seed. Large seeds would also do best in a system that is dark or nutrient poor, as it is better able to compete. There is a case of sacrifice for the greater cause. ? As a Restio you produce a mass of seeds. Rodents come to this bush rather than another bush as the seeds are edible. After a while they are full, but these are still the best seeds. The seeds are then buried with the stylopodium eaten as a reward. This is to cover the cost of the removal such that more seeds than necessary are not eaten.

A paper by Caddick and Linder (2002) examines the effects of ecological components on diaspore (nut) size. They discuss the trade-offs between fecundity and seedling survivorship. Carrick and Linder (2002) found that larger nuts can grow faster and larger in the first few months and are therefore better able to survive summer drought. As *Willdenowia incurvata* primarily grows on tertiary sands, the effects of summer drought would be accentuated due to the rapid drainage of water in this substrate. This thus may explain the size of *Willdenowia incurvata*.

Caddick & Linder (2002) cite fire as a major factor influencing seed size. While many of the Restionaceae survive fires through resprouting, the obligate reseeders rely on seeds germinating and growing in winter and spring for their continued existence. It is crucial that the seedlings roots grow deep enough to tap into moist soil during the arid summer months. The trade off in seed size is through many small seeds that stand a better chance of at least a few finding a favourable habitat, and producing larger seeds that are better able to survive difficult environmental conditions. This theory suggests a bimodal distribution with either large seeded or small seeded nuts occurring, but few inbetween. Figure 8 appears to contradict this as there is a continuum of nut sizes, the majority being small tending towards several big species.

Two major clades exist in the Restionaceae – the *Restio* clade, and the *Willdenowia* clade. In the *Willdenowia* clade a unilocular nut is present with a lignified ovary wall, with three exceptions important to this study. *Nevillea* develops from a two-locular ovary, and the genera Anthochortus and Hydrophilus which both have small and soft walled.

In the Restio clade, diaspores are seeds or soft-walled nutlets. *Askidiosperma, Chondroptealum, Restio, Dovea, Platycaulos* and *Rhodocoma* all have dehiscent, tricarpellary ovaries.

relevance

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References

Bond W.J., Ferguson M. & Forsyth G. 1980. Small mammals and habitat structure along altitudinal gradients in the Southern Cape mountains. *South African Journal of Zoology* **15**(1): 98-117.

Bond W.J. & Breytenbach G.J. 1985. Ants, rodents and seed predation in Proteaceae. *South African Journal of Zoology* **20**(3): 35-52.

Bond W.J., & Slingsby, P. 1983. Seed dispersal by ants in shrublands of the Cape Province and its evolutionary implications. South African Journal of Science **79**: 231-233

Bond, W.J., Honig, M. & Maze, K.E. 1999. *Seed size and seedling emergence: an allometric relationship and some ecological implications.* Oecologia. **120**: 132-136.

Botha S.A. 1989. Effect of sowing season and granivory on the establishment of the Clanwilliam cedar. *South African Journal of Scientific Research* **19**(3): 126-148.

Breytenbach G.J. 1987. *Small mammal dynamics in relation to fire*. In: Disturbance and the dynamics of fynbos biome communities. (Eds) Cowling,

Brown, J.H., Reichman, O.J. and Davidson D.W. 1979. Granivory in desert ecosystems. *Annual Review of Ecology and Systematics* **10**:201-227.

Caddick L.R. & Linder H.P. 2002. *Evolutionary strategies for reproduction and dispersal in African Restionaceae. Austrian Journal of Botany* **50**: 339-355.

Cowling, R.M., Le Maitre, D.C., McKenzie, B.M., Prys-Jones, R.P. & van Wilgen, B.W. 1987. *South African National Science Programme Report* 135.

Dempster, E. 1996. Are *Tatera afra* and *T. brandtii* reproductively isolated? *African Small Mammals Newsletter* **16**: 56-60.

Fleming P. A. & Nicholsan S.W. 2002. Opportunistic breeding in the Cape spiny mouse *(Acomys subspinosus). African Zoology* **37**(1):101-105.

Fraser M.W. 1990. Small mammals, birds and ants as seed predators in post-fire mountain fynbos. *South African Journal of Scientific Research* **20**(2): 188-198.

Grodzinki, W. & Sawicka-Kapusta, K. 1970. Energy value of tree seeds eaten by small mammals. *Oikos* **21**:52-58.

Jacobs, L.F. 1992. The effect of handling time on the decision to cache by grey squirrels. *Animal Behaviour* **41**:103-110.

Janzen, D. 1986. Seeds as products. *Oikos* **46**:1-2.

Le Roux, A. Rosch, H. Theron, H. & Cillers, C. 2002. SKEP sub-regional report draft. http://www.dlist.org/docs/SKEP_HTR_subregional_report.doc

Linder, H.P. 2000. *The* African Restionaceae. *Contrib. Bolus. Herb.* **20**:

Linder, H.P. 2001. Two new species of Ceratocaryum (Restionaceae). *Kew Bulletin* **56**: 465-477.

Midgley J. C. 2002. *Mutualistic seed dispersal by the cape spiny mouse (Acomys Subspinosus).* Botany Honours Thesis. University of Cape Town.

Midgley J.J. 2002a. More fynbos mouse stories. *Veld & Flora*. June 2002.

Midgley J.J. & Clayton P. 1990. Short-term effects of an autumn fire on small mammal populations in Southern Cape Coastal Mountain Fynbos. *Suid-Afrikaanse Bosboutydskrif* **153**: 123-136.

Newton, R.J., Bond, W.J. & Farrant, J.M. 2000. *An investigation into seed germination cues for Cape Restionaceae.* Poster at University of Cape Town.

Pettifer H.L. & Nel J. A.J 1977. Hoarding in four Southern African Rodent Species. *Zoologica Africana* **12**(2): 409-418.

Smith, C.C. & Follmer, D. 1972. Food preferences of squirrels. *Ecology* **53**: 82-91.

Stapanian, M. A. & Smith, C.C. 1978. A model for seed scatterhoarding: Coevolution of fox squirrels and black walnuts. *Ecology* **59**: 884-896.

Theimer, T.C. 2003. Intraspecific variation in seed size affects scatterhoarding behaviour of an Australian tropical rain-forest rodent. *Journal of Tropical Ecology* **19**: 95-98.

Vander Wall, S.B. 2002. Masting in animal-dispersed pines facilitates seed dispersal. *Ecology* **83**(12): 3508-3516

Vlok J. 1995. Fynbos and rodents. *Veld & Flora* **72**(4): 105-107.

Wilson, D.E. & D.H. Janzen. 1972. Predation on Scheelea paltm seeds by bruchid beetles : Seed density and distance from parent palm. *Ecology* **53**:954-959.