

Chapter 3

Ecology

Abstract

The highveld mole-rat occurs in a region of seasonal precipitation. Burrow extension and active foraging for new food resources (bulbs) can therefore only occur in summer when the soil moisture content is high enough. In this resource limited environment, these subterranean rodents would be expected to be energy maximizers and preferences should be evident relating to bulb size and patch density. It was expected that preferences would be in favour of bulbs that gave the most reward per unit handling time. Feeding trials investigated which bulb sizes were handled most efficiently in terms of animal size and sex. These bulbs were then expected to be preferred during foraging trials which gave animals choices between patch densities, bulb sizes and combinations thereof. Animal sex did not affect handling time while animal mass did. Larger animals spent a greater proportion of time handling bulbs. As bulb size increased from 1-2g to >2g, the proportion of time spent handling bulbs decreased. This can be translated into an increased proportion of time spent actually consuming the bulbs (acquiring energy). Less costs (handling time = no energy gain) mean greater profits (energy acquisition). However, although these bulbs were expected to be preferred during foraging trials, empty patches were generally preferred. Thus, individuals can not be strictly classified as short-term energy maximizers. In the long-term however, the further exploration of empty patches may lead to energy maximization as further resources could be discovered once patches containing bulbs have been found.

Introduction

A large branch of animal behaviour concerns the study of how animals, whether they are herbivores or carnivores, generalists or specialists, forage for their energy and nutrient requirements in the wild and how (if at all) animals optimise their search for food resources in terms of the benefits of feeding. These benefits include energy gain, nutrient gain and, in some cases, water gain and are evaluated relative to the cost of locating the food (energy expenditure, time and predation risk). The process of locating a food resource that will give maximum benefits to the animal at the least expenditure is termed optimal foraging. Optimal Foraging Theory is an important field of behavioural ecology. There are several definitions used by ecologists to describe optimal foraging theory most pertaining to the maximization of the rate of energy gain and energy acquisition and how natural selection shapes foraging behaviour in this way (Barnett 1991, Nevo 1979, Vleck 1981, Kaufman & Collier 1981). Several predictions have been made regarding Optimal Foraging Theory including predictions with regard to optimal diet, optimal foraging space, optimal foraging period and optimal foraging group size (Nevo 1979). As this study deals only with the diet of the animals, the other predictions will be ignored. Optimal Foraging Theory relating to diet predicts that an animal should never specialise on lower-ranked food regardless of abundance while when the food is in higher abundance increased specialisation should be found (Nevo 1979). In other words, when there are fewer resources available, animals should generalise. When food abundance is low, food generalists are favoured (Nevo 1979) as they can make use of a more diverse range of food. Food generalism in subterranean mammals is primarily related to low net energy harvestable (Nevo 1979).

In the subterranean environment the energetic costs of finding food are very high as soil is a dense and cohesive medium (Vleck 1979). Although bathyergids have a lower resting metabolic rate than that of other rodents their digging metabolic rate may be five times higher than their resting metabolic rate (Spinks *et al.* 1999). The energetic cost of burrowing is proportional to the mass of soil removed and therefore to burrow diameter

(Spinks *et al.* 1999). This places an evolutionary limit on animal size. It has also been found that soil moisture content plays a major role in determining when bathyergids extend their burrow system in search of new food resources as they dig with their extra-buccal incisors which, although growing continuously, are worn down faster than their replacement rate (Jarvis & Bennett 1990).

Studies on the bathyergids suggest that resting metabolic rate scales independent of body mass (Lovegrove & Wissel, 1988) that is unlike any other rodent group. Other subterranean rodents tend to forage above ground and it is thought that the metabolic rate of African mole-rats has been selected for in response to a high energy cost and low probability of finding widely distributed food resources by random burrowing (Lovegrove & Painting 1987). Geophytes are the primary food resource of these subterranean rodents. Geophytes typically have a clumped and patchy distribution due to their predominantly asexual mode of reproduction (Barnett 1991). In the subterranean environment foraging is blind and animals are unable to distinguish distance, direction or quality of an unexploited food patch (Barnett 1991 and Jarvis *et al.* 1998).

Because of the high energetic cost of excavation, it would be advantageous to select food of high nutrient quality since this would increase foraging efficiency (Bennett & Jarvis 1995). Geophytes have concentrated nutrients and low fibre (especially after handling which removes the outer husk) and are essential in maintaining a positive water balance (Bennett & Jarvis 1995) in animals that do not drink any free water.

There are several ways in which foraging in the subterranean environment can be optimised. Where food is heterogeneously distributed (patchy), animals optimise foraging by concentrating their search in the most favourable resource patches (in other words, if all else is constant, the animals will concentrate their efforts in the patch with the highest density of resources) (Barnett 1991). Central place foraging assumes that foragers optimise energy delivery to the central place (store) (Barnett 1991). The Orians-Pearson Model of Central Place Foraging has four main assumptions (Hegner 1982). The animal can search simultaneously for prey of many types or energy values, prey is encountered



randomly in a Poisson manner (this means that the expected time to encounter a specific item is independent of length of time foraging in the area), prey handling time is trivial and the animal is attempting to maximise the rate at which energy is delivered to the central place. These assumptions are generally thought to hold for social bathyergids except for the assumption regarding handling time. Determining whether handling times are indeed trivial was investigated in the present study as handling time is thought to be expensive. If a choice for the animal exists, it would be more efficient to pursue a food item that would require less handling time, if handling time is not trivial. Orians-Pearson predict that there would be an increase in load size (and therefore foraging time) for an animal using a patch of a given quality at an increased distance from the central place. This infers that optimal exploitation of a patch is dependent upon the distance between the patch and the central place (Hegner 1982). When the density of food is increased (a patch is encountered), foragers can change their food search from being blind to being directed (Barnett 1991). This is often evident in bathyergids when a sudden branching of the tunnel system is observed. Thus, foraging efficiency can be optimised with food and soil conditions (Barnett 1991). The optimal diet model predicts that selectivity should decrease as search costs increase (Barnett 1991), thus no longer choosing diets that give a maximum energy yield per unit foraging time in these conditions. Animals should choose large bulbs over smaller bulbs as, for equivalent foraging times, larger bulbs are a greater source of energy (Barnett 1991). These last few ways of optimising efficiency are based on an animal's ability to judge a food resource item accurately (Kaufman & Collier 1981).

However, it is unlikely that true optimal foraging is found in nature as evolution results from a series of compromises (Smith & Sweatman 1974). Also, intraspecific variation (Gustafsson 1988) could be high in an environment where a series of decisions regarding the selection of a food item must be made. It must be kept in mind that optimal foraging theory describes typical individuals (Gustafsson 1988). In natural populations, feeding behaviour can differ between animals of different sex and age (Gustafsson 1988) and other factors such as size. There are three main sources of individual variation. Firstly in a patchy environment with different patches, different behaviours could be applicable to

each patch. Secondly, there can be phenotypic differences (including individually acquired skills) that affect the most appropriate behaviour for each individual to use. Finally, if individuals have identical phenotypes, behaviour can depend on the presence of other individuals. Individual differences are probably not mutually exclusive (Gustafsson 1988) especially in a closed, social environment.

In this study, optimal foraging was studied into two ways. Firstly, the response of animals to different sized geophytes (quantified as components of total consumption time) as well as how individual variation (sex and size) played a role in determining the components of total consumption time. It was predicted that larger animals, especially males, would feed on larger bulbs as well as being more efficient at handling the bulbs presented to them. Secondly, patch preference was investigated with patch density and bulb size being varied independently. It was predicted that patches containing the highest density of bulbs would be favoured and that large bulbs would be selected over smaller bulbs. This was investigated in terms of patch visitation as well as excavation distance.

Methods and Materials

Feeding

Three colonies containing a total of 23 individuals of variable body mass were used in the feeding trials. On the day of a feeding trial, animals were housed in separate chambers and deprived of all food for a period of at least six hours. Feeding trials were conducted at approximately the same time of day at which the animals were normally fed. Although it was not possible to standardize motivational states completely (as it was not known when each animal ate last), it was possible, by depriving the animals of food for six hours prior to each study, to state that none of the animals had eaten for at least six hours prior to each study.

A feeding trial consisted of presenting an individual with a naturally occurring geophyte (*Onithogalum secundum*), of a certain size class (mass). Once the individual had accepted the geophyte, two parameters were recorded; handling time (the time taken to handle and/or prepare the geophyte for consumption; excluding mastication) and total consumption time which is the total time taken by an individual to handle and consume the bulb; from the beginning of handling to the end of consumption. Total consumption time = handling time + consumption time, and it was therefore possible to calculate consumption time (the time taken by an individual to eat the bulb beginning at mastication).

Bulbs of three size classes were used, namely; less than 1 g, 1 – 2 g and more than 2 g. Geophyte size classes were determined according to availability. Most of the 23 individuals were subjected to 15 trials; 5 repeats for each size class for statistical integrity. It was not possible to conduct 15 trials for five animals due to their level of stress. The number of repeats for each individual and test were never less than three.

The data was converted to proportions of total consumption time (handling time relative to total consumption time and consumption time relative to total consumption time).

Mean \pm SD's (mostly $n = 5$) were then calculated for each individual and bulb size class. All data analyses were conducted on the proportion of time spent handling the food item relative to total consumption time (ht/tct) as the proportion of time spent consuming the geophyte (ct/tct) would simply be $1 - (\text{ht}/\text{tct})$ and relationships analyzed would all be relative. It is important to note here that all results are thus in a ratio format (thus no units being given).

Handling time was analysed for significant differences between animal mass, animal sex and bulb mass respectively. Before the data could be analysed, an arcsine transformation was carried out. Statistical procedures were carried out by the Statistics Department at the University of Pretoria that consisted of analysis of variance (ANOVA) using a LS MEANS technique. In order to differentiate between results of the ANOVA, a multiple comparison procedure was undertaken. F statistics are only reported for major distinctions while probability values are reported for all tests undertaken.

Foraging

Two functionally complete colonies were used in all foraging trials. The colonies consisted of seven and eight individuals respectively. Foraging trials were conducted in an apparatus specifically designed for the trials; and is illustrated below (Figure I). The apparatus consisted of four foraging trays each comprising 250 cm of available packed soil to burrow. This distance was not limiting. Each tray was filled to capacity with a sandy soil typical of the region. The soil is a red, fine sandy/clay soil. Prior to use, the soil moisture content was standardized to 16% (of wet mass) as soil moisture limits burrow excavation (Jarvis *et al.* 1994).

Each tray was subjected to varied density and size class combination treatments of the geophyte *Ornithogalum secundum* during the experimental procedure. Control runs were undertaken to determine any directional or sensory preference to the four trays; of which no preference was evident (see Figures 7a and 7b). The control procedures were

undertaken for each colony separately and consisted of soil-filled trays but with no geophyte content in any tray.

At the colony's usual feeding time, all individuals of a single colony were placed in the central arena and were left for a few minutes (not longer than 3 minutes) in order to reduce their stress levels. Scan sampling was conducted on the four trays each minute, a single day session lasting 90 minutes. Data gathered consisted of counts of the number of individuals *actively* digging/excavating each of the trays as well as the total distance excavated in each tray after the 90-minute session each day. Each colony and experimental procedure was repeated three times for statistical integrity.

Bulb size classes that were used when varying size class were < 1 g, 1 - 2 g and > 2 g while when varying density were <1 g and >2 g. Similarly to bulb size classes, tray geophyte density was assigned as a function of geophyte size class availability. Tray densities that were used were 2 m⁻¹, 4 m⁻¹, 6 m⁻¹ and 0 m⁻¹ respectively.

Thus, each colony was subjected to the same series of encounters with the soil arenas varying in bulb density and bulb size class *independently*. Data was analyzed for significant differences between mean (n=3) patch visitation ± SE (count data) using an analysis of variance (ANOVA) technique comparing LS MEANS that were executed by the statistics department of the University of Pretoria. In the same way, data was analyzed for significant differences between mean excavation distances (n=3). This method of comparison employs a multiple comparison technique in order to differentiate between significantly different statistical outcomes of the ANOVA. It is important to note here (foraging section only) that only those statistical outcomes that had p < 0.025 were considered to be significant. F statistics are only reported for major distinctions while probability values are reported for all tests undertaken.

Table 1: The following patch density/bulb size class combinations were experimentally investigated.

Experimental Condition	Tray 1 Density (m ⁻¹)	Tray 2 Density (m ⁻¹)	Tray 3 Density (m ⁻¹)	Tray 4 Density (m ⁻¹)	Bulb Size Class (g)
Control	0	0	0	0	No bulbs used.
Vary Size	2	4	6	0	<1
	2	4	6	0	1-2
	2	4	6	0	>2
Vary Density	2	2	2	0	<1
	4	4	4	0	<1
	6	6	6	0	<1
	2	2	2	0	>2
	4	4	4	0	>2
	6	6	6	0	>2

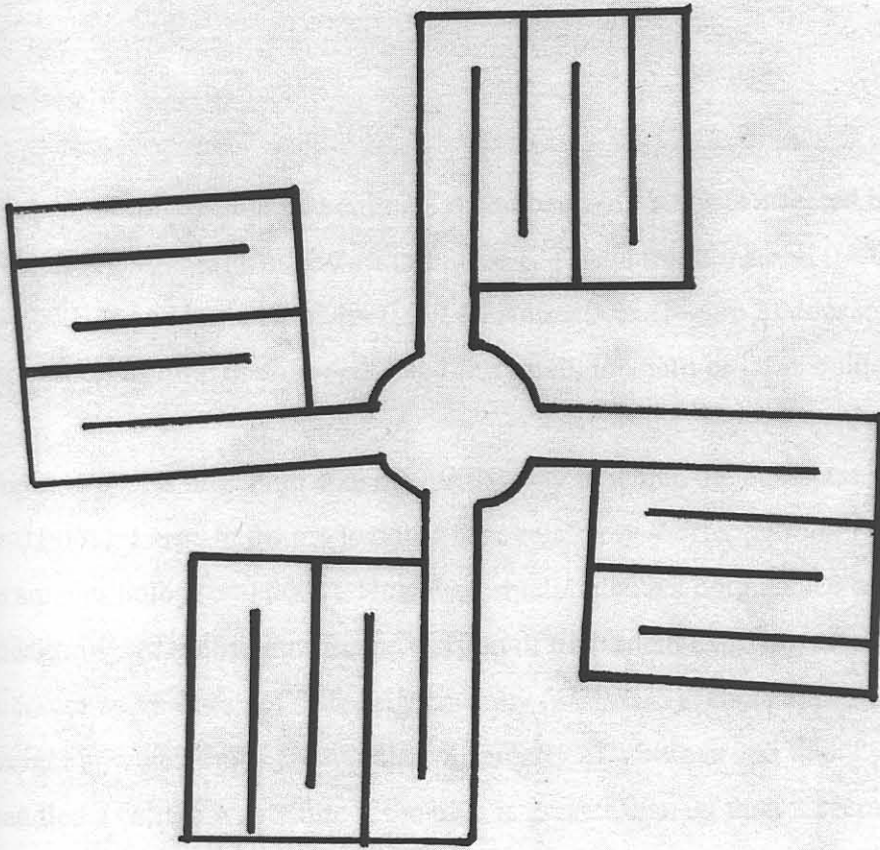


Figure I: Schematic representation of the apparatus used in the foraging trials. Each tray consisted of 250 cm of available burrowing distance. Each tray lead from a central arena into which each entire colony was placed at the beginning of each trial.

Results

Feeding

The proportion of time that animals spend handling bulbs is affected by animal size ($F=28.29$, $p<0.0001$), as shown in Figure 1. This is true for small ($p=0.0020$), medium ($p=0.0024$) and large bulbs ($p=0.0014$). Animal sex (Figure 2) does not affect the proportion of time that is spent handling small, medium or large bulbs ($F=0.82$, $p=0.37$).

Figure 4 shows how bulb size affects the way in which the bulbs are handled ($F=45.96$, $p<0.0001$). Large bulbs are handled for a relatively shorter period of time than compared to smaller bulbs ($p<0.0001$). However, small bulbs are not handled any differently to medium sized bulbs since the proportion of time spent handling small bulbs compared to medium bulbs does not differ significantly ($p=0.0235$). There appears to be a cut-off weight at which bulbs are handled differently. If a bulb is less than 2g in mass it is handled a certain way while if the bulb is greater than 2g then it seems to be handled for a significantly shorter period of time.

Small animals spend the same proportion of time handling small and medium sized bulbs ($p=0.1233$) (Figure 3 and Figure 6). This is also true for large animals ($p=0.1028$). Small animals spend a greater proportion of time handling small bulbs when compared to large bulbs ($p<0.0001$). This is also true for large animals ($p<0.0014$). Small animals also spend a greater proportion of time handling medium bulbs when compared to large bulbs ($p<0.0001$). This is also true for large animals ($p<0.0001$).

Figure 5 shows how males spend the same proportion of time handling small bulbs as they do medium bulbs ($p=0.0891$). This is also true for females ($p=0.1549$). Males spend a greater proportion of time handling small bulbs when compared to large bulbs ($p<0.0001$). Males also spend a greater proportion of time handling medium bulbs when compared to large bulbs ($p=0.0005$). These trends are similar for females ($p<0.0001$ and $p<0.0001$ respectively).

Absolute values

Overall, small animals handle geophytes for about a third of total consumption time, whereas large animals handle geophytes for slightly longer. Differences in the proportion of time spent handling geophytes is independent of animal sex for both animal size classes.

All bulbs were handled for less than half of total consumption time with the greatest proportion of handling time being used by large animals on small and medium sizes geophytes (0.46 ± 0.10). The smallest proportion of time spent handling geophytes was performed by small animals who fed on large geophytes (0.24 ± 0.09).

Time spent handling geophytes thus varied between 24 % and 46 % of total consumption time. The proportion of handling time was always less than half of total consumption time.

Foraging

In order to test whether individuals had a preference to certain trays, a control experiment was carried out. In these experiments, the four trays were filled with soil only geophytes being absent in all trays. It was important to test the null hypothesis for the control experiment. This hypothesized that there would be no preference to certain trays in terms of visitation (quantified as counts and total distance excavated). If the null hypothesis was rejected, showing that there was a preference to certain trays, this could possibly be explained by odour trails or directional preference when foraging. In this study, there was no evidence that there was any preference to any tray(s) when geophytes were absent from the four trays (Figure 7). Counts varied between 71 and 97 ($p=0.0838$). Individuals excavated a total distance of between 117 and 144 cm ($p=0.2367$).

The trend observed was that no preference existed between the four trays in terms of visitation (count and total excavation distance). This result allowed further,

uncomplicated investigations into possible preferences to trays varying in geophyte size and patch density independently as well as various combinations of geophyte size and patch density.

When comparing the preferences that individuals showed to patch density, independent to geophyte size, it was evident that there was no statistically significant preference to any of the patches of different geophyte density. This trend was equally evident when using either of the methods of quantification of visitation (count and total excavation distance; see Figure 8 and 9 respectively). Counts varied between 64 and 80 individual visitations that excavated a total distance of between 100 and 128 cm.

When comparing the preferences that individuals showed to geophyte size, independent to patch density, it was evident that there were statistically significant preferences to several of the patches of different geophyte size. This trend was not equally evident when using either of the methods of quantifying visitation (count and total excavation distance).

In terms of count data (Figure 10), it was apparent that individuals preferred empty patches (86.4 ± 5.6) when compared to patches containing medium sized geophytes (58.9 ± 9.7) ($p=0.0089$). Also, individuals apparently preferred empty patches when compared to patches with large sized geophytes (66.4 ± 4.7) ($p=0.0074$). No preference was evident between patches where different sized geophytes were present.

In terms of total excavation distance (Figure 11), it was apparent that individuals preferred empty patches (133.6 ± 8.6) when compared to patches containing medium sized geophytes (87.9 ± 13.3) ($p=0.0048$). Although this trend correlates well to the preference showed by count data, individuals showed no preference to large sized geophytes when compared to empty patches ($p=0.0405$). However, individuals did show a preference to small sized geophytes (123.3 ± 7.5) when compared to medium sized geophytes ($p=0.0211$).

When combining geophyte size together with geophyte patch density it is possible to determine whether certain geophyte size/density patch combinations are preferred over others. In undertaking this analysis, it was evident that very few combinations are preferred over other combinations. A total of four statistically significant preferences were observed. Only one of these combination comparisons was confirmed with both methods of visitation quantification (count and total excavation distance). The other three statistically significant preferences were only evident for either count or total excavation distance data.

When geophyte size and density are combined as a factor for comparison, it is evident that, for large geophytes, empty patches are preferred over patches with a density of 2 geophytes m^{-1} ($p=0.0224$). This is only evident when analysing excavation distance data (Figure 13). Similarly, for large geophytes, empty patches are preferred over patches with a high density of geophytes (6 geophytes m^{-1}) ($p=0.0205$).

When patch densities are 2 geophytes m^{-1} , it is evident that patches with small geophytes are preferred over those with medium geophytes. This observation is confirmed for both methods of visitation quantification (count data; $p=0.0067$ and total excavation distance; $p=0.0046$).

Finally, when preference is compared in low-density patches (2 geophytes m^{-1}) it is evident that patches with small geophytes are preferred over those patches that contain large geophytes ($p=0.0218$). This is only evident for count data (Figure 12).

Visitation quantification correlation

Figure 14 shows an assessment that was made to determine whether any correlation existed between the two methods used to quantify patch visitation, and ultimately, patch preference. The methods that were compared to each other were count data (number of animals in a patch) and the total distance that was excavated in that patch. Strong correlations were found to exist. The linear correlation and power correlation gave

correlation coefficients of 0.758 and 0.805 respectively. The exponential correlation was found to provide the best-fit to the data; giving a correlation coefficient of 0.814.

Although not perfect correlations, either of the correlations could be used to estimate one type of data provided that the other is known. Note that these correlations were estimated on colonies of seven and eight individuals respectively.

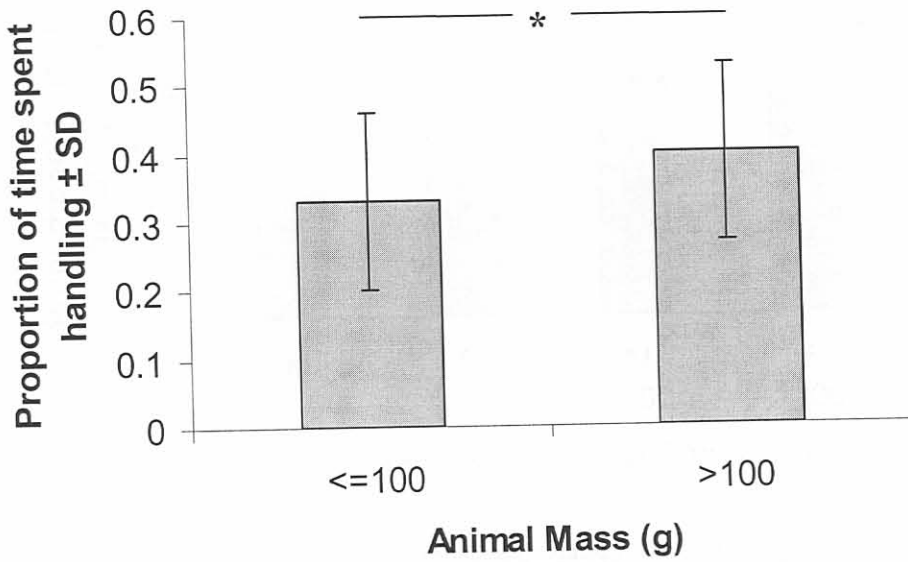


Figure 1: The mean proportion of time (\pm standard deviation) different sized animals (both sexes) spent handling geophytes. *=significant difference detected.

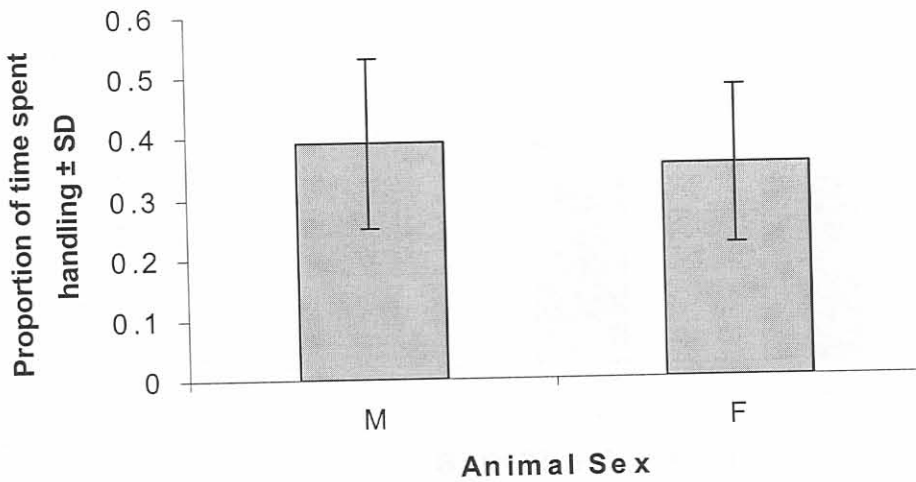


Figure 2: The mean proportion of time (\pm standard deviation) that animals of different sex (all animal size classes) spent handling geophytes. No significant differences were detected.

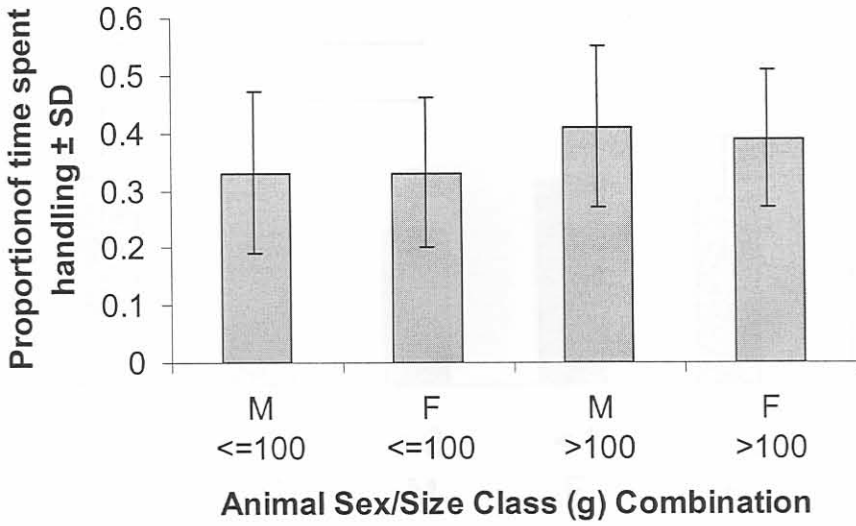


Figure 3: The mean proportion of time (\pm standard deviation) that different sized animals (of each sex) spent handling geophytes. *=significant differences detected.

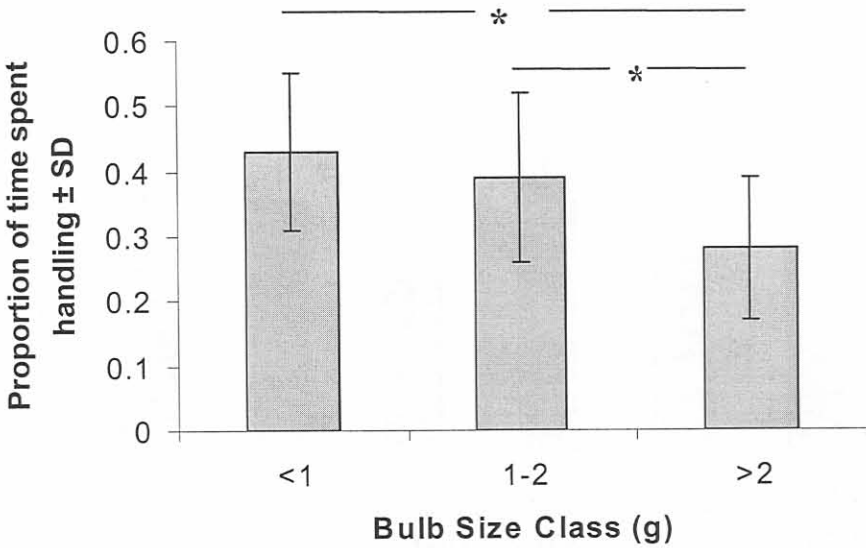


Figure 4: The mean proportion of time (\pm standard deviation) that was spent (for all animals) on different sized geophytes. *=significant differences detected.

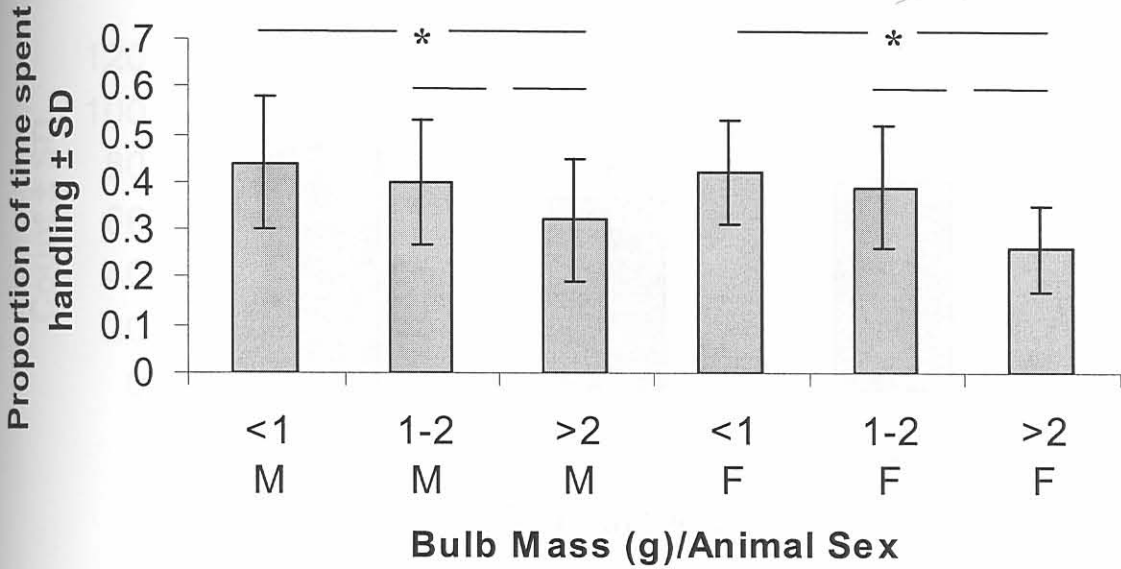


Figure 5: The mean proportion of time that animals of different sex spent handling different sized geophytes. *=significant differences detected.

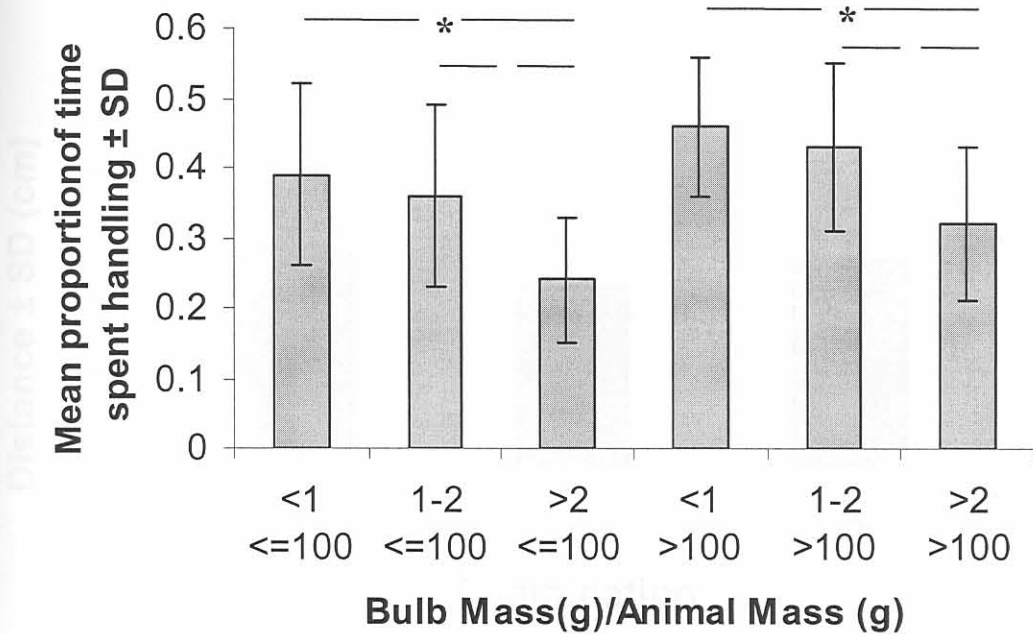


Figure 6: The mean proportion of time (± standard deviation) that different sized animals (of both sexes) spent handling different sized geophytes. *=significant differences detected.

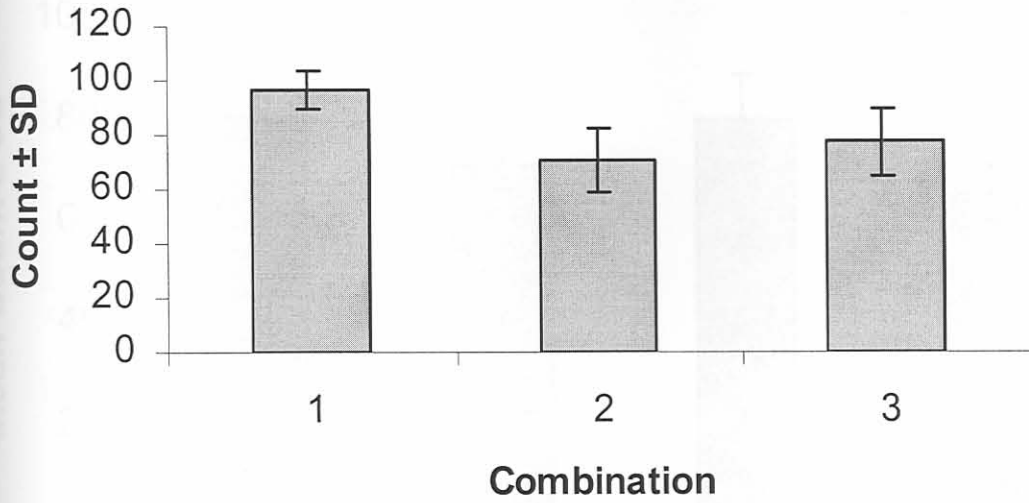


Figure 7a: Mean count (\pm standard deviation) of individuals observed in each soil filled tray (devoid of any geophytes). No significant differences were detected.

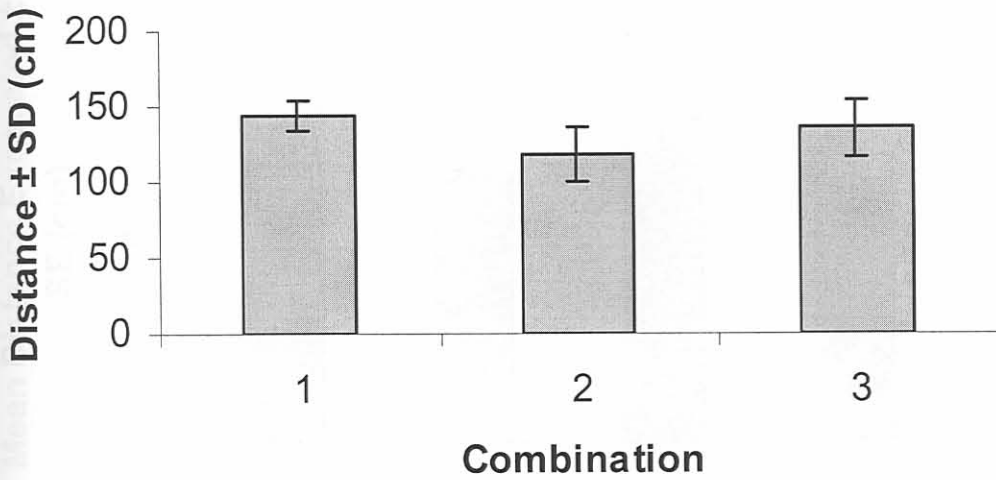


Figure 7b: Mean excavation distance (\pm standard deviation) dug by animals in each soil filled tray (devoid of any geophytes). No significant differences were detected.

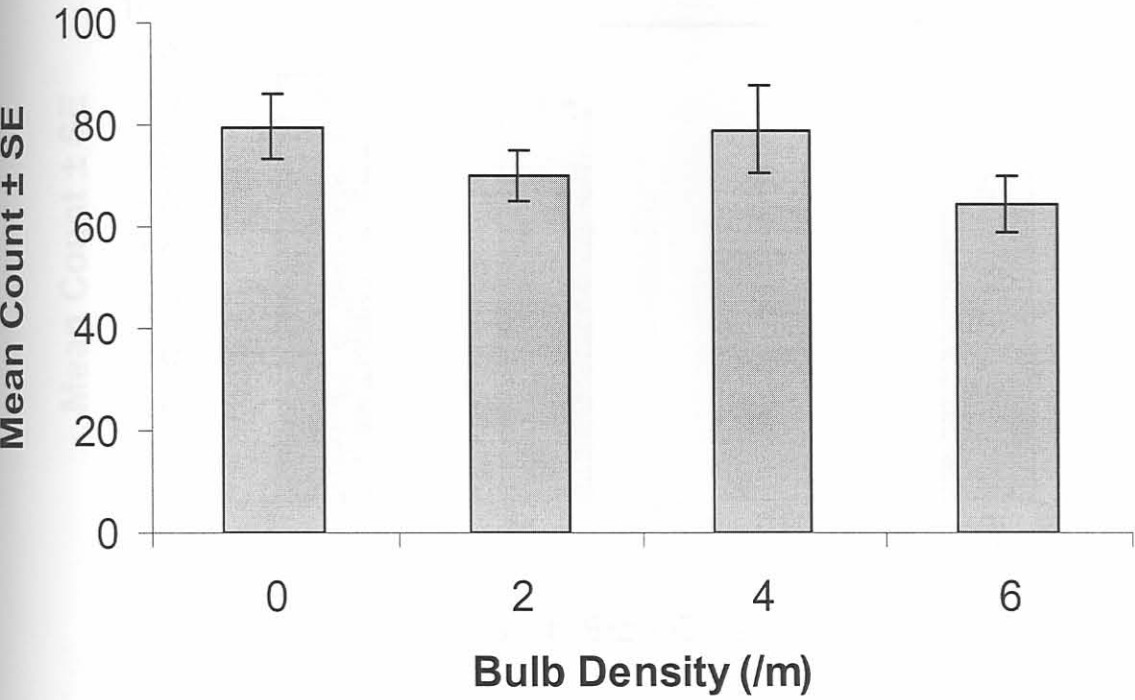


Figure 8: Mean count (\pm standard error) of animals observed in patches of different geophyte densities (for all bulb sizes). No significant differences were detected.

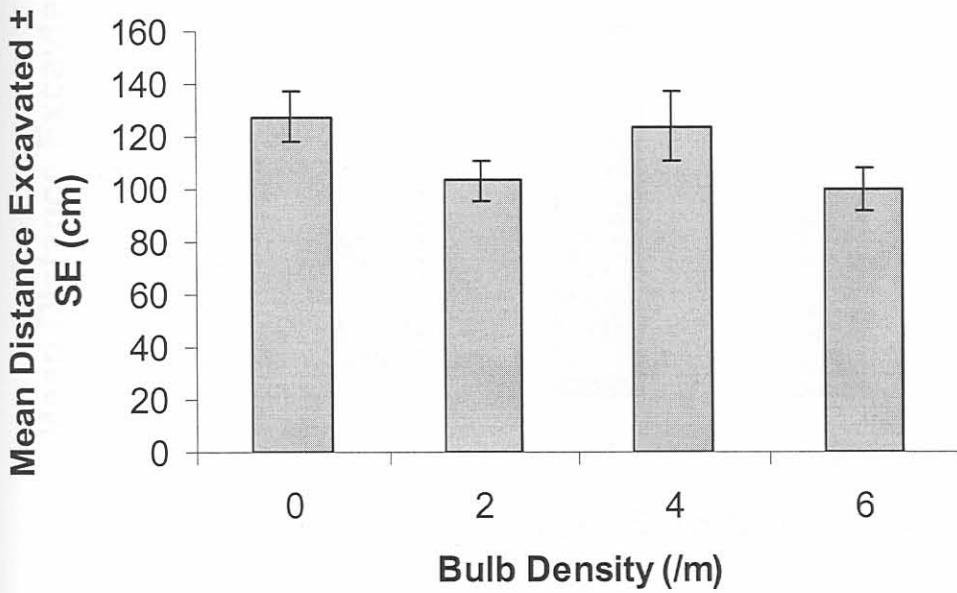


Figure 9: Mean excavation distance (\pm standard error) dug by individuals in patches of different geophyte densities (for all bulb sizes). No significant differences were detected.

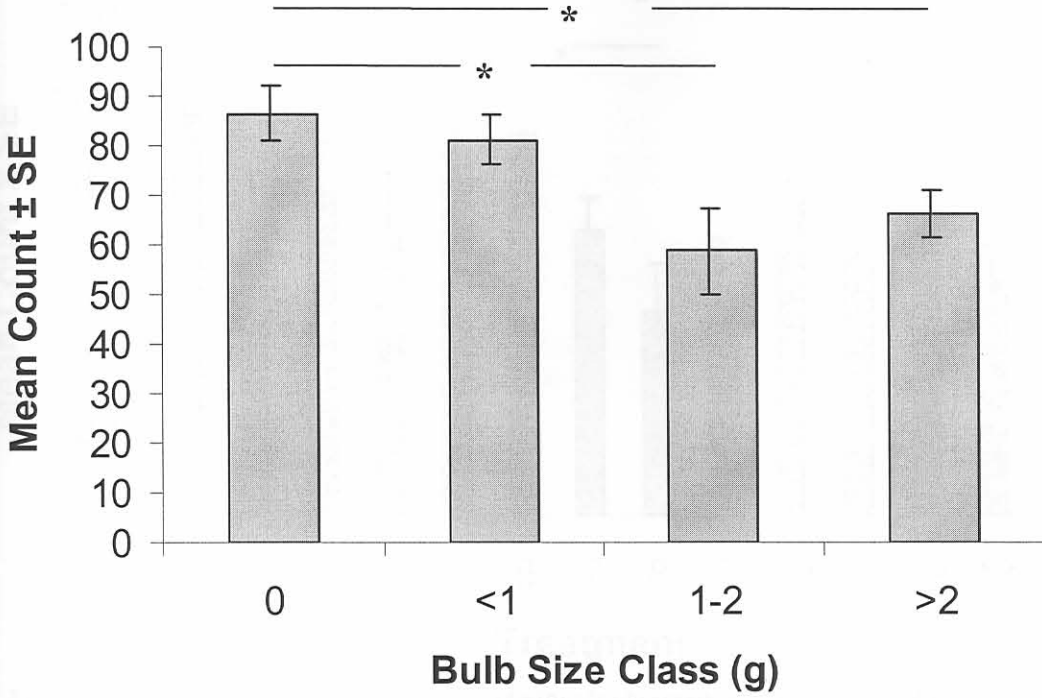


Figure 10: Mean count (\pm standard error) of animals observed in patches of different geophyte sizes (for all bulb densities). *=significant differences detected.

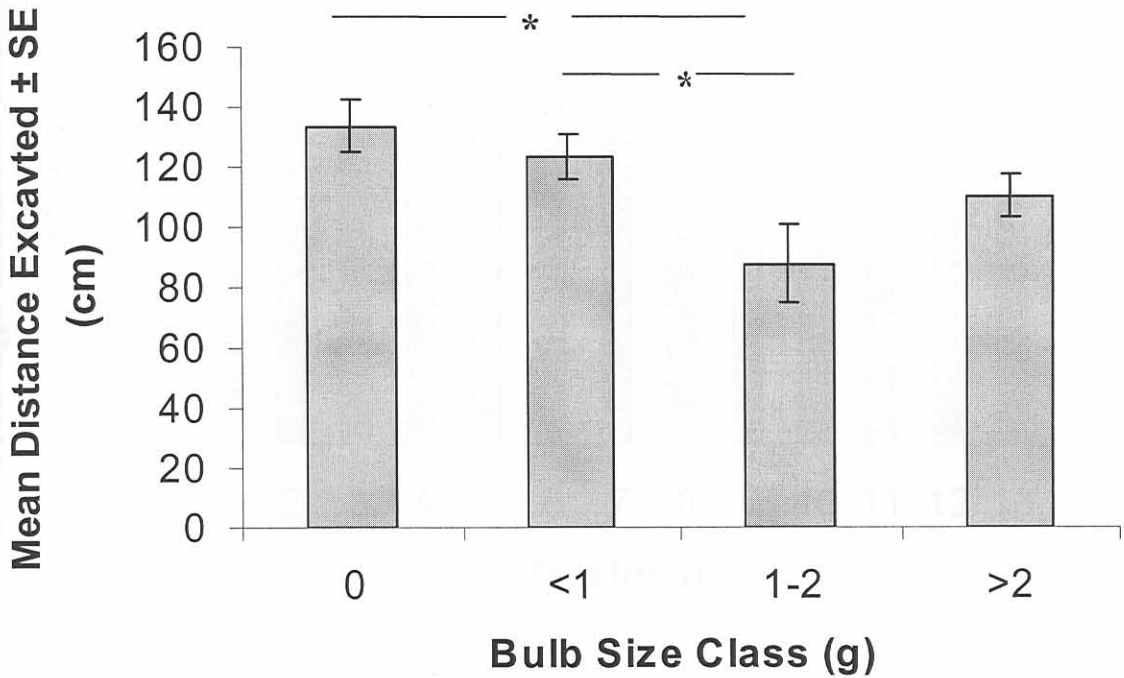


Figure 11: Mean excavation distance (\pm standard error) dug by individuals in patches of different geophyte sizes (for all bulb densities). *=significant differences detected.

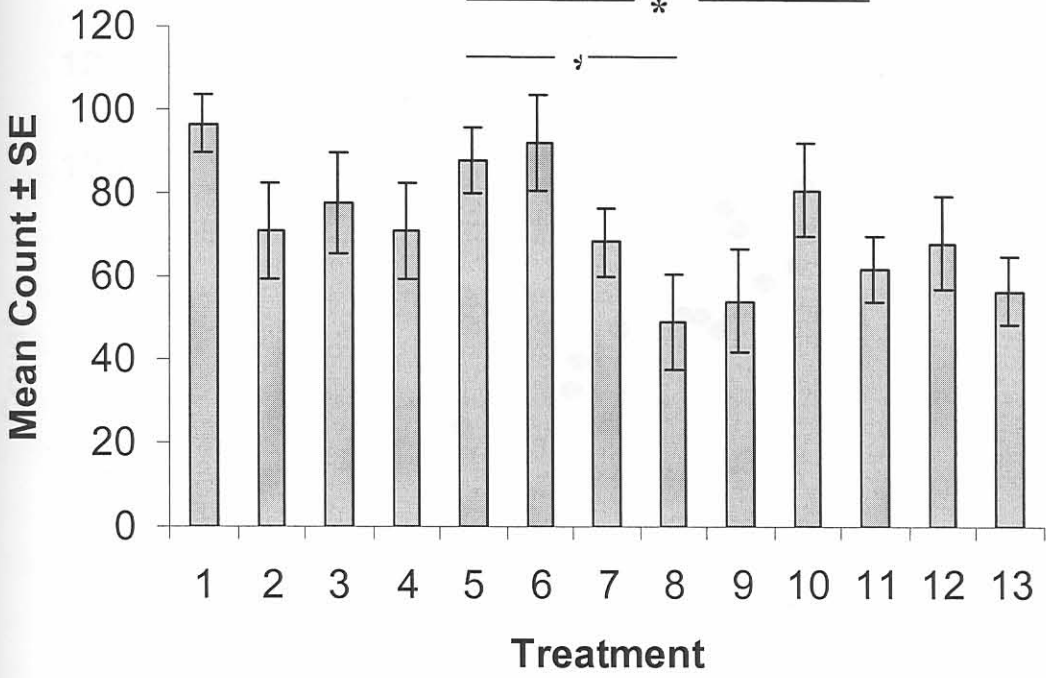


Figure 12: Comparison of the number of individuals observed (count ± standard error) in patches with different geophyte size/density combinations. *=significant differences detected.

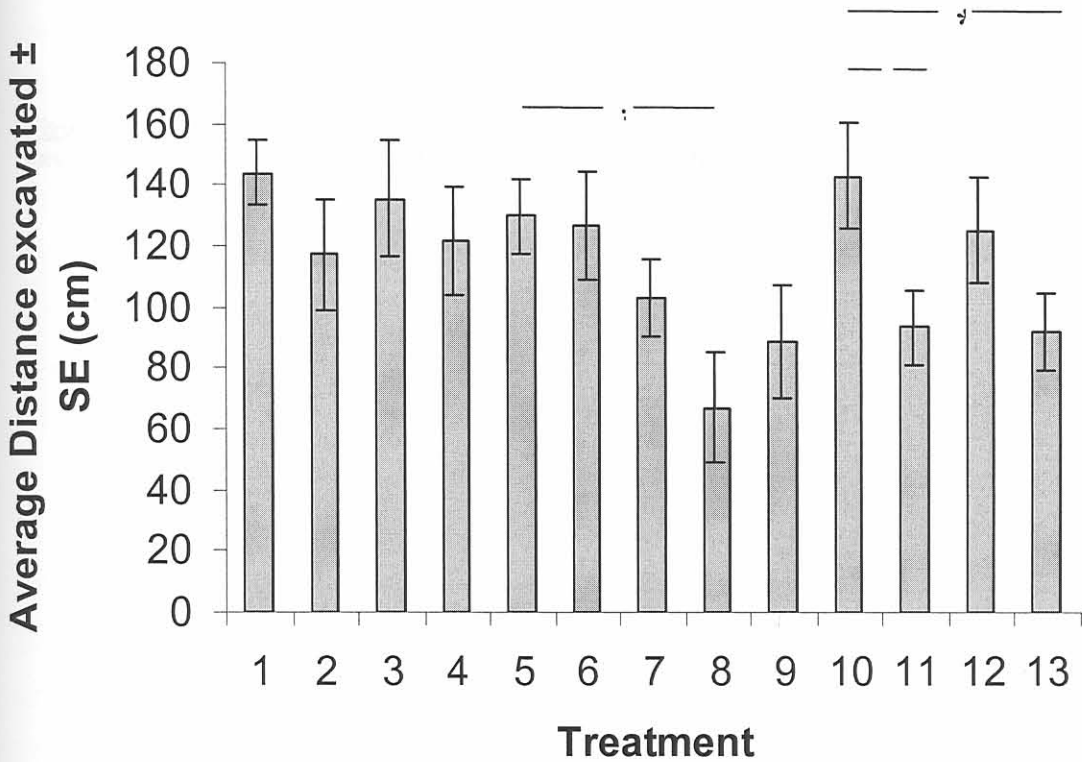


Figure 13: Comparison of the distance excavated by individuals (excavation distance ± standard error) in patches with different geophyte size/density combinations. *=significant differences detected.

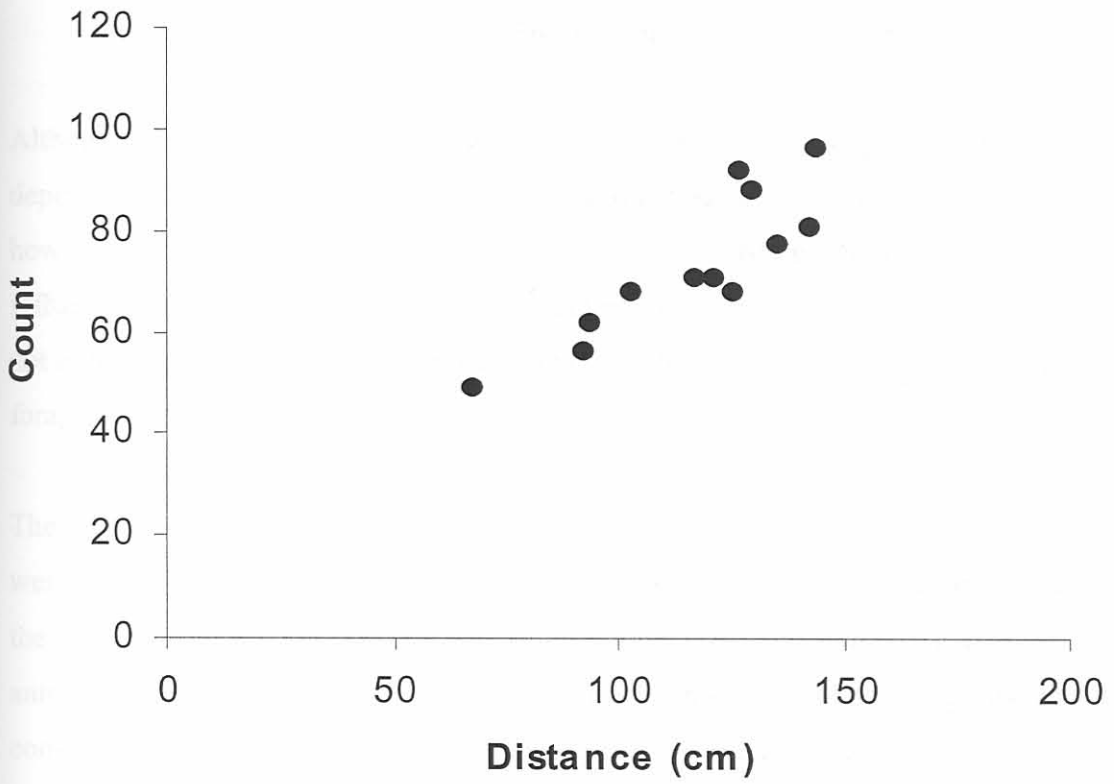


Figure 14: A comparison of the quality of data used in this study in order to determine whether any correlation exists between the two types of patch visitation quantification.

Discussion

Although it was not possible to study optimal foraging *per se*, as optimal foraging theory depends on the individual's resulting fitness and natural selection (Sih 1982), it was however possible to estimate feeding efficiency and identify possible factors which influence feeding behaviour. Using these factors, it was possible to estimate whether or not individuals within colonies of the highveld mole-rat could be classified as optimal foragers.

The responses that animals of different size and sex showed to geophytes of varying size were quantified in terms of the time which animals spent handling geophytes relative to the total consumption time. Total consumption time was measured as the time that an animal took to deal with a geophyte in its entirety. This included handling time as well as consumption time. Handling time is an energetically expensive activity as time is taken (and energy used) in order to make the geophyte suitable for consumption. Energy is only acquired once the geophyte has been consumed and for this reason handling time was assumed to be more important than consumption time as the energy cost of consumption time is minimal compared to the amount of energy that is acquired – while no energy is acquired during handling. Barnett (1991) showed in the eusocial *Cryptomys damarensis*, that handling time was expensive and important in determining resource selection.

Feeding

In natural populations, feeding behaviour can vary intra-specifically (Gustafsson 1988). In birds, an individual's sex (eg Selander 1966 cited in Gustafsson 1988), age (e.g. Partridge & Green 1985 cited in Gustafsson 1988) as well as other individual traits (e.g. Grant *et al.* 1976 cited in Gustafsson 1988), such as an individual's position in a social hierarchy and its mass, can influence feeding behaviour. Since bathyergid age determination is difficult to accomplish non-invasively, individual sex and mass were only used to investigate differences in feeding behaviour.

It was evident that there was no relationship between animal sex and the proportion of time spent handling geophytes. It was expected that males, being the more aggressive of the sexes, would handle geophytes more efficiently. Females apparently spend the same proportion of time handling geophytes of different sizes as males do.

Animal size appears to play a role in determining the proportion of time an individual spends handling a particular sized geophyte. It was predicted that larger animals, because of their assumed older age, would handle geophytes more efficiently as experience is assumed to increase with age. It was further postulated that this would be evident from a difference in handling times where larger animals would handle geophytes for a relatively shorter period of time than younger animals. There was a significant difference in the proportion of time that larger and smaller animals spent handling geophytes of different sizes but was not as expected. It was evident that larger animals spend a greater proportion of their total consumption time handling the geophytes than smaller animals do. However, this can be explained by rather looking at this trend in terms of consumption time. A larger animal would consume a bulb of a certain size faster than a smaller animal simply due to the volume of the oral cavity. Therefore, if a large animal spends a smaller proportion of its time consuming than a smaller animal, the opposite trend will be evident when comparing handling times and a larger proportion of time will be seen being invested in handling when compared to smaller animals.

It was apparent that geophytes of varying size were handled differently. Small geophytes were handled for a longer time relative to total consumption time when compared to large ones. In both males and females, the trend observed was that as geophyte size increased, so the proportion of time spent handling the geophyte decreased. Animal size had no effect on this trend, since both small and large animals showed the same pattern. This trend was expected as a larger bulb has more tissue for consumption compared to the smaller bulb. Thus, it would be expected that a greater proportion of time (and energy) would be spent on handling smaller bulbs than larger ones. This is an interesting finding since this trend would favour optimal foraging when an abundance of geophytes of varying sizes is available. Individuals should favour larger bulbs, since less time (and

energy) would be spent on preparing the geophyte for consumption and energy acquisition. Also, once the geophyte has been handled and made suitable for consumption, more energy would be acquired than if a smaller bulb had been handled. This observation leads to the formation of an energy maximizing hypothesis which could result in the animals being termed optimal foragers. In an abundant resource (geophyte) patch, individuals should preferentially select larger geophytes over smaller ones. This hypothesis is tested in the next section (foraging).

It is interesting that there appears to be a cut-off mass at which size classes of bulbs are handled differently. Bulbs of less than 2g (small and medium bulbs) showed no significant difference in the proportion of time that animals spent handling them, while geophytes of greater than 2g were handled for shorter periods of time. Also, the proportion of time spent handling geophytes was always less than the amount of time spent consuming the geophyte – evidence that the consumption of the geophyte is more important in terms of energy acquisition as the greatest amount of time should be spent on acquiring energy.

It is therefore concluded that the proportion of time that an individual spends handling a geophyte is a function of bulb and animal size. Animal sex played no role in determining the way in which geophytes are handled. Larger bulbs are handled for a relatively shorter period of time than smaller bulbs and larger animals handle bulbs for a relatively longer proportion of time than smaller animals. It is hypothesized that, given an abundant patch of resources (geophytes) varying in size, individuals should preferentially select larger geophytes over smaller ones as the handling time of a larger bulb is less and energy acquired from a larger bulb is greater than that obtained from a smaller geophyte. It is therefore predicted that individuals would be energy maximizers in a resource abundant patch.

Foraging

A foraging animal is assumed to exhibit two major patterns of behaviour; travelling between patches and feeding within patches (Arditi & Dacorogna 1998). If patches have not yet been found, subterranean consumers should forage blindly (randomly) until prey patches are encountered (Glasser 1984). Once prey patches are encountered, foraging should become directed as the probability of finding food increases (Barnett 1991). Consumers are faced with choices when foraging in particular patches (Hirakawa 1997). These choices determine which prey item to consume, which patch to visit, how long to stay in a particular patch and the best route to take in order to get to the patch (Hirakawa 1997). The first two of these choices are important in this study, while the length of time in a patch as well as the route taken to the patch are not investigated in this study.

Two questions have been identified concerning how prey patches are used by foragers: (1) do foragers concentrate their efforts in more profitable patches? and, (2) do the decisions that foragers make follow rules predicted by optimal foraging theory? (Sih 1982). This study attempts to answer these questions. It is important to note, again, that these questions do not test optimality of patch use but the efficiency of patch use by foragers (Sih 1982). Studies concerning optimality need to take fecundity, growth rate and survivorship (fitness) into account (Sih 1982).

Patch preference was not evident when all four experimental trays were filled only with soil (no geophytes). Hence, no directional or sensory preference played a role in preferences that were evident with different geophyte size/patch density combinations. Results can therefore be explored in a meaningful way – the preferences evident only being attributable to geophyte size, density or a combination of the two.

It is apparent that patch density, when analysed independent of geophyte size, plays no role in determining geophyte patch preference while geophyte size, when analysed independent of patch density does play some part in determining patch preference.

It was shown that individuals generally prefer empty patches when compared to either patches containing medium or large geophytes. This was evident from an analysis of visitation (count) data and excavation distance data. It was also evident from excavation distance data that there was a preference for small geophytes when compared to large geophytes.

When comparing preferences of geophyte size/patch density combinations, it was evident that very few preferences existed. The only trend that can be discussed is that, generally, individuals tend to prefer empty patches when compared to patches with geophytes size/density combinations present (particularly for large geophytes at densities of 2 m^{-1} and 6 m^{-1}). Also, at low patch densities ($2 \text{ geophytes m}^{-1}$), small geophytes are preferred over medium and large geophytes.

Although it has been found that foragers generally follow the qualitative predictions of optimal foraging theory, foragers also appear to fall somewhat short of being energy maximizers (Sih 1982). This is thought to be due to other foraging or fitness considerations being taken into account (Sih 1982). For example, studies on rats have shown that they show a preference for food items with the lowest handling cost but this was not an absolute preference (Kaufman & Collier 1981). It has also been shown that differences in the increase of handling time between small and large prey items might alter profitability and reward rate of different size classes during feeding (Barnett 1991).

Bathyergids have lower resting metabolic rates than other rodents; resting metabolic rate being independent of body mass (Lovegrove & Painting 1987). Lower resting metabolic rates are thought to have been selected for in response to high energy costs of burrowing and the low probability of finding widely dispersed geophytes by random burrowing (Lovegrove & Painting 1987). From the results presented from this study it appears as though individuals of the highveld mole-rat are not maximizing their immediate energy consumption. If individuals were foraging in order to maximize their immediate net energy intake it would be expected that they would show preferences to patches with large bulbs, a high density of bulbs, or a combination of high density/large geophyte

patches. This appears not to be the situation since patches with no geophytes occurring within them appeared to be favoured.

As the definition of optimal foraging takes into account that individuals would attempt to maximize their net energy intake (independent of fitness requirements mentioned above), the highveld mole-rat cannot be classed as an optimal forager. Rather, it appears, individuals prefer patches with the lowest density of geophytes when other patches that contain geophytes have been investigated. These trends were evident using both methods of preference quantification; count data as well as excavation distance data.

In an environment with a patchy food distribution, a forager may sample a number of patches prior to more intensive exploitation (Hodapp & Frey 1982). This appears to be just what is happening with the highveld mole-rat. It appears as though all of the patches in the study were explored and then choices were made that caused more intense exploration of patches where no geophytes had yet been located. This foraging strategy may be allowing individuals in the colonies to “hedge their bets”. In other words, once patches have been located which contain geophytes (irrespective of the size or density of the geophytes) other patches are explored which have not yet given evidence of geophytic presence. These patches are then explored further in order to determine whether a new source of geophytes can be found not far away from the other patches. Patches that contain geophytes will be used as a resource while exploring the other (empty), less profitable patches.

It has also been shown that in dominance-related social contexts and when constraints of limited feeding time exist, the problem of choosing the optimum balance between exploring food arenas and exploitation of food arenas is intensified because of competition (Hodapp & Frey 1982). In other studies it has also been shown that an increase in activity was found in patches of lower food quality and quantity (Hodapp & Frey 1982).

Although optimal foraging theory can predict and explain food choice and food patch choice by animals, for an animal that does not forage widely and whose food selection abilities may be limited, regulation of ingestive and digestive processes may be an especially important component of a strategy to optimize feeding energetics (Barnett 1991). This could be the case for the highveld mole-rat where very low resting metabolic rates and restricted food selection abilities select for the foraging strategy that has been observed in this study.

Correlation of quantification methodologies

It is interesting to observe that a relatively strong correlation exists between the two types of methods of preference quantification used, namely; individual count data and excavation distance data. It appears that either of these methods can be used to estimate patch preference with reasonable accuracy. This correlation also shows that excavation distance is positively correlated to the number of animals found to be in a patch at any particular time.

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