Foraging Decisions in the Bushveld Gerbil (*Gerbilliscus leucogaster*) using Cost/Benefit Scenarios

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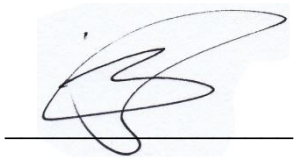
Declaration

I declare that this dissertation is my own unaided work. It is being submitted for the degree of Master of Science to the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination to any other university.



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8 February 2013

Abstract

Foraging is an essential part of an animal's everyday life, during which it has to balance out many costs and rewards while making decisions on where, what, when and how to forage. The aim of my study was to investigate how different cost/benefit foraging scenarios affect foraging decisions in captive Bushveld gerbils. The foraging behaviour of Bushveld gerbils was studied in four experiments to establish the effect of cost/benefit scenarios on their foraging behaviour, specifically I tested i) how much gerbils will work for seeds of different quality; ii) how seed presentation (piled/scattered) influences foraging behaviour; and iii) the effect of potential predation risk on foraging decisions. Initial seed preference studies for five commercially available seeds (sunflower, sorghum, oats, maize and wild rice) indicated that the gerbils displayed individual seed preferences, and this information was then used to tailor the experiments to the preferences of individual gerbils. The experimental apparatus consisted of 2 joined tanks, one of which, the experimental tank, was designed to impose a cost (weighted door) to access reward (food). The weight of the door was altered to create a low cost door (light door) or a high cost door (heavy door) that was individually tailored to the gerbils by using their individual body weights to create a heavy door approximately the same weight as the gerbil. Most and least preferred seeds were used to create a high reward and a low reward, respectively. Using the door in combination with the preferred seeds, 4 treatments were created, namely, low cost low reward, low cost high reward, high cost low reward, and high cost high reward. These treatments were run in 4 different experiments that were designed to assess the decisions Bushveld gerbils made during foraging. My results indicated that the gerbils employed foraging strategies which, firstly, favoured a reduced cost, possibly linked to reduced energy expenditure, and secondly, gaining the highest rewards. The gerbils consumed less in high cost and low reward treatments, and consumed more in low cost and high reward treatments. The data also revealed that the presentation of the seeds influenced foraging decisions, where seed consumption and exploratory behaviour differed when seeds were piled rather than scattered, depending on the cost/reward structure. Under potential predation risk, the gerbils employed predator avoidance strategies by using cover more and reducing foraging, indicating they were trading-off foraging against predation risk. Demand curves generated to assess decision-making indicated that the gerbils made consistent decisions except under particular circumstances, such as when there was a large difference in food value and cost. Ultimately, my study showed that Bushveld gerbils change

their foraging decisions in a predictable way to exploit low cost and high reward situations. Their decision-making was largely inelastic, indicating that foraging decisions were similar under different circumstances, except when there is a large discrepancy between the qualities of seeds presented.

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Chapter 1: Introduction

1.1 Decision Making

Each behaviour an animal performs is driven by the motivational state(s) it is experiencing at that time (Mason, 2006). These motivational states are a continuous characteristic within the animal, with many conflicting stimuli occurring simultaneously at any moment in time (MacFarland, 1989). These motivational states or 'tendencies' are formed by the interplay between the animal's internal state and external stimuli (Mason, 2006). An animal may have a tendency (or motivation) for more than one behaviour at any point in time, which is known as behavioural conflict (e.g. a tired hungry mouse has a tendency to go look for food as well as rest). These tendencies compete for a single final behavioural pathway or expression, and the decision of which behaviour the animal will perform is driven by the strongest tendency (MacFarland, 1989). Each tendency has associated costs and benefits that an animal must weigh up to determine which behaviour will be best for that situation, ultimately enhancing its fitness. Therefore, the animal will trade-off between competing behaviours before the final decision-making step (MacFarland, 1989); there are instances when decisions cannot be reached between competing behaviours, resulting in a mixture of behaviours, such as ambivalence, displacement or redirected behaviours, which while important will not be considered further in my study.

In the case of the hypothetical example of a tired hungry mouse, if it leaves the safety of its nest to forage, it will benefit from the food it will gain but it will need to pay a cost of energy loss in order to obtain food and also a cost of predation risk. If it stays in its burrow, it will benefit from lowering energy expenditure but will pay a cost in missed foraging opportunities. Therefore, if predation risk is very high, the mouse might find it more beneficial to save energy and rest, but under extreme hunger, the mouse might risk predation to obtain some food, indicating that embedded in decision-making are states when risks and rewards are reassessed, resulting in a dynamic process reflecting changing motivational states. Motivation is established by internal states (e.g. hunger) and external stimuli (e.g. food, predation) together with a cognitive ability to make decisions. Motivation is difficult to measure directly, at least with the current available methodologies, and instead inferences from observed behaviour are used to infer motivation (Drickamer and Vessey, 1986).

The literature indicates that the complexity of the brain and attendant anatomical structure and physiological processes is a result of natural selection and therefore it can be assumed that behaviour is also a consequence of such selection (Walton *et al*., 2006). This leads to the conclusion that the goal of an animal's behaviour is to maximise its fitness (MacFarland, 1989). The notion of weighing up costs and benefits in relation to the animal's fitness has formed the foundation of behavioural ecology for the better part of half a century (Walton *et al*., 2006). As shown in many studies, in conflicting situations, an animal will choose a behaviour that will be beneficial for its survival. In situations where an animal is faced with predation, an animal will balance out the benefits of risk reduction and the associated costs (Winnie *et al*., 2006).

Foraging under high predation risk may possibly lead to death and therefore animals have the delicate task of trading off between foraging gains and mortality (Scarratt and Godin, 1992). Thus, it is expected that a forager will delay its responses to predation (such as fleeing) when the benefits that can be gained from continued foraging exceed the costs of delaying foraging (Scarrat and Godin, 1992; Diego-Rasilla, 2003). This type of risky behaviour is said to be irrational but can be advantageous in certain circumstances where an animal has a need to change its present state to a desired state (Mishra and Lalumière, 2010). An example of a kind of risky behaviour is shown by three-spined sticklebacks (*Gasterosteus aculeatus*), which apparently engage in predator inspection (Walling *et al*., 2004). The benefits of this behaviour are to gather valuable information about the predator as well as signalling its detection to both the predator and nearby conspecifics, whereas the costs to predator inspection are increased risk of predation and lost opportunity costs, such as missed foraging opportunities.

In many situations, animals may also have to decide how much effort they are willing to expend in order to obtain particular rewards (Van den Bos *et al*., 2006). In these situations, animals assess many different options and the associated costs and benefits before making a decision (Van den Bos *et al*., 2006; Walton *et al*., 2006). Walton *et al.* (2006) suggest that animals may work a little harder to obtain a higher reward but as the cost to obtain a reward increases substantially, animals will choose the lower, less costly, reward. The animals choose the outcome based on a work/reward ratio, as shown by experiments done with

macaque monkeys (*Macaca mulatta*) where they are offered a food reward attached to a performance task, and they assess this ratio and choose either the option that offers a high reward or the option with less effort to obtain the reward (Walton *et al*., 2006). Through these experiments, it was also established that the response speed was faster for high rewards than low rewards (Walton *et al*., 2006).

To make a decision, animals gather information through their ability to detect stimuli. They perceive these stimuli through sensory receptors that provide information about what is available and where it is located (Celikel and Sakmann, 2007). Therefore, the more sensory receptors or senses that are stimulated, the shorter the time taken to make a decision. For example, laboratory mice which possess all their whiskers require less sensory exploration time before making decisions and completing tasks, as compared to those that had their number of whiskers experimentally reduced to a single whisker (Celikel and Sakmann, 2007). However, multiple whiskers do not increase the probability of success in decision-making but decreases the duration of sensory integration needed to make a decision.

Accuracy or success in making a decision depends on the time taken to make a decision (Celikel and Sakmann, 2007; Chittka *et al*., 2009). Speed in making decisions depends on the receptor properties, difficulty of task and previous experience. Bees that have to choose flowers by discriminating colour tend to be more error prone when sampling quickly, whereas others that take a longer time to choose are less prone to errors (Chittka *et al*., 2009). Where predation is concerned, the cost of an error may be death and therefore animals which have previously encountered a predator, take longer to make decisions, as occurs in guppies (*Poecilia reticulata*) in high-predation environments (Chittka *et al*., 2009)

1.2 Foraging Theory

Many theories have been developed to explain the foraging strategies of animals, the embodiment of which is known as the Optimal Foraging Theory (OFT). This theory assumes that the fitness of the animal is a "function of the efficiency of foraging measured in some 'currency' " (Pyke *et al*., 1977, pp 138–139). The currency in almost all cases is the net rate of energy intake and, due to the need for animals to maximise their fitness, the main assumption in OFT is that net rate of energy gain is maximized (Pyke *et al*., 1977; Taghon

and Jumars, 1984; Ritchie, 1990). During foraging, an animal can be placed in one of two categories depending on what strategy it adopts. If the animal has a fixed energy requirement (it will gain little fitness beyond a threshold level of energy intake) and there are also demands made on its time for other activities, minimizing the time to obtain this fixed level of energy will be the most optimal strategy to maximise fitness. These animals are referred to as *time minimizers* (Pyke *et al*., 1977; Taghon and Jumars, 1984). On the other hand, if the animal has a fixed amount of time to forage and increasing the amount of energy gained increases the animal's fitness, the maximum fitness will be attained when the animal can obtain the maximum amount of energy in a particular time period. These animals are referred to as *energy maximizers*. For both time minimizers and energy maximizers, the net rate of energy intake while foraging is maximized (Pyke *et al*., 1977; Ritchie, 1990). Therefore, the goal of a foraging animal is to maximize its fitness by obtaining the maximum net rate of energy intake. There are, however, factors that influence the foraging behaviour of animals by increasing or decreasing energy obtained and/or time spent foraging, such as predation risk, nutritional requirements, patch selection and competition.

Animals use environmental cues to assess the risk of predation. As an example, many rodents use illumination level, odour or the level of cover to assess predation risk (Brown *et al*., 1988; Vasquez, 1994; Wisenden, 2000; Pillay *et al*., 2003). Prey trade off their foraging time according to predation risk in such a way that they can meet their energy needs and minimize risk of being killed (i.e. the predation risk allocation hypothesis; see Lima and Bednekoff, 1999; Sundell *et al*., 2004). This hypothesis states that foraging will be low during high risk of predation and foraging will be high during low risk of predation. For example, Vasquez (1994) suggested that, on moonlight nights, rodents tended to have a lower energetic return because they foraged less and spent energy carrying food to cover to reduce predation risk. Predation risk has many other effects on foraging decisions apart from decreasing overall foraging behaviour. Many studies have shown that in high predation risk situations, animals will decrease the distance travelled in order to obtain food (Dill and Fraser, 1984), use more protected habitats, decrease food harvesting, increase food handling time and decrease overall activity (Lima, 1985; Brown *et al*., 1988; Vasquez, 1994). Therefore, predation risk can have a marked affect on where an animal will chose to eat, how much it will eat and what it will chose to eat. With predation having such a significant effect on the decisions animals make while foraging, it is not surprising that predation plays a role in microhabitat partitioning

(Kotler *et al*., 1991), where species more suited to risky microhabitats can become dominant and thrive in those environments and others suited to the less risky microhabitats are dominant there (Kotler, 1984; Brown *et al*., 1988; Abrahams and Dill, 1989).

Habitat choices are also influenced by other factors, such as competitors (Mitchell *et al*., 1990), the richness (in terms of net energy gained) of the patches in the habitat and the potential energetic benefit that these can have for the animal (Hanson and Green, 1989). Food resources tend to have patchy distributions in nature and according to foraging models, an animal will choose a patch according to its richness, such that patch-types are differentially valued according to net energy gain (Hanson and Green, 1989). Lewis (1980) suggested that grey squirrels (*Sciurus carolinensis*) chose a patch of lower quality acorns instead of high quality acorns, as the overall abundance of the lower quality acorns yields a higher net rate of energy intake. In a patch, however, the higher quality acorns are selected first, showing that in each case the squirrel selects for the higher energy yield option (Lewis, 1980). This is not always the case, however, since energy intake can be superseded by nutrient requirement, as occurs in dark-eyed juncos (*Junco hyemalis*) which maximise lipid and not energy intake (Thompson *et al*., 1987).

It is a complicated balance among patch richness, environment quality, search cost, and encounter rate that lead to the decisions of whether the animal will accept the patch, how long it will spend in that patch and what it eats in the patch (Hanson and Green, 1989; Johnson and Collier, 1989). The encounter rate of good and poor foraging opportunities can affect the choices of patch acceptance; as the encounter rates of good patch types decreases, animals should become less selective and accept patches of lower quality (Hanson and Green, 1989). Animals have to search for their food which incurs a cost, and minimizing this cost is beneficial. Therefore, as encounter rate with poor patches decreases, the cost of searching for food will increase and animals should accept more of these lower quality patch opportunities (Hanson and Green, 1989). More time and effort is spent exploiting all patch-types when environmental quality is poor (when the rates of acquiring food decreases), and consequently more food removed from a patch (Hanson and Green, 1989). High quality patches and food are usually exploited because these yield the greatest benefit (Vickery, 1984). However, similar to patch choice, Hanson and Green (1989) found that as the encounter rate with poor-food type increased (i.e. an abundance of a food type), the tendency was to reject the food but

as the encounter rate decreased, more poor-food types were accepted. The acceptance of poor patch/food types due to a low encounter rate with rich resources is seen as a generalist strategy, whereas in food rich environments animals should implement a specialist strategy and only select for rich patches (Hanson and Green, 1989).

1.3 Economic models

Consumer demand approaches using a demand curve have been used in behavioural studies to interpret the motivation of animals to acquire particular resources (Mason *et al.*, 1998). The demand curve takes into account the elasticity of demand for a particular resource, where consumption or usage changes in response to an increase in cost (Mason *et al.*, 1998). From this, an indication of the importance of particular resources that an animal is willing to work for can be determined (MacFarland, 1989, Mason *et al.*, 1998). Elasticity of demand can be evaluated using the equation:

$$E_d = \frac{(\Delta Q / \bar{Q})}{(\Delta P / \bar{P})} \qquad (1)$$

Where Q is the quantity demanded, P is the price of the item under consideration, $\bar{Q}$ is the average difference in quantity between two treatments and $\bar{P}$ is the average difference in price between two treatments. If the demand elasticity (E_d) is greater than 1, the demand is elastic and if the value is less than 1, the demand is inelastic (McConnel and Brue, 2005). The elasticity of demand from an ecological point of view can be seen as a change in consumption of a resource (Q) over the change in cost (P).

Elasticity describes the relationship between demand and cost, in which the demand is elastic when it changes more rapidly than a change in cost (i.e. when the value is <1). Therefore, if consumption of a resource decreases as it becomes more costly to obtain the resource, the response is elastic, whereas if the consumption of the resource does not change with increased cost, the response is inelastic (Faure and Lagadic, 1994). Resources with an inelastic demand are classified as necessities whereas resources with an elastic demand are luxuries (Mason *et al.*, 1998). However, if there is not a valid cost: reward ratio, true elasticity cannot be measured (Mason *et al.*, 1998). The cost and reward must co-vary as the

animal can compensate for an increase in cost by visiting the reward less often but increasing its time using the reward, and therefore the use of the reward remains unchanged for an increase in cost. An example where the cost and reward do not co-vary is when an animal has to pay a cost to reach an unlimited amount of food (reward). Therefore, when the cost increases, the animal can visit the food less often but can compensate by eating more each visit, leaving the total amount of food consumed unchanged regardless of the cost (Mason *et al*., 1998).

1.4 Rodent feeding behaviour

Rodents feed to meet a number of energetic and nutritional needs and use a variety of behavioural and physiological methods during foraging to satisfy these needs (Johnson *et al*., 1986; Johnson and Collier, 1987). 'Partial sampling' is common in rodents where they sample all the foods available to them; this behaviour may play a large role in determining the nutritional quality of the different foods available (Barnett, 1966; Barnet et al., 1978; Parshad and Jindal, 1991; Murray and Dickman, 1997). It is also suggested that different seeds are sampled to different degrees as they might satisfy different dietary needs of an individual (Murray and Dickman, 1997). In addition to the nutritional qualities of food, many other factors such as size, shape, texture and palatability can influence preference and consequently the diet of a rodent (Parshad and Jindal, 1991; Murray and Dickman, 1997; Johnson and Collier, 2001; Munoz and Bonal, 2008). For example, previous studies have shown that granivorous rodents prefer large over small seeds, because large seeds contain a greater nutritional content (Kerley and Erasmus, 1991; Garb *et al*., 2000; Vander Wall 1994, 2003). The lesser bandicoot rat (*Bandicota bengalensis*) prefers softer smaller seeds such as millet, and its lesser preference for larger maize seeds might be due to the hardness of maize, although maize is hoarded the most (Sridhara and Krishnamoorthy, 1978).
Palatability can influence the meal size and rate at which food is eaten, with more palatable foods eaten in greater amounts and at a faster rate (Johnson *et al*., 1986; Johnson and Collier, 1987; Johnson and Collier, 2001). Intake rate controls caloric ingestion, where rodents are thought to use sensory information, perhaps from the stomach or mouth, to monitor and control intake (Johnson *et al*., 1986). Meal size, intake rate, meal frequency, palatability and caloric intake are some of the parameters deciding the feeding patterns of rodents, indicating

that behavioural strategies as well as physiological outcomes of ingestion determine the meal patterning (Johnson *et al*., 1986; Johnson and Collier, 1987).

1.5 Bushveld gerbil biology

The Bushveld gerbil (*Gerbilliscus leucogaster*) is a medium-sized (48–98 g) rodent that presents no sexual dimorphism (Skinner and Chimimba, 2005; Lötter, 2010). It has large eyes and well-developed ear bullae, indicating high visual acuity and a nocturnal habit, as well as well-developed hearing. The well-developed hind legs, characteristic of all gerbils, enable bipedal and thereby rapid locomotion, freeing the forelimbs for processing food (Mares, 1993). Other distinctive morphological features of Bushveld gerbils include tawny-coloured upper parts with white under parts, white hands and feet, and a distinctive dark band down the entire length of its tail. The dark tail band distinguishes the Bushveld gerbil from its congener *G. brantsii*, an important diagnostic characteristic that can be used to tell the species apart in syntopy (Skinner and Chimimba, 2005; Stuart and Stuart, 2007; Lötter, 2010).

Bushveld gerbils have a widespread distribution in Africa, and in the southern African sub region, they occur in large parts of Namibia, Botswana, Zimbabwe, Mozambique and Swaziland. In South Africa, they are found in north-eastern KwaZulu-Natal, Limpopo, the North-West Province, and parts of Gauteng, Mpumalanga, the Free State and the Northern Cape, north of the Orange River (Skinner and Chimimba, 2005). The Bushveld Gerbil occupies a wide variety of different biomes in South Africa, such as open grassland and woodland as well as Bushveld and Thornveld (De Graaff, 1981; Downs and Perrin, 1994; Skinner and Chimimba, 2005).

Gerbilliscus leucogaster is nocturnal and burrows in sandy soils, usually at the base of trees or bushes but also in the open (De Graaff, 1981; Lötter and Pillay, 2008). It constructs small scattered warrens, comprising of excavated burrows 40–50 mm in diameter in sandy soils, whereas in harder soil, it uses existing holes in termite mounds or shallow excavations under logs (De Graaff, 1981).

Gerbilliscus leucogaster is an unspecialised granivore which consumes a wide range of seeds but also consumes insects and other plant material (Perrin and Swanepoel, 1987; Skinner &

Chimimba, 2005), which is also revealed in its unspecialised gut structure (Kinahan & Pillay, 2008). Therefore, the Bushveld gerbil is likely to be faced with an array of different types of food and it needs to make decisions about the food it consumes, under various motivational states (as discussed above). It is therefore an ideal model to test how small rodents in general and a granivore in particular make decisions about food consumption. My study tests motivation and decision-making in Bushveld gerbils but goes a step further by investigating the responses of individual gerbils, which to my knowledge makes mine the first study to consider individual effects.

1.6 Aims, Objectives and Predictions

To gain insight into motivation and decision-making in Bushveld gerbils, I studied their foraging behaviour to ascertain how different cost/benefit situations would affect their foraging decisions. I also used elasticity of demand to further investigate the consistency of their decision making. I had three main objectives.

1. *Seed Preference*.
To establish whether Bushveld gerbils displayed individual seed preference, I presented the gerbils with 5 different commercial seeds and analysed their seed choice (which seeds they chose to eat) and consumption. I then used their least and most preferred seeds to set up high and low rewards in further experiments.

2. *Foraging behaviour*.
a) In order to establish the decisions made under varying costs to obtain seeds of different reward values, I presented gerbils with different costs (i.e. impeded their access to a feeding areas) to access their least and/or most preferred seeds (presented separately) and then assessed how much the gerbils were willing to work to access food of different quality. I also recorded whether/how their foraging behaviour was influenced by varying costs and rewards. I predicted that the gerbils would be willing to work harder to access seeds they most preferred than those they least preferred, possibly because it can be assumed that the most preferred seeds would provide more energy/nutrients.

b) I also used the preference tests to select two seeds that all gerbils preferred (to be presented at the same time) and then to investigate how cost (access to a feeding area) would affect seed choice and consumption. Again, I recorded whether/how foraging behaviour was affected. I predicted that with increased cost to access the seeds, the gerbils would choose seeds with high energy content to offset the cost. When the cost to access the seeds is lower, the gerbils will expend less energy obtaining the seeds and are likely to be less selective in their seed choice.

c) Depending on the experiment, I presented the seed as piled and/or scattered to assess how the presentation of the seeds affected the gerbils' decisions in seed choice, consumption, willingness to work, and their foraging behaviour. I predicted that scattered seeds would increase the cost of obtaining seeds and would therefore lead to decisions that would minimise this cost. I also predict that gerbils would be more willing to work, forage and consume more in piled situations.

3. *Predation Risk*.

To establish how the perceived cost of predation affects foraging behaviour under different cost/benefit scenarios, I used the odour of a potential predator and a light source as proxies of predation risk. I investigated seed choice and consumption and foraging behaviour by the gerbils. I predicted that under the perceived cost of predation, the gerbils would most likely consume fewer seeds and spend more time in an area offering protection (cover).

CHAPTER 2: MATERIALS AND METHODS

2.1 Animal housing

Five male and six female wild caught adult Bushveld gerbils (*Gerbilliscus leucogaster*), trapped near Orkney (26.935423 S; 26.694667 E), North-West Province, South Africa, were used as study subjects in all experiments. The animals were trapped by Dr Mark Keith early January 2010 using live traps placed in a random pattern and baited with peanut butter. I used few gerbils due to limited availability and to comply with ethics regulations of using fewer test subjects. The gerbils were housed at the Milner Park Animal Unit of the University of the Witwatersrand, under standard environmental conditions of 14 hour light and 10 hour dark cycle (lights on at 05h00; simulating summer on the highveld) at a temperature of approximately 24°C. They were housed alone in standard Lab-o-tec™ cages (410 x 245 x 230 mm) and provided with coarse wood shavings for bedding and hay for nesting material; Bushveld gerbils are usually solitary (Lötter and Pillay, 2008), such that the solitary housing conditions in captivity did not provide additional stress. Gerbils were acclimated to laboratory conditions for 3 months prior to experiments. Before experiments, the gerbils were fed approx 3 g mouse cubes, 3 g seeds, 2 g fruit or vegetable (e.g. lettuce, apple) daily and had water at all times. Two weeks before experiments, the gerbils were housed individually in tanks (450 x 290 x 350 mm), designated home tanks, for the remainder of the study and provided with coarse wood shavings, hay, cover (nest box) and water (*ad libitum*). The gerbils were then placed on a restricted diet consisting of a reduced quantity of approx 1 g mouse cubes, 2 g commercial rice cereal (Pick n' Pay no name brand) and 1–2 g lettuce. The gerbils were fed the cereal in order to reduce their protein and fat intake. The rice cereal had a protein content of 6 g/100 g and fat of 0.2 g/100 g. Between treatments in each experiment, gerbils received only the 2 g of rice cereal (apart from the seed rewards given during experiments; see below) in their home tank throughout the experiment, while gerbils not used in experiments received the restricted diet only (as described above).

2.2 Test Apparatus

Experiments took place in an experimental tank (identical to the home tank) that was connected to the home tank with a PVC pipe (30 cm long x 5 cm wide with an internal

diameter at 4.5 cm) that allowed the gerbils to move freely between the tanks. The experimental tanks were modified to include a Perspex partition, 14 cm from the entrance, and a perspex door (6 x 6 cm) fitted at the bottom centre of the partition that moved freely in both directions (Figure 1a, 1b), allowing the gerbils to move back and forth between the two parts of the experimental tank. The door was not fixed to the partition, so that I could unhinge and change the door when required for experiments (see below); the gerbils could not remove the door. Small holes were drilled in the perspex partition, allowing the gerbils to smell the seeds placed on the other side of the partition during experiments. The experimental tanks were furnished with river sand into which seeds (described below) were placed.

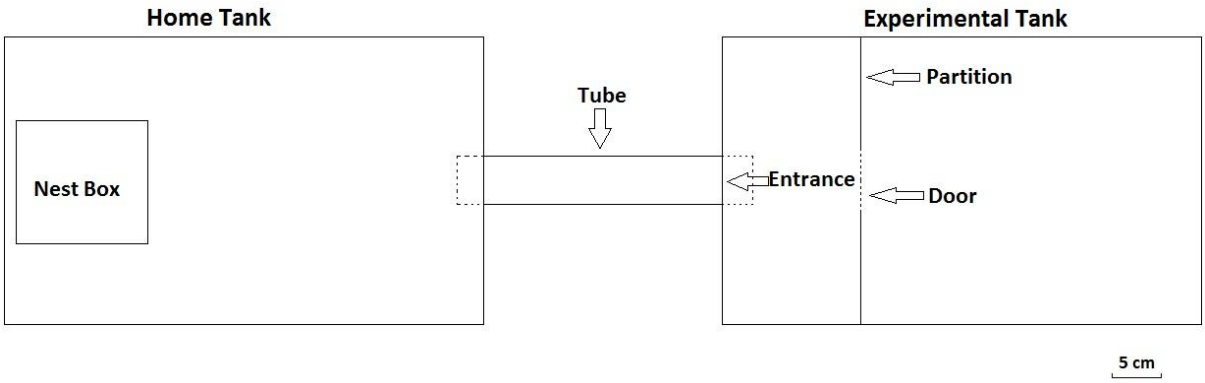

Figure 1a. Top view of the experimental set up with the home tank containing nest box connected to the experimental tank via a plastic tube. The entrance, partition and door are shown.

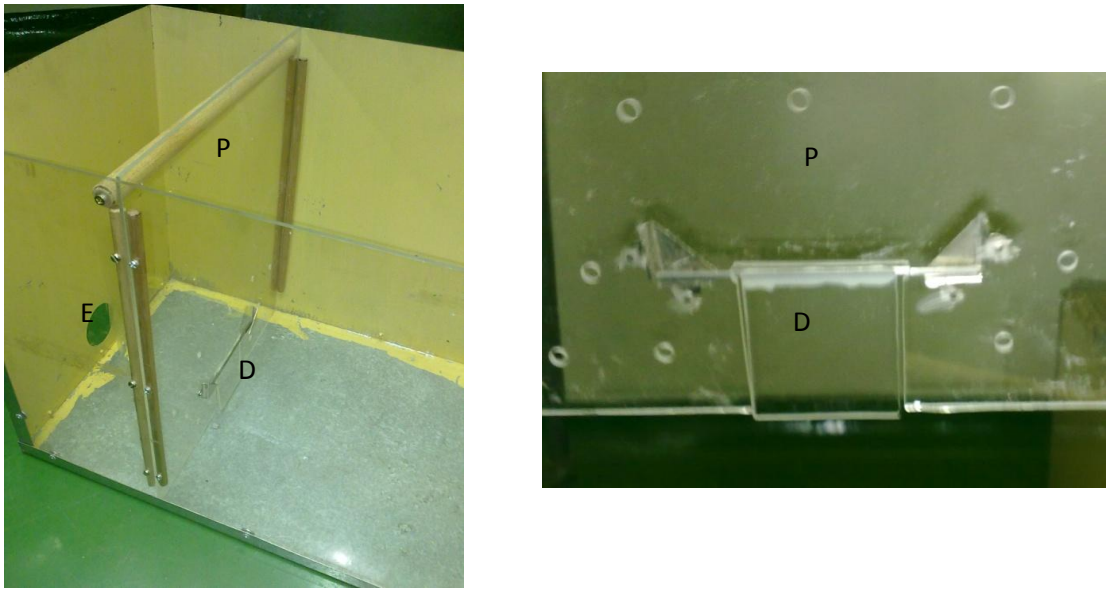

Figure 1b. Experimental tank with the entrance at the front (E) and perspex partition (P) with door (D) at the bottom centre of the partition.

2.3 Seed preference

Individual gerbils underwent a seed preference test a month before experiments commenced, during which each animal was provided with five commercial seeds, namely maize, sunflower seeds, wild rice, sorghum and wild oats (Table 1). Commercial seeds were used as they are easily obtained, the energy and nutrient content are known from the suppliers (Table 1) and have been consumed previously by gerbils (Kinahan & Pillay, unpublished). All five seed types were presented at once in the experimental tank, representing a cafeteria choice test (Murray and Dickman, 1997). A standard quantity of 50 seeds of each seed type (250 in total) were weighed and presented to each gerbil. The seeds were placed in the tanks at approximately 13h00 when the experiment began and then left overnight. The following morning (at approximately 10h00), the remaining seeds were weighed (to the nearest 0.1 gram) and counted. The weight data were then used to determine the most preferred (seeds eaten the most) and least preferred (seeds eaten the least) seeds for individual gerbils, which were used in further experiments to create a low and high reward. The food preference tests allowed the gerbils to become familiar with the experimental tank and the action of the perspex door and partition (Figure 1).

Table 1. The energy and nutritional content, morphology and mass of the five commercial seeds used to test seed preference in Bushveld gerbils. CHO = carbohydrate. Data provided on the seed packaging.

Seed	Energy (KJ/g)	% protein	% fat	% CHO	% fibre	toughness	Length (mm)	Mass per seed (g)
Sunflower	25.16	11	13	86	6	coat but not tough	11.88	0.070
Dried maize	17.37	12.8	3	82.4	2.4	hard coat	10.65	0.330
Sorghum	17.37	11	3	75	0	hard	4.15	0.027
Wild oats	16.3	14	7.2	67	22	soft coat	10.43	0.036
Wild rice	15.27	4	1.5	35	3	hard	8.19	0.034

2.4 Decisions made under different cost/reward scenarios

A behaviour an animal performs has different associated costs and benefits. Therefore, animals must weigh up the costs and benefits before making a decision about which behaviour to perform (MacFarland, 1989). An important type of cost-benefit decision making

occurs when animals must decide whether to invest a greater effort in a particular behaviour to receive a greater reward (Walton *et al*., 2006). Four experiments, as detailed below, were conducted to test foraging decisions made by Bushveld gerbils. The general protocol was to impose a low cost or a high cost for individual gerbils to access seeds that they most preferred (high reward) and least preferred (low reward) in an experimental tank. The cost was the weight of the door leading from the home tank to the experimental tank (Figure 1).

Pilot experiments were run to determine the maximum weight of the door that individual gerbils could push through, which I calculated to be more or less 100% of the gerbil's mass. Steel plates were then stuck onto Perspex doors to create a heavy door approximately 100% of each gerbil's mass. These weighted doors were used in experiments to create a known high cost. The perspex door (i.e. no additional mass) and weighted door therefore represented low and high costs respectively. Based on the data obtained from the food preference trials (above), the most or least preferred seeds were used and placed in the experimental tank to create low and high rewards. The preference of each gerbil was taken into consideration, so that both the costs and rewards were individually tailored to each gerbil. The gerbils were weighed regularly before and after every experiment to monitor any weight changes. When the gerbils mass changed by more or less than 5 g, another weighted door was constructed for that particular gerbil. I chose 5 g variation as this was approximately the upper limit to which the gerbils could push and any change beyond this weight would have made the door too heavy or too light (information from pilot studies) for the purpose of the experiments.

Each experiment comprised of 4 treatments, the sequence of which was randomly run for each gerbil, and each experiment was a repeated measures design. Each treatment was run for one hour during the dark part of the light-dark cycle, between approximately 19h00 and 20h00 (i.e. as soon as the lights in the animal room went off). When a gerbil was used in an experiment, it was randomly subjected to all four treatments consecutively (i.e. each gerbil underwent four consecutive days of treatments per experiment). Only four gerbils could be run at a time due to restrictions on equipment and space. Therefore, there were a few weeks between re-use of gerbils in the subsequent experiments. The behaviours of the gerbils were video recorded (using Sony DCR SX 44E cameras) for this hour (19h00-20h00) under red lights to facilitate recording in the dark.

The first two experiments were designed to establish the cost that the gerbils were willing to pay to access seeds they preferred the most and least (Objective 2a). Two grams of seeds were weighed and counted, and presented as either piled or scattered. Piled referred to seeds placed in a pile in the centre of the experimental tank and scattered referred to seeds scattered and tossed in the sand lightly, ensuring the gerbils had to search and dig for the seeds. Scattered seeds placed an extra cost on the gerbils because they had to work to obtain the seeds. Both piled and scattered presentations were used to cover all possibilities of how gerbils would encounter seeds under natural conditions. Below, I provide the four treatments in each experiment in relation to the combination of cost-reward of the weighted door and the seed preference. The abbreviations used to represent each treatment are shown below alongside each treatment.

<u>Experiment 1. Piled seed experiment</u>

1. Low cost (low weight door)/ Low reward (least preferred seeds) - LcLr
2. Low cost (low weight door)/ High reward (preferred seeds) - LcHr
3. High cost (weighted door)/ Low reward (least preferred seeds) - HcLr
4. High cost (weighted door)/ High reward (preferred seeds) - HcHr

<u>Experiment 2. Scattered seed experiment</u>

1. Low cost (low weight door)/ Low reward (least preferred seeds) - LcLr
2. Low cost (low weight door)/ High reward (preferred seeds) - LcHr
3. High cost (weighted door)/ Low reward (least preferred seeds) - HcLr
4. High cost (weighted door)/ High reward (preferred seeds) - HcHr

<u>Experiment 3. Mixed seed experiment</u>

A third experiment was conducted to establish the decisions made by the gerbils in experiments 1 and 2, after experiencing the cost induced by the weighted doors, the seeds they choose, how much they ate and for how long they foraged. Experiment three investigated seed choice under different cost/reward situations (Objective 2b). I used two seeds of different size and quality (nutritional value; Table 1) that all the gerbils preferred (namely, sunflower and sorghum). Presenting the gerbils with two seeds they prefer at the same time gave the gerbils a ‘choice’ of which seed to eat rather than just whether it was worth eating the seed they were presented with, as in experiment 1 and 2. Two grams of both

seeds were offered at the same time (mixed), creating the same reward in each experiment and therefore the presentation (piled/scattered) was varied to provide a low or high reward. The piled presentation was a high reward as seeds were easily obtained while scattered was a low reward as the gerbils had to search to obtain the seeds.

1. Low cost (low weight door)/ Low reward (scattered) - LcLr
2. Low cost (low weight door)/ High reward (piled) - LcHr
3. High cost (weighted door)/ Low reward (scattered) - HcLr
4. High cost (weighted door)/ High reward (piled) - HcHr

2.5 Decisions made under perceived predation

Animals use cues such as illumination level and odour to measure the risk of predation (Vasquez, 1994; Brown *et al*., 1988; Wisenden, 2000). Thus, a white light source was placed above the experimental tanks to simulate a full moon and thereby greater predation risk. In addition, fresh Badger urine obtained from the Johannesburg Zoo, South Africa was used to provide odour cues of a potential predator through smell. Both predation risks were present in all four treatments. A series of cost/reward treatments were conducted in order to ascertain whether predation risk affected the behaviour and decisions made by the gerbils (below). I chose to use the same protocol as experiment three because providing gerbils with a choice of seeds rather than only one option would provide for a more insightful experiment.

<u>Experiment 4. Predation experiment</u>

1. Low cost (low weight door)/ Low reward (scattered) - LcLr
2. Low cost (low weight door)/ High reward (piled) - LcHr
3. High cost (weighted door)/ Low reward (scattered) - HcLr
4. High cost (weighted door)/ High reward (piled) - HcHr

At the end of all experiments, the seeds after each hour of treatment were counted and weighed (to the nearest 0.1 g) to establish the quantity and mass of seeds eaten during the treatments. The percentage of seeds eaten for each treatment in all experiments was then calculated. Using Observer XT 9™ (Noldus Information Technologies), the frequency, duration and rates of the behaviours exhibited by the gerbils during the experiments in the

experimental tank were scored for the hour of a treatment. The behaviours scored are provided in Table 2. Foraging behaviour comprises of three components, including acquisition (including searching for food), processing/handling food and ingestion. Because of the difficulties of separating out these components in the video footage under red light, food acquisition was included under Explore behaviour, and handling and ingestion were grouped under Seed consumption (Table 2).

Table 2. Descriptions of the different behaviours for gerbils scored during experiments. The types of behavioural recording (duration and/or frequency) are presented for each behaviour.

Behaviour	Description
Home	Use of the home tank (duration/frequency)
Enter	Entering the experimental tank (frequency)
Door	Passing through the experimental door (frequency)
Seed Consumption	Seed was held in the forepaws for consumption or carrying back to home tank (duration)
Alert/Attentive	Raising of the front paws off the ground, standing on the hind legs, ears up and gerbil motionless (duration/frequency)
Dust bathing	Rolling onto their backs in the sand (duration)
Inactive	Motionless for more than 5 seconds (not including attentive behaviour) (duration)
Explore	Moving around the experimental tank, including sniffing, scratching and food acquisition (duration)
Other	Other behaviour that does not fall into the above categories (duration)

2.6 Data analysis

All analyses were performed using Statistica 7.1 (Statsoft Inc, www.statsoft.com). The dataset met the assumptions of normality (Shapiro-Wilk's test) and homogeneity of variances (Levene's test) or were square root transformed to meet the assumptions of normality. For each experiment, I used a repeated measures general linear model (GLM) to assess whether the responses of individual gerbils were different across treatments. The sex of the gerbil was included as a categorical predictor and mass as a continuous predictor. For the duration data, six behaviours (Other was excluded because few behaviours occurred in this category) were included as multiple response variables, resulting in a repeated measures MANCOVA design. For the frequency data (home, enter, door and attentive), each variable was analysed separately using a repeated measures ANOVA; mass was not a significant predictor of behaviours and was not included in these analyses (see Results). For the seed consumption data, I ran a repeated measures design for each treatment for the percentage number and

percentage mass of seeds consumed. Rate (frequency) and percentage (seed consumption) data were arcsine square-root transformed to meet the assumptions of normality prior to analyses. A Fisher's post hoc test was used to obtain pairwise comparisons of levels for significant categorical predictors. Energy obtained from seeds in experiments was calculated using the energy (Kj/g) of each seed (Table 1) multiplied by the total mass (g) of seed eaten. I ran a repeated measures design for each treatment for the energy obtained from seeds and Fisher's post hoc tests were used to obtain pairwise comparisons of levels for significant categorical predictors. In all cases the model level significance was $\alpha = 0.05$.

The demand elasticity (E_d) for seeds eaten during treatments for each gerbil and all gerbils in each experiment was calculated using the economic equation (1) in the introduction. The mass of seeds eaten was used to calculate the quantity demanded (Q) to standardise measurements across all experiments, since all the gerbils received the same initial mass of seeds. Pricing (P) was calculated differently depending on the experiments.

For experiments 1 and 2, high cost was assigned a value of 6 because the door during high cost was approximately six times greater than that of the low cost door; consequently, low cost was assigned a value of 1. High reward was assigned a value of 1 (most preferred seed out of 5 seeds) and low reward was assigned a value of 5 (Least preferred seed out of 5 seeds). The Price (P) values for treatments were:
LcHr: 1x1 = 1
LcLr: 1x5 = 5
HcHr: 6x1 = 6
HcLr: 6x5 = 30

For experiments 3 and 4, high cost and low cost was the same as for experiments 1 and 2, above. Low reward (scattered) was assigned a value of 18 as the area the seeds covered was approximately 18 times greater than that of high reward (piled); consequently, high reward was given a value of 1. The Price (P) values for treatments were:
LcHr: 1x1 = 1
LcLr: 6x1 = 6
HcHr: 1x18 = 18
HcLr: 6x18 = 108

CHAPTER 3. RESULTS

3.1 Seed preference

Seed preference tests showed that individual gerbils preferred different seeds (Table 3), with the majority of gerbils preferring sunflower seeds (gerbils 5, 6, 8, 9, 10, 11), 2 gerbils preferring oats (gerbils 1, 7) and 3 preferring sorghum (gerbils 2, 3 and 4). Interestingly, all gerbils showed a clear preference (i.e. there was no ambiguity in seed preference).

Table 3. Seed consumption (by mass) of the five commercial seeds during the seed preference test, Values highlighted in red indicate the seed most preferred by the individual gerbils while values highlighted in blue indicate seeds least preferred.

			% Seed Eaten				
Gerbil	**Sex**	**Mass (g)**	**Wild Rice**	**Sunflower**	**Maize**	**Oats**	**Sorghum**
1	**male**	**97.5**	52.94	51.72	20.00	94.44	92.31
2	**female**	**90.8**	64.71	83.33	8.43	33.33	100.00
3	**female**	**132.3**	36.84	78.57	18.99	87.50	100.00
4	**male**	**113.3**	88.89	40.00	9.20	43.75	100.00
5	**male**	**98.3**	27.78	73.33	22.37	68.75	61.54
6	**female**	**100.8**	29.41	100.00	18.06	18.75	76.92
7	**female**	**69**	12.50	61.29	8.50	100.00	69.23
8	**female**	**81.3**	6.67	75.76	10.06	16.67	23.08
9	**male**	**101.3**	0.00	62.07	14.67	6.67	30.77
10	**male**	**105.2**	10.53	100.00	14.09	0.00	30.77
11	**female**	**77.8**	16.67	85.29	7.79	37.50	53.85

3.2 Decisions made under different cost/reward scenarios

3.2.1 Experiment 1 - Piled seed experiment

In this experiment, I tested the costs gerbils were willing to pay to access seeds they preferred the most and seeds they preferred the least in a piled presentation of the seeds. Treatment significantly influenced seed consumption for both number of seeds eaten ($F_{3,27} = 5.82$, $P =$

0.003) and mass of seeds eaten ($F_{3,27}$ = 5.17, P = 0.006). Post hoc tests revealed that most seeds were consumed in the LcHr treatment and the least seeds consumed in the HcLr treatment (Figure 2), with the LcLr and HcHr treatments occupying an intermediate position. A similar pattern was observed for the mass of seeds consumed (Figure 3). Neither the sex of the gerbil nor the sex*treatment interaction influenced the number of seeds consumed ($F_{1,9}$ = 0.002, P = 0.969 ; $F_{3,27}$ = 0.58, P = 0.632, respectively) and the mass of seeds eaten ($F_{1,9}$ = 0.05, P = 0.822 ; $F_{3,27}$ = 0.83, P = 0.487, respectively).

No gerbils showed any elastic responses in the LcHr versus HcLr treatment comparison and gerbils 1, 2, 5, 7 showed no elastic responses to any treatment comparison. However, gerbils 3, 4, 6, 8, 9,10 and 11 showed at least one elastic response in the varied treatment comparisons (Table 4). Comparisons of treatments revealed that 18% were elastic and 82% were inelastic. However when looking at the demand curves for all the gerbils (total), all were inelastic responses.

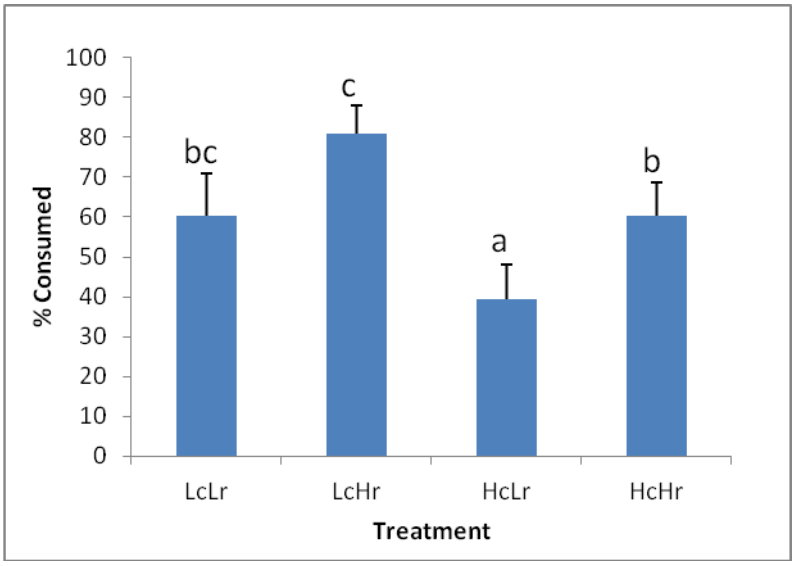

Figure 2. Mean (+SE) number of seeds eaten in 4 treatments. LcLr = Low cost Low reward, LcHr = Low cost High reward, HcLr = High cost Low reward and HcHr = High cost High reward. The LcHr treatment had the highest percentage number of seeds eaten while the HcLr treatment has the least. Bars sharing the same letters indicate non-significant differences (Fisher's post hoc tests).

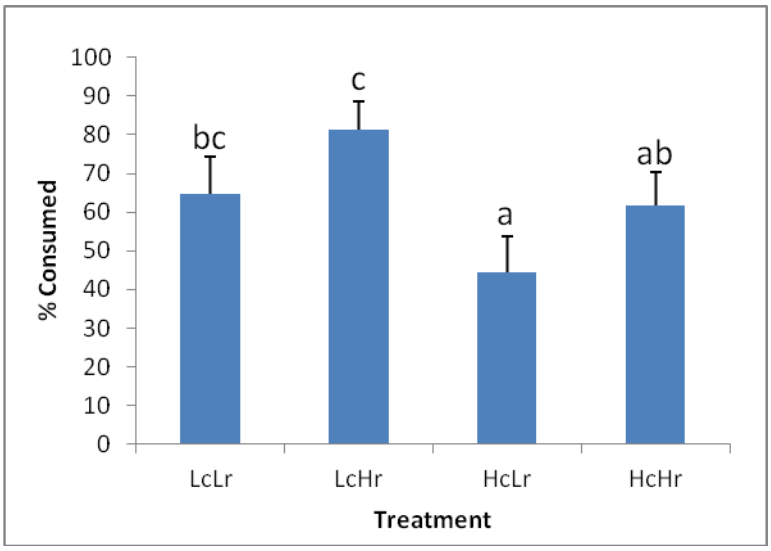

Figure 3. Mean (+SE) mass of seeds eaten in 4 treatments. LcLr = Low cost Low reward, LcHr = Low cost High reward, HcLr = High cost Low reward and HcHr = High cost High reward. The LcHr treatment has the highest percentage number of seeds eaten while the HcLr treatment has the least. Bars sharing the same letters indicate non-significant differences (Fisher's post hoc tests).

Table 4. Pairwise comparisons of demand curve functions between treatments for Bushveld gerbils provided with piled seeds. Low reward being seeds least preferred and high reward being seeds most preferred. Elastic responses are highlighted in red.

Gerbil	LcHr vs LcLr	LcHr vs HcHr	LcHr vs HcLr	LcLr vs HcHr	LcLr vs HcLr	HcLr vs HcHr
1	0.000	0.000	0.189	0.000	0.247	0.265
2	0.125	0.000	0.143	0.917	0.300	0.200
3	0.122	0.297	0.356	1.467	0.363	0.196
4	1.093	0.311	0.238	9.000	1.145	0.000
5	0.038	0.036	0.382	0.000	0.531	0.569
6	0.000	0.467	0.000	3.667	0.000	0.500
7	0.318	0.200	0.405	0.786	0.255	0.375
8	0.625	0.000	0.844	4.583	0.778	1.184
9	0.136	0.108	0.097	1.833	0.000	0.250
10	0.079	1.145	0.967	8.800	1.253	0.500
11	0.794	0.056	0.566	5.500	0.000	0.750
Total	**0.235**	**0.099**	**0.398**	**0.955**	**0.320**	**0.464**

Treatment significantly influenced the energy intake from the seeds consumed ($F_{3,27} = 6.87$, $P = 0.001$) but there was no effect of sex ($F_{1,9} = 0.23$, $P = 0.640$) or treatment*sex ($F_{3,27} = 0.39$, $P = 0.761$). Energy acquisition from seeds was greater in the high reward treatments, with the LcHr treatment having the most energy consumed while HcLr the least (Figure 4)

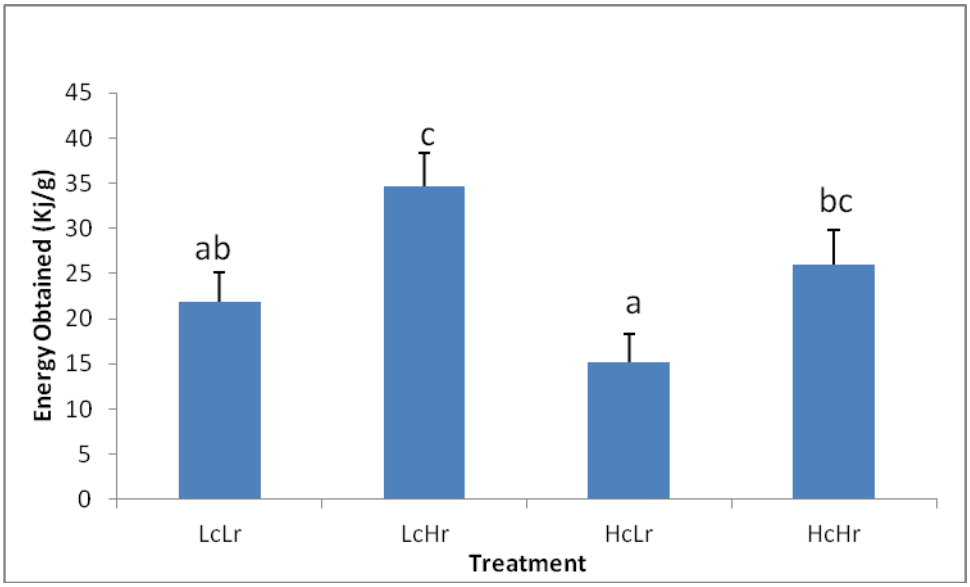

Figure 4. Mean (+SE) energy (Kj/g) obtained from seeds in 4 treatments. LcLr = Low cost Low reward, LcHr = Low cost High reward, HcLr = High cost Low reward and HcHr = High cost High reward. The most energy obtained was in the LcHr treatment while the least occurred in the HcLr treatment. Bars sharing the same letters indicate non-significant differences (Fisher's post hoc tests).

Treatment was a significant predictor for the duration of only explore behaviour (Wilks $\lambda_{3,8}$ = 0.38, P = 0.045; MANCOVA; Figure 5), but none of the other behaviours was predicted by treatment (Figure 6): home (Wilks $\lambda_{3,8}$ = 0.86, P = 0.729), attentive (Wilks $\lambda_{3,8}$ = 0.81, P = 0.624), dust bath (Wilks $\lambda_{3,8}$ = 0.69, P = 0.366), seed (Wilks $\lambda_{3,8}$ = 0.71, P = 0.407), inactive (Wilks $\lambda_{3,8}$ = 0.93, P = 0.895) and scratching (Wilks $\lambda_{3,8}$ = 0.76, P = 0.512). There was no sex (Wilks $\lambda_{7,3}$ = 0.11, P = 0.136) or mass effect (Wilks $\lambda_{7,3}$ = 0.43, P = 0.690) on duration of behaviours. The highest duration of explore behaviour was in the LcHr treatment and the least in HcHr (Figure 5).

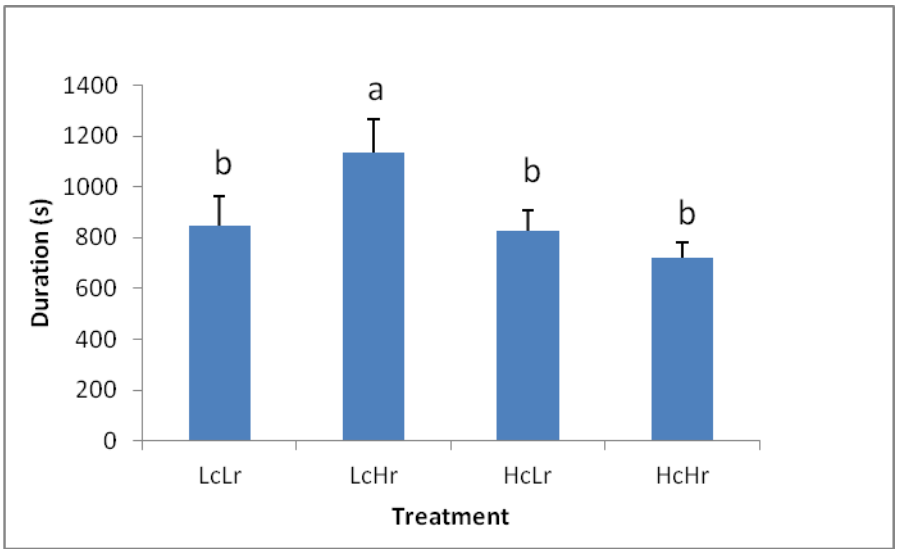

Figure 5. Mean (+SE) duration of explore behaviour in 4 treatment s. LcLr = Low cost Low reward, LcHr = Low cost High reward, HcLr = High cost Low reward and HcHr = High cost High reward. The highest duration of explore behaviour occurred in the LcHr treatment and the least in HcHr treatment. Bars sharing the same letters indicate non-significant differences (Fisher's post hoc tests).

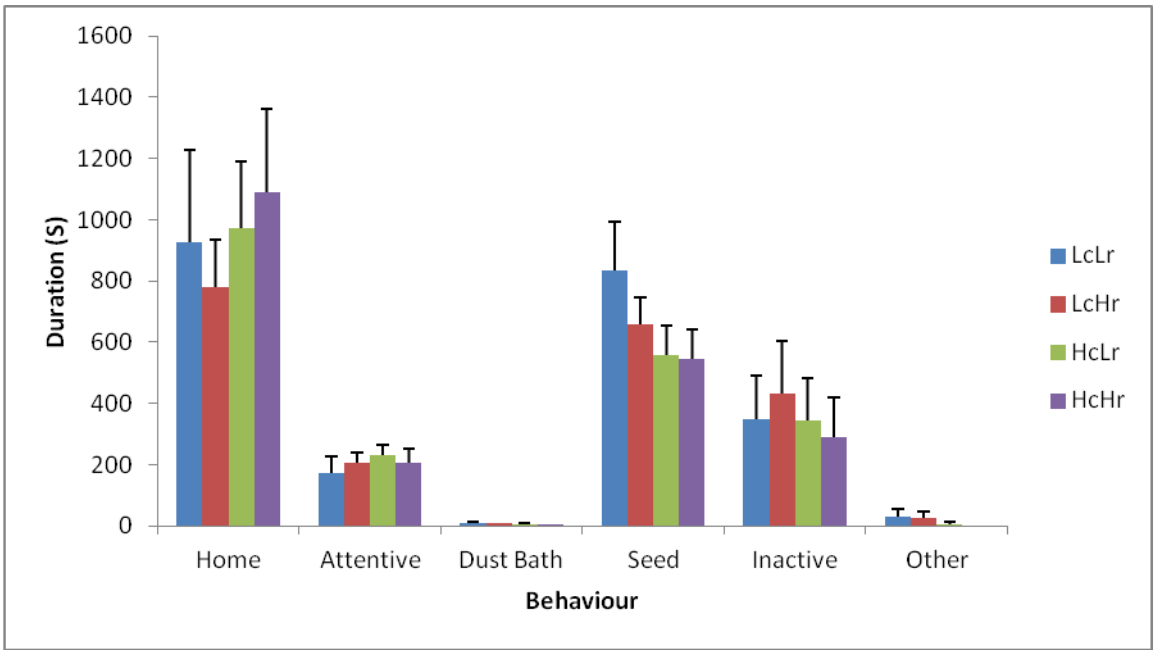

Figure 6. Mean (+SE) duration of non-significant behaviours in 4 treatments. LcLr = Low cost Low reward, LcHr = Low cost High reward, HcLr = High cost Low reward and HcHr = High cost High reward.

For the frequency of behaviours, treatment was a significant predictor of door usage ($F_{3,27}$ = 9.65, P < 0.001) only, with door usage occurring significantly more frequently in low cost treatments than high cost treatments (Figure 7). There was no significant sex ($F_{1,9}$ = 0.09, P = 0.776) and treatment*sex ($F_{3,27}$ = 1.29, P = 0.297) effects for door usage. Frequency of enter,

home and attentive were not affected by treatment ($F_{3,27}$ = 1.59, P = 0.215 ; $F_{3,27}$ = 1.64, P = 0.204 ; $F_{3,27}$ = 1.36, P = 0.275, respectively), sex ($F_{1,9}$ = 0.08, P = 0.778 ; $F_{1,9}$ = 0.06, P = 0.819; $F_{1,9}$ = 0.05, P = 0.834, respectively) and treatment*sex ($F_{3,27}$ = 0.38, P = 0.765 ; $F_{3,27}$ = 0.45, P = 0.721 ; $F_{3,27}$ = 1.32, P = 0.298, respectively); these data are provided in Appendix 1.

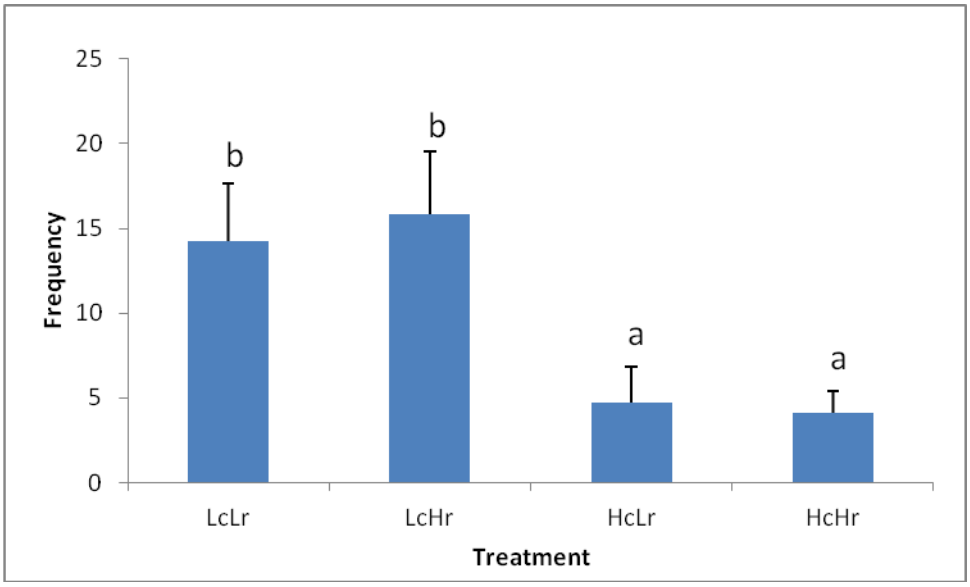

Figure 7. Mean (+SE) frequency of door usage in 4 treatments. LcLr = Low cost Low reward, LcHr = Low cost High reward, HcLr = High cost Low reward and HcHr = High cost High reward. The highest amount of door use occurred in the LcHr treatment and the least in the HcHr treatment. Bars sharing the same letters indicate non-significant differences (Fisher's post hoc tests).

3.2.2 Experiment 2 - Scattered seed experiment

In this experiment, I tested the costs gerbils were willing to pay to access seeds they preferred the most and seeds they preferred the least in a scattered presentation of the seeds.

Again (as in Experiment 1), treatment significantly influenced seed consumption for both number of seeds eaten ($F_{3,27}$ = 6.22, P = 0.002) and mass of seeds eaten ($F_{3,27}$ = 5.51, P = 0.004). Fisher's post hoc tests revealed the greatest number and mass of seeds were consumed in the high reward treatments, with the LcHr treatment having the highest number and mass of seeds consumed and the HcLr treatment having the least (Figures 8 and 9).

Neither sex nor the sex*treatment interaction influenced the number of seeds consumed ($F_{1,9}$ = 1.96, P = 0.195 ; $F_{3,27}$ = 0.67, P = 0.577, respectively) and the mass of seeds eaten ($F_{1,9}$ = 2.60, P = 0.141 ; $F_{3,27}$ = 0.64, P = 0.593, respectively).

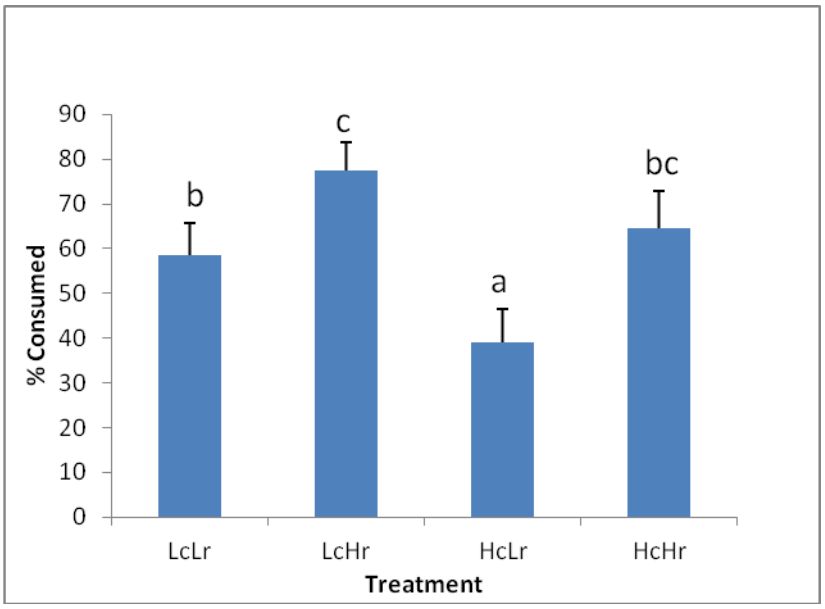

Figure 8. Mean (+SE) number of seeds eaten in 4 treatments. LcLr = Low cost Low reward, LcHr = Low cost High reward, HcLr = High cost Low reward and HcHr = High cost High reward. The LcHr treatment has the highest percentage number of seeds eaten while the HcLr treatment has the least. Bars sharing the same letters indicate non-significant differences (Fisher's post hoc tests).

No gerbil displayed any elastic responses in the LcHr versus LcLr and LcHr versus HcHr comparisons (Table 5). However, all gerbils showed an elastic response when comparing the LcLr and HcHr treatments. Gerbils 1 and 4 also showed elastic responses with the LcHr versus HcLr, LcLr versus HcLr and HcLr and HcHr treatments. For the comparisons between treatments for individual gerbils, 26% were elastic and 74% were inelastic. When looking at the demand curves for all the gerbils (total), however, all were inelastic responses.

Treatment significantly influenced the energy intake from the seeds consumed ($F_{3,27} = 9.11$, $P < 0.001$) but there was no effect of sex ($F_{1,9} = 1.15$, $P = 0.311$) or treatment*sex ($F_{3,27} = 0.30$, $P = 0.826$). Energy acquisition from seeds was greater in the high reward treatments, with the LcHr treatment having the most seed energy obtained while HcLr the least (Figure 10).

Treatment was a significant predictor for the duration of only explore behaviour in the gerbils (Wilks $\lambda_{3,8} = 0.29$, $P = 0.015$; MANCOVA; Figure 11). Treatment did not influence any other behaviour (Figure 12): home (Wilks $\lambda_{3,8} = 0.79$, $P = 0.569$), attentive (Wilks $\lambda_{3,8} = 0.83$, $P = 0.676$), dust bath (Wilks $\lambda_{3,8} = 0.78$, $P = 0.545$), seed (Wilks $\lambda_{3,8} = 0.52$, $P = 0.134$), inactive (Wilks $\lambda_{3,8} = 0.92$, $P = 0.881$) and scratching (Wilks $\lambda_{3,8} = 0.55$, $P = 0.163$). There was no sex (Wilks $\lambda_{7,2} = 0.001$, $P = 0.257$) or mass effect (Wilks $\lambda_{7,2} = 0.004$, $P = 0.125$) on duration of

behaviours. The duration of explore behaviour was significantly greater in the low cost treatments than in the high cost treatments, with explore occurring most in the LcHr treatment and the least in HcLr (Figure 11).

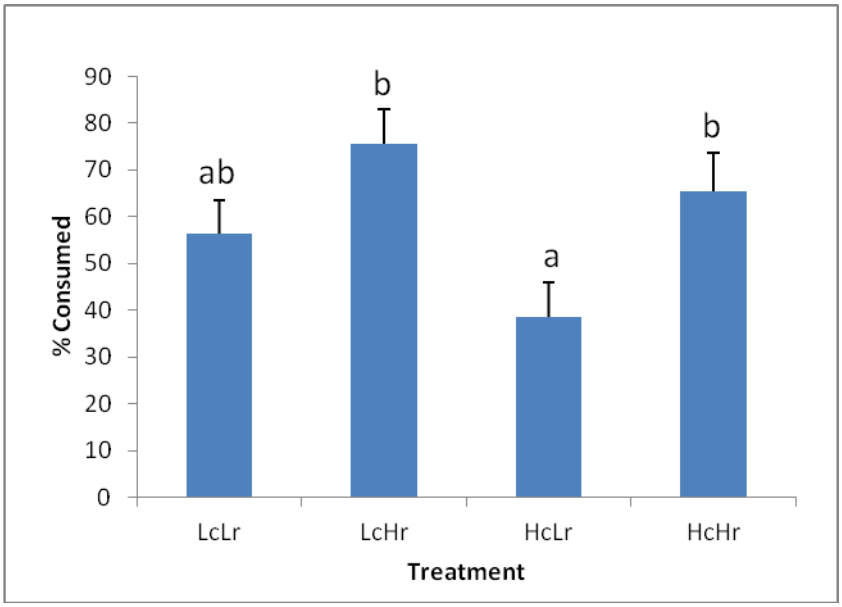

Figure 9. Mean (+SE) mass of seeds eaten in 4 treatments. LcLr = Low cost Low reward, LcHr = Low cost High reward, HcLr = High cost Low reward and HcHr = High cost High reward. The LcHr treatment has the highest percentage number of seeds eaten while the HcLr treatment has the least. Bars sharing the same letters indicate non-significant differences (Fisher's post hoc tests).

Table 5. Pairwise comparisons of demand curve functions between treatments for Bushveld gerbils provided with scattered seeds. Low reward being seeds least preferred and high reward being seeds most preferred. Elastic responses are highlighted in red.

Gerbil	LcHr vs LcLr	LcHr vs HcHr	LcHr vs HcLr	LcLr vs HcHr	LcLr vs HcLr	HcLr vs HcHr
1	0.318	0.875	1.053	8.130	1.386	1.403
2	0.326	0.052	0.178	2.000	0.074	0.196
3	0.326	0.168	0.232	1.100	0.000	0.150
4	0.500	0.127	1.051	2.750	1.354	1.470
5	0.750	0.400	0.356	2.750	0.280	0.079
6	0.079	0.467	0.087	3.143	0.040	0.389
7	0.079	0.467	0.267	4.172	0.280	0.808
8	0.569	0.156	0.576	3.080	0.280	0.682
9	0.250	0.525	0.178	2.444	0.000	0.333
10	0.214	0.000	0.405	1.571	0.350	0.569
11	0.318	0.000	0.267	2.333	0.056	0.375
Total	**0.172897**	**0.191111**	**0.312586**	**0.23741**	**0.256667**	**0.24359**

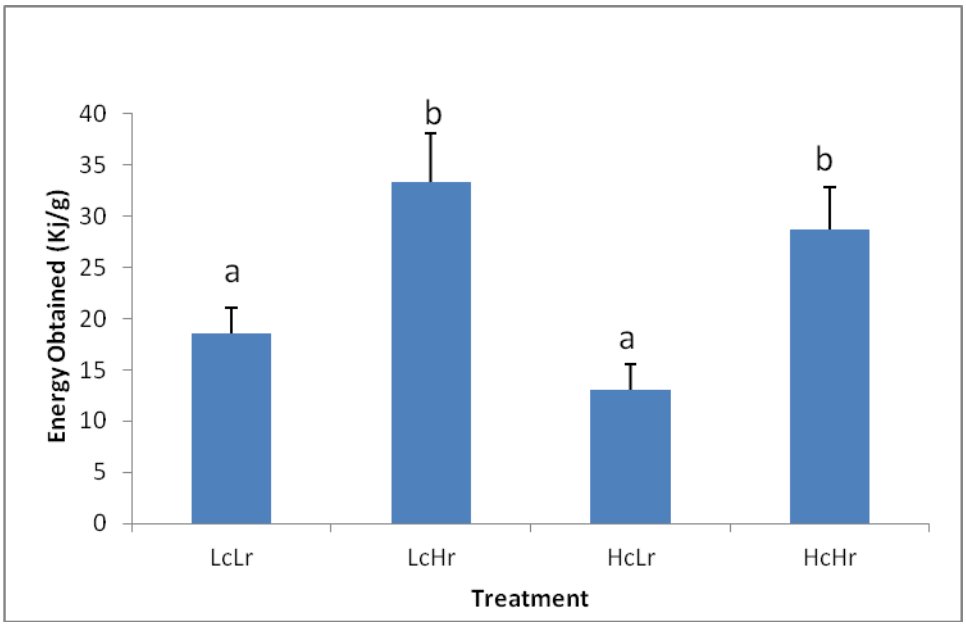

Figure 10. Mean (+SE) energy (Kj/g) obtained from seeds in 4 treatments. LcLr = Low cost Low reward, LcHr = Low cost High reward, HcLr = High cost Low reward and HcHr = High cost High reward. The most energy consumed was in the LcHr treatment while the least occurred in the HcLr treatment. Bars sharing the same letters indicate non-significant differences (Fisher's post hoc tests).

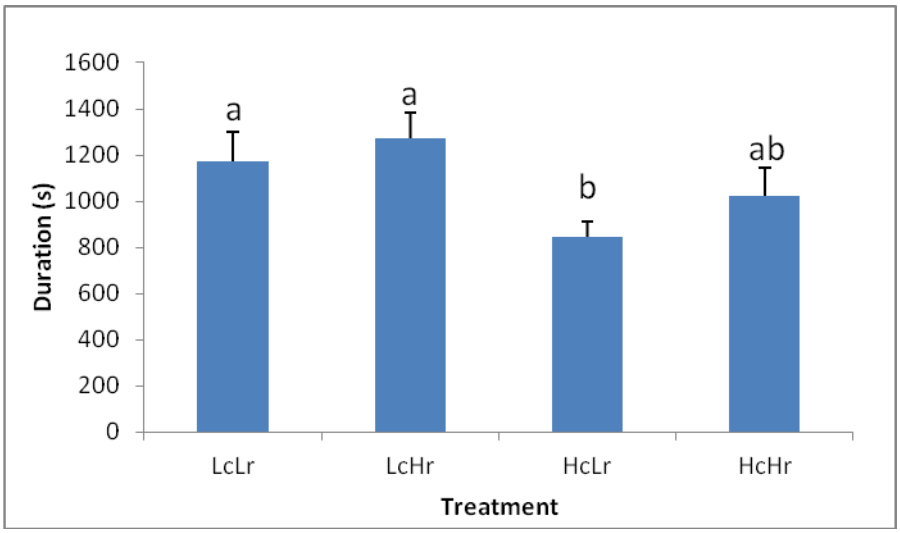

Figure 11. Mean (+SE) duration of explore behaviour in 4 treatments in experiments.. LcLr = Low cost Low reward, LcHr = Low cost High reward, HcLr = High cost Low reward and HcHr = High cost High reward. The highest duration of explore behaviour occurred in the LcHr treatment and the least in the HcHr treatment. Bars sharing the same letters indicate non-significant differences (Fisher's post hoc tests).

For frequency of behaviours, treatment was a significant predictor of door usage ($F_{3,27}$ = 19.23, P < 0.001) only, with low cost treatments having significantly more door usage than high cost treatments (Figure 13). There was no significant sex ($F_{1,9}$ = 0.05, P = 0.828) and treatment*sex ($F_{3,27}$ =1.19, P = 0.331) effects for door usage. Frequency of enter, home and attentive (data in Appendix 2) were not affected by treatment ($F_{3,27}$ = 0.77, P = 0.522 ; $F_{3,27}$ = 0.84 , P = 0.481 ; $F_{3,27}$ = 1.48, P = 0.241, respectively), sex ($F_{1,9}$ = 0.19, P = 0.673 ; $F_{1,9}$ = 0.20, P = 0.664; $F_{1,9}$ = 0.23, P = 0.645, respectively) and treatment*sex ($F_{3,27}$ = 0.48, P = 0.697 ; $F_{3,27}$ = 0.48, P = 0.702; $F_{3,27}$ = 1.49, P = 0.239, respectively) effects for frequency.

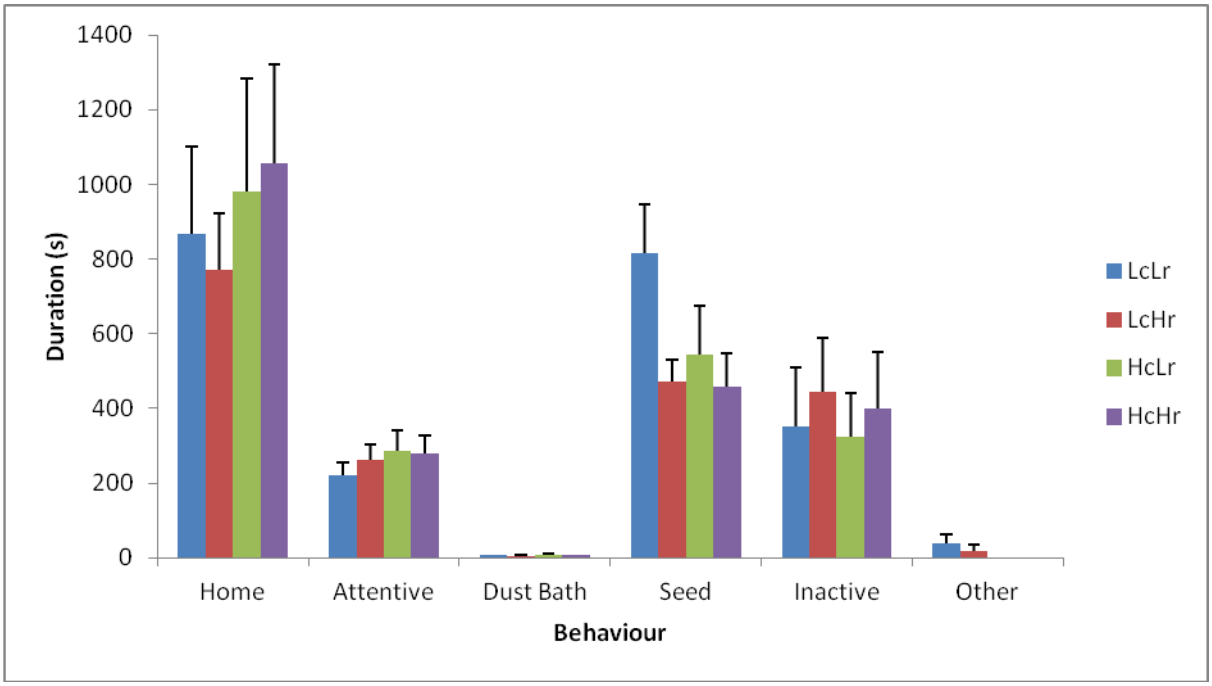

Figure 12. Mean (+SE) duration of non-significant behaviours in 4 treatments. LcLr = Low cost Low reward, LcHr = Low cost High reward, HcLr = High cost Low reward and HcHr = High cost High reward.

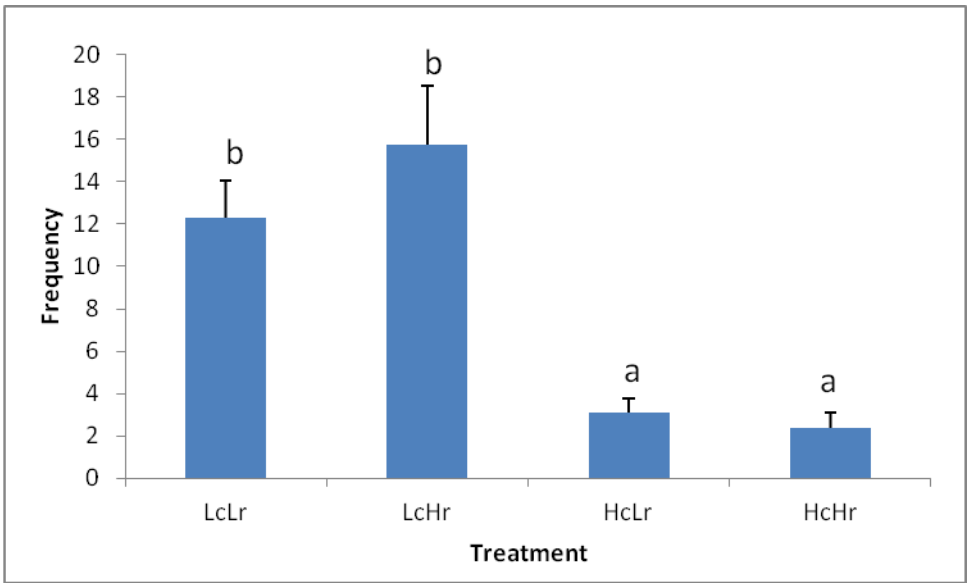

Figure 13. Mean (+SE) frequency of door usage in 4 treatments. LcLr = Low cost Low reward, LcHr = Low cost High reward, HcLr = High cost Low reward and HcHr = High cost High reward. The highest duration of explore behaviour occurred in the LcHr treatment and the least in the HcLr treatment. Bars sharing the same letters indicate non-significant differences (Fisher's post hoc tests).

3.2.3 Experiment 3 - Mixed Seed experiment

In this experiment, I tested whether the cost/presentation would influence the gerbil's seed choice when offered two seeds they preferred. Treatment and seed type significantly influenced the number ($F_{3,27} = 3.04$, $P = 0.046$; $F_{1,9} = 35.90$, $P < 0.001$, respectively) and mass ($F_{3,27} = 3.03$, $P = 0.047$; $F_{1,9} = 35.36$, $P < 0.001$, respectively) of seeds consumed. Post hoc tests revealed that the most number and mass of seeds were consumed in the low cost treatments, with the LcHr treatment having the highest number and mass of seeds consumed, the HcLr treatment having the least number of seeds consumed and the HcHr treatment having the least mass of seeds consumed. Sunflower seeds were the most consumed seed in all treatments (Figure14 and Figure 15).

Neither sex ($F_{1,9} = 0.06$, $P = 0.812$; $F_{1,9} = 0.10$, $P = 0.758$), treatment*sex ($F_{3,27} = 0.18$, $P = 0.910$; $F_{3,27} = 0.27$, $P = 0.845$), treatment*seed type ($F_{3,27} = 2.87$, $P = 0.056$; $F_{3,27} = 1.88$, $P = 0.157$), seed*sex ($F_{1,9} = 0.07$, $P = 0.804$; $F_{1,9} = 0.69$, $P = 0.428$) nor the treatment*seed*sex ($F_{3,27} = 2.21$, $P = 0.110$; $F_{3,27} = 2.25$, $P = 0.105$) influenced the number or mass of seeds consumed, respectively.

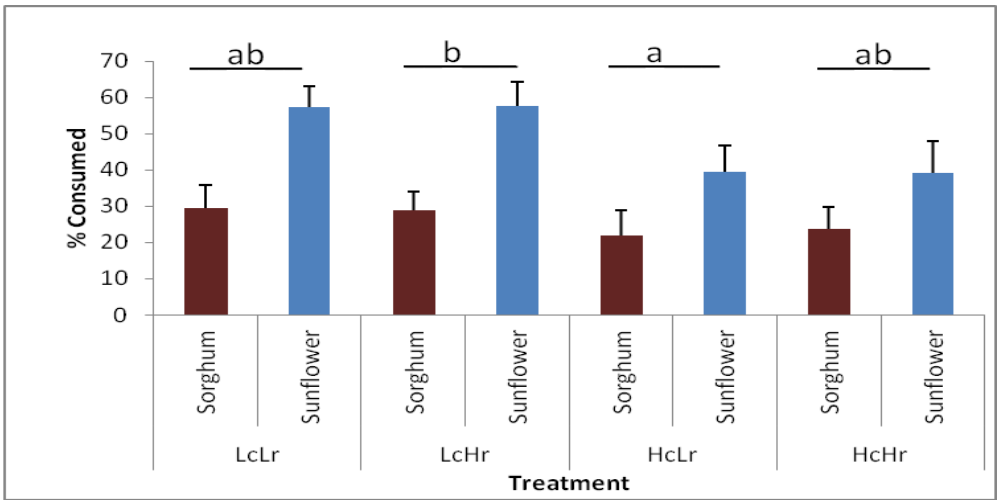

Figure 14. Mean (+SE) number of seeds eaten for each seed type in 4 treatments. LcLr = Low cost Low reward, LcHr = Low cost High reward, HcLr = High cost Low reward and HcHr = High cost High reward. The LcHr treatment has the highest percentage number of seeds eaten while the HcLr treatment has the least. Treatments sharing the same letters indicate non-significant differences (Fisher's post hoc tests).

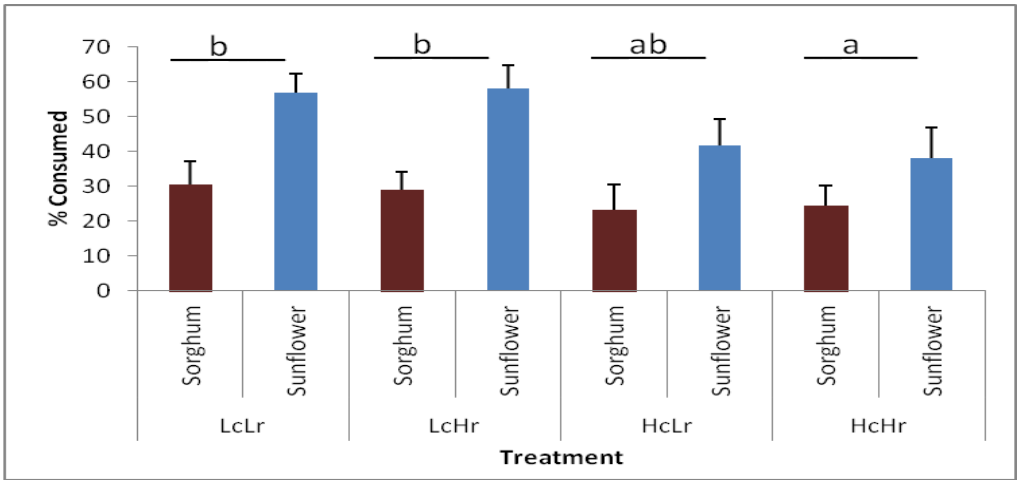

Figure 15. Mean (+SE) mass of seeds eaten for each seed type in 4 treatments. LcLr = Low cost Low reward, LcHr = Low cost High reward, HcLr = High cost Low reward and HcHr = High cost High reward. The LcHr treatment has the highest percentage mass of seeds eaten while the HcHr treatment has the least. Treatments sharing the same letters indicate non-significant differences (Fisher's post hoc tests).

Table 6 shows that there were varied elastic responses in treatment comparisons, with no gerbils showing elastic responses in the LcHr versus HcHr comparisons regarding sorghum seed consumption and no gerbils showed any elastic responses in the LcHr versus HcHr and LcLr versus HcLr treatment comparisons regarding sunflower seed consumption. Gerbils 1, 2, 4, 5, 7 and 8 showed no elastic responses in any treatment comparisons. Gerbils 3, 6 and 11 showed elastic responses for sorghum consumption and gerbils 3, 9 and 10 showed elastic responses for sunflower consumption. Of the comparisons between treatments for each

gerbil, 14% were elastic and 86% inelastic for sorghum, compared to 11% elastic and 89% inelastic for sunflower seeds. The demand curves for all the gerbils (total) together, revealed inelastic responses.

Treatment significantly influenced the energy intake from sunflower seeds only ($F_{3,27}$ = 4.18, P = 0.015) but there was no effect of sex ($F_{1,9}$ = 0.02, P = 0.882) or treatment*sex ($F_{3,27}$ = 0.97, P = 0.421). Energy acquisition from sunflower seeds was greater in the low cost treatments with LcHr treatment having the most sunflower seed energy consumed and HcHr the least (Figure 16). Energy intake from sorghum and the combined total of energy from both seeds were not influenced by treatment ($F_{3,27}$ = 0.50, P = 0.687; $F_{3,27}$ = 2.95, P = 0.051, respectively) sex ($F_{1,9}$ = 0.86, P = 0.776; $F_{1,9}$ = 0.0002, P = 0.988, respectively) nor treatment*sex ($F_{3,27}$ = 0.48, P = 0.696; $F_{3,27}$ = 0.36, P = 0.779, respectively).

Treatment was a significant predictor for the duration of only explore behaviour in the gerbils (Wilks $\lambda_{3,8}$ = 0.36, P = 0.036 ; MANCOVA; Figure17). Again, treatment did not affect any of the other behaviours (Figure 18): home (Wilks $\lambda_{3,8}$ = 0.67, P = 0.338), attentive (Wilks $\lambda_{3,8}$ = 0.59, P = 0.210), dust bath (Wilks $\lambda_{3,8}$ = 0.81, P = 0.620), seed (Wilks $\lambda_{3,8}$ = 0.59, P = 0.222), inactive(Wilks $\lambda_{3,8}$ = 0.88, P = 0.784) and scratching (Wilks $\lambda_{3,8}$ = 0.76, P = 0.512). There was no sex (Wilks $\lambda_{7,2}$ = 0.13, P = 0.394) or mass effect (Wilks $\lambda_{7,2}$ = 0.14, P = 0.420) on durations of any behaviours. The duration of explore behaviour was significantly greater in the low cost treatments than in the high cost treatments, with explore occurring most in the LcHr treatment and the least in the HcHr treatment (Figure 17).

For the frequency of behaviours, treatment was a significant predictor of door usage ($F_{3,27}$ = 13.87, P < 0.001) only, with door usage occurring significantly more frequently in low cost treatments than high cost treatments (Figure 19). There was no significant sex ($F_{1,9}$ = 0.002, P = 0.964) and treatment*sex ($F_{3,27}$ = 0.90, P = 0.456) effects for door usage. Frequency for enter, home and attentive were not affected by treatment ($F_{3,27}$ = 1.11, P = 0.364 ; $F_{3,27}$ = 0.79, P = 0.511 ; $F_{3,27}$ = 0.28, P = 0.840, respectively), sex ($F_{1,9}$ = 0.82, P = 0.388 ; $F_{1,9}$ = 0.73, P = 0.416; $F_{1,9}$ = 0.88, P = 0.372, respectively) and treatment*sex ($F_{3,27}$ = 1.09, P = 0.371 ; $F_{3,27}$ = 1.13, P = 0.353 ; $F_{3,27}$ = 2.17, P = 0.115, respectively); these data are given in Appendix 3.

Table 6. Pairwise comparisons of demand curve functions between treatments for Bushveld gerbils provided with sunflower and sorghum seeds. Low reward being a scattered presentation of seeds and high reward being a piled presentation of seeds. Elastic responses are highlighted in red.

Sorghum							**Sunflower**						
Gerbil	**LcHr vs LcLr**	**LcHr vs HcHr**	**LcHr vs HcLr**	**LcLr vs HcHr**	**LcLr vs HcLr**	**HcLr vs HcHr**	**Gerbil**	**LcHr vs LcLr**	**LcHr vs HcHr**	**LcHr vs HcLr**	**LcLr vs HcHr**	**LcLr vs HcLr**	**HcLr vs HcHr**
1	0.560	0.086	0.407	0.667	0.000	0.467	**1**	0.183	0.146	0.375	0.000	0.279	0.350
2	0.140	0.093	0.085	0.364	0.203	0.000	**2**	0.000	0.039	0.035	0.069	0.039	0.000
3	1.375	0.093	1.000	1.969	0.000	1.379	**3**	1.377	0.160	1.002	1.975	0.000	1.383
4	0.350	0.479	0.679	0.400	0.559	0.467	**4**	0.778	0.186	0.078	0.857	0.559	0.127
5	0.200	0.066	0.221	0.400	0.086	0.382	**5**	0.000	0.032	0.029	0.057	0.032	0.000
6	0.350	0.224	0.953	0.857	1.074	1.267	**6**	0.280	0.102	0.204	0.222	0.000	0.156
7	0.156	0.373	0.146	0.857	0.279	0.280	**7**	0.247	0.294	0.170	0.182	0.373	0.576
8	0.108	0.086	0.170	0.000	0.102	0.127	**8**	0.117	0.000	0.000	0.167	0.093	0.000
9	0.000	0.373	0.566	0.667	0.621	0.382	**9**	1.145	0.197	0.340	1.500	0.745	0.233
10	0.538	0.479	0.146	0.105	0.559	0.754	**10**	0.867	0.193	0.487	1.000	0.224	0.467
11	1.145	0.000	0.340	1.636	1.011	0.467	**11**	0.156	0.430	0.509	0.571	0.460	0.200
Total	**0.118644**	**0.025595**	**0.115156**	**0.214876**	**0.031933**	**0.189831**	**Total**	**0.290566**	**0.013253**	**0.166695**	**0.392344**	**0.050802**	**0.212903**

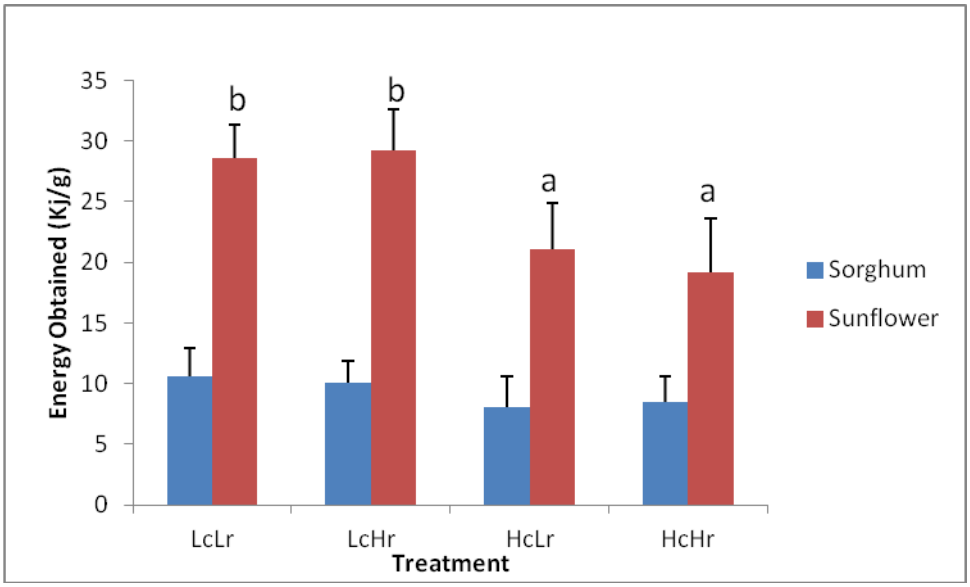

Figure 16. Mean (+SE) energy (Kj/g) obtained from seeds in 4 treatments. LcLr = Low cost Low reward, LcHr = Low cost High reward, HcLr = High cost Low reward and HcHr = High cost High reward. Energy intake for sunflower seed only was significant across treatments with the most energy obtained in the LcHr treatment while the least occurred in the HcHr treatment. Bars for the sunflower seeds sharing the same letters indicate non-significant differences (Fisher's post hoc tests).

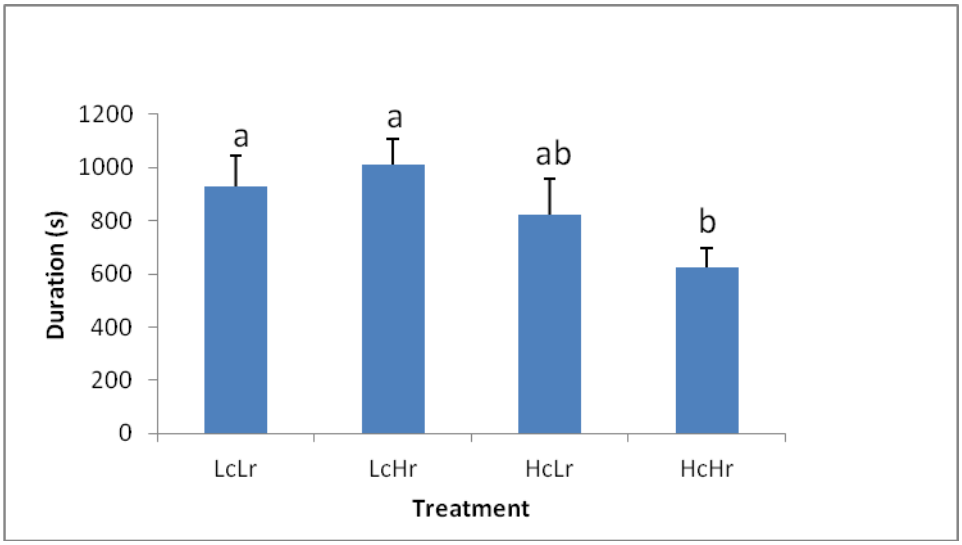

Figure 17. Mean (+SE) duration of explore behaviour in 4 treatments. LcLr = Low cost Low reward, LcHr = Low cost High reward, HcLr = High cost Low reward and HcHr = High cost High reward. The highest duration of explore behaviour occurred in the LcHr treatment and the least in HcHr treatment. Bars sharing the same letters indicate non-significant differences (Fisher's post hoc tests).

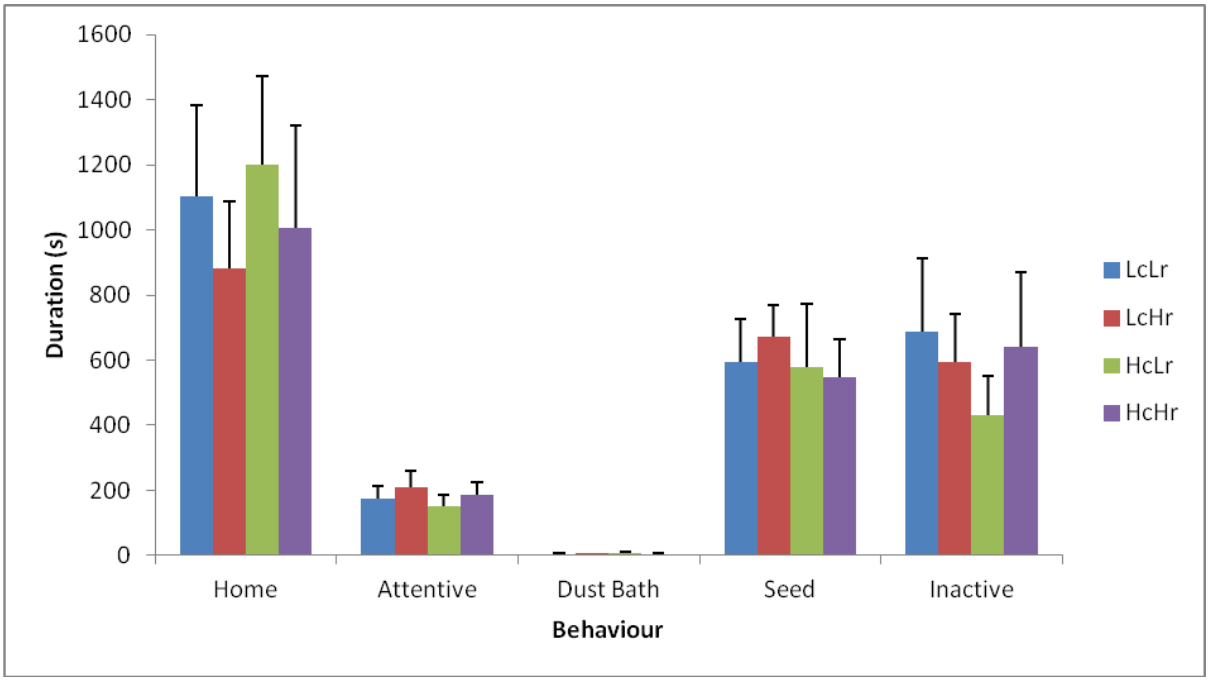

Figure 18. Mean (+SE) duration of non-significant behaviours in 4 treatments. LcLr = Low cost Low reward, LcHr = Low cost High reward, HcLr = High cost Low reward and HcHr = High cost High reward.

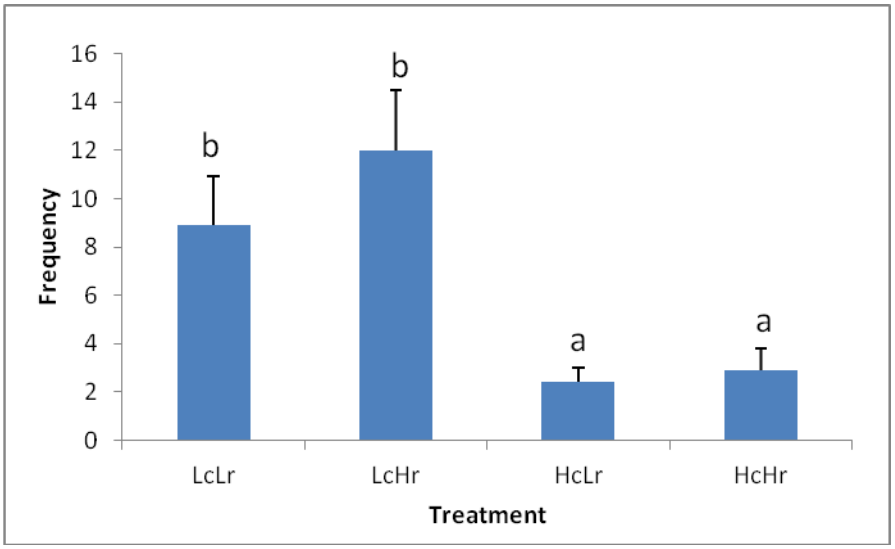

Figure 19. Mean (+SE) frequency of door usage in 4 treatments. LcLr = Low cost Low reward, LcHr = Low cost High reward, HcLr = High cost Low reward and HcHr = High cost High reward. The highest frequency of door use occurred in the LcHr treatment while the lowest in the HcLr treatment. Bars sharing the same letters indicate non-significant differences (Fisher's post hoc tests).

3.2.4 Experiment 4 - Predation

In this experiment, I tested how predation risk would affect the gerbils foraging behaviour under the same conditions as experiment 3. Only seed type significantly influenced the number ($F_{1,9}$ = 25.97 , P < 0.001) and mass of seed consumed ($F_{1,9}$ = 26.61, P < 0.001), where sunflower seeds were the most consumed in all treatments (Figure 20 and Figure 21). There was no influence of treatment ($F_{3,27}$ = 1.78, P = 0.174 ; $F_{3,27}$ = 1.97, P = 0.143), sex ($F_{1,9}$ = 0.11, P = 0.743 ; $F_{1,9}$ = 0.11, P = 0.750), treatment*sex ($F_{3,27}$ = 1.61, P = 0.211 ; $F_{3,27}$ =1.69, P = 0.193), treatment* seed type ($F_{3,27}$ = 1.67, P = 0.197 ; $F_{3,27}$ = 1.41, P = 0.263), seed*sex ($F_{1,9}$ = 0.73, P = 0.415 ; $F_{1,9}$ =0.75, P = 0.408) and treatment*seed*sex ($F_{3,27}$ = 0.98, P = 0.417 ; $F_{3,27}$ = 1.12, P = 0.360) on the number or mass of seeds consumed, respectively.

No gerbils showed elastic responses for LcHr versus HcHr and LcHr versus HcLr treatment comparisons in sorghum seed consumption, whereas with sunflower seed consumption, in the treatment comparisons at least one gerbil showed an elastic response (Table 7). Gerbils 1, 3, 4, 7, 8, 10 and 11 showed at least one elastic response in sorghum seed consumption while gerbils 3, 8 and 10 showed at least one elastic response in sunflower seed consumption. Treatment comparisons revealed that 18% were elastic and 82% inelastic for sorghum, while 17% were elastic and 83% inelastic for sunflower seeds. The total demand curves for all gerbils together were inelastic.

Energy intake from sorghum and sunflower seeds was not influenced by treatment ($F_{3,27}$ = 1.98, P = 0.141; $F_{3,27}$ = 1.78, P = 0.175, respectively), sex ($F_{1,9}$ = 0.03, P = 0.865; $F_{1,9}$ = 0.16, P = 0.697, respectively) nor treatment*sex ($F_{3,27}$ = 0.50, P = 0.685; $F_{3,27}$ = 2.11, P = 0.122, respectively; Figure 22). The total combined energy intake of both sorghum and sunflower seeds was also not influenced by treatment ($F_{3,27}$ = 1.87, P = 0.159), sex ($F_{1,9}$ = 0.11, P = 0.745) nor treatment*sex ($F_{3,27}$ = 1.73, P = 0.184).

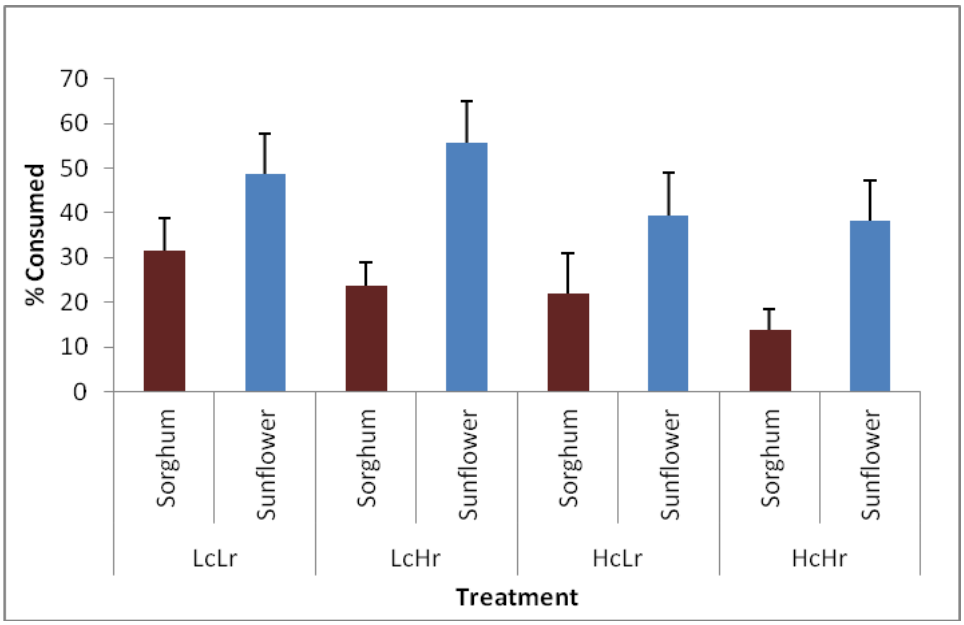

Figure 20. Mean (+SE) number of seeds eaten for each seed type in 4 treatments. LcLr = Low cost Low reward, LcHr = Low cost High reward, HcLr = High cost Low reward and HcHr = High cost High reward. The consumption of neither sorghum nor sunflower seeds differed across treatments.

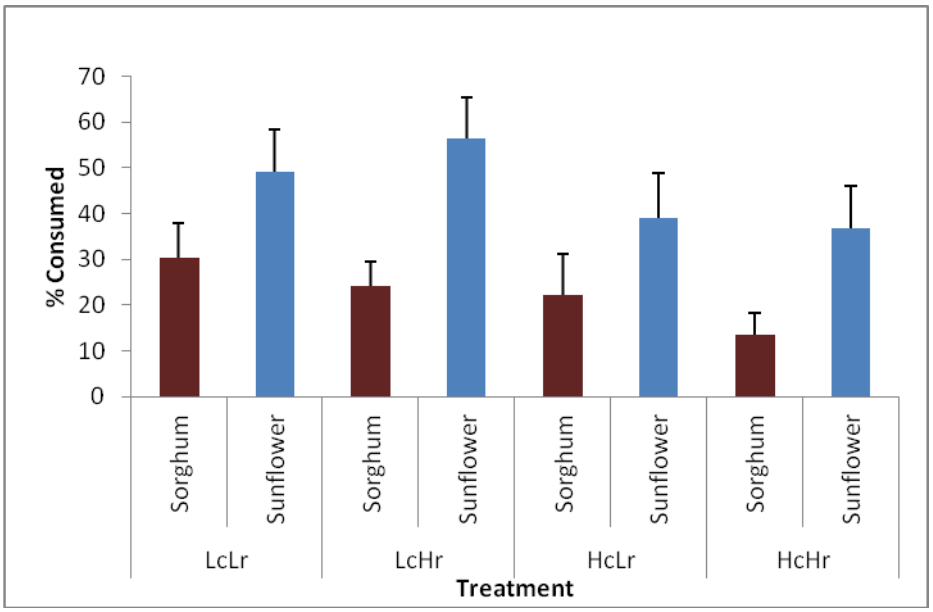

Figure 21. Mean (+SE) mass of seeds eaten for each seed type in 4 treatments. LcLr = Low cost Low reward, LcHr = Low cost High reward, HcLr = High cost Low reward and HcHr = High cost High reward. The consumption of neither sorghum nor sunflower seeds differed across treatments.

Table 7. Pairwise comparisons of demand curve functions between treatments for Bushveld gerbils provided with sunflower and sorghum seeds under predation risk. Low reward being a scattered presentation of seeds and high reward being a piled presentation of seeds. Elastic responses are highlighted in red.

	Sorghum							Sunflower					
Gerbil	**LcHr vs LcLr**	**LcHr vs HcHr**	**LcHr vs HcLr**	**LcLr vs HcHr**	**LcLr vs HcLr**	**HcLr vs HcHr**	**Gerbil**	**LcHr vs LcLr**	**LcHr vs HcHr**	**LcHr vs HcLr**	**LcLr vs HcHr**	**LcLr vs HcLr**	**HcLr vs HcHr**
1	0.700	0.279	0.255	1.333	0.745	0.000	**1**	0.074	0.000	0.049	0.105	0.112	0.067
2	0.156	0.146	0.000	0.476	0.124	0.183	**2**	0.117	0.149	0.375	0.429	0.329	0.670
3	1.365	0.224	0.994	1.967	0.000	1.377	**3**	1.383	0.207	1.006	1.964	0.000	1.375
4	0.700	0.000	0.000	1.000	0.559	0.000	**4**	0.700	0.279	0.463	0.571	0.066	0.323
5	0.538	0.112	0.146	0.933	0.559	0.061	**5**	0.052	0.039	0.035	0.143	0.080	0.000
6	0.700	0.224	0.509	0.667	0.000	0.467	**6**	0.467	0.176	0.000	0.933	0.373	0.221
7	1.267	0.224	0.000	1.871	1.011	0.280	**7**	0.653	0.053	0.226	0.857	0.305	0.247
8	1.145	0.914	0.833	0.000	0.000	0.000	**8**	1.375	1.098	0.000	0.000	1.098	1.375
9	0.000	0.000	0.000	0.000	0.000	0.000	**9**	0.000	0.000	0.000	0.000	0.000	0.000
10	0.000	0.197	0.990	0.353	1.086	1.372	**10**	0.040	0.270	1.007	0.429	1.105	1.375
11	0.636	0.066	0.367	1.000	0.782	0.431	**11**	0.247	0.059	0.000	0.250	0.197	0.074
Total	**0.387952**	**0.130392**	**0.039949**	**0.762887**	**0.268801**	**0.217241**	**Total**	**0.187166**	**0.010445**	**0.106114**	**0.285714**	**0.033462**	**0.158763**

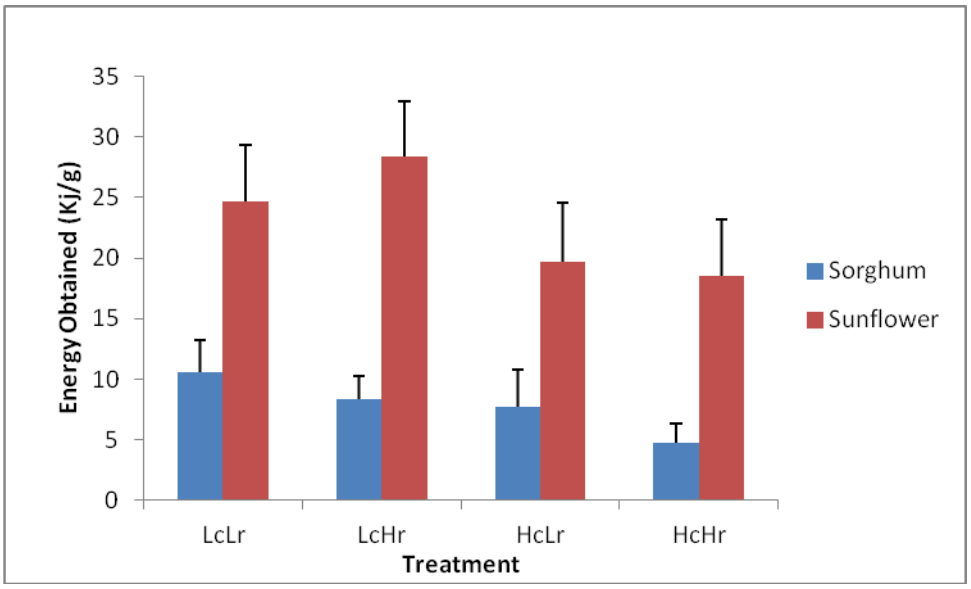

Figure 22. Mean (+SE) energy (Kj/g) obtained from seeds in 4 treatments. LcLr = Low cost Low reward, LcHr = Low cost High reward, HcLr = High cost Low reward and HcHr = High cost High reward. There were no significant effects of energy obtained from any seed across any treatment.

Treatment was a significant predictor for duration of both explore and home behaviour (Wilks $\lambda_{3,8} = 0.30$, $P = 0.044$; Wilks $\lambda_{3,8} = 0.36$, $P = 0.048$, respectively; Figure 23). The duration of explore behaviour was significantly greater in the low cost treatments than in the high cost treatments, with explore occurring most in the LcHr treatment and the least in HcLr (Figure 23). The duration of home behaviour was significantly greater in the high cost treatments than the low cost treatments, with the most home behaviour occurring in the HcLr treatment and the least in LcHr (Figure 23). Treatment did not influence duration of attentive (Wilks $\lambda_{3,8} = 0.62$, $P = 0.263$), dust bath (Wilks $\lambda_{3,8} = 0.67$, $P = 0.339$), seed (Wilks $\lambda_{3,8} = 0.66$, $P = 0.316$), inactive (Wilks $\lambda_{3,8} = 0.82$, $P = 0.633$) and scratching (Wilks $\lambda_{3,8} = 0.55$, $P = 0.165$) behaviours (Figure 24). There was no sex (Wilks $\lambda_{7,2} = 0.24$, $P = 0.625$) or mass effect (Wilks $\lambda_{7,2} = 0.50$, $P = 0.913$) on durations of any behaviours.

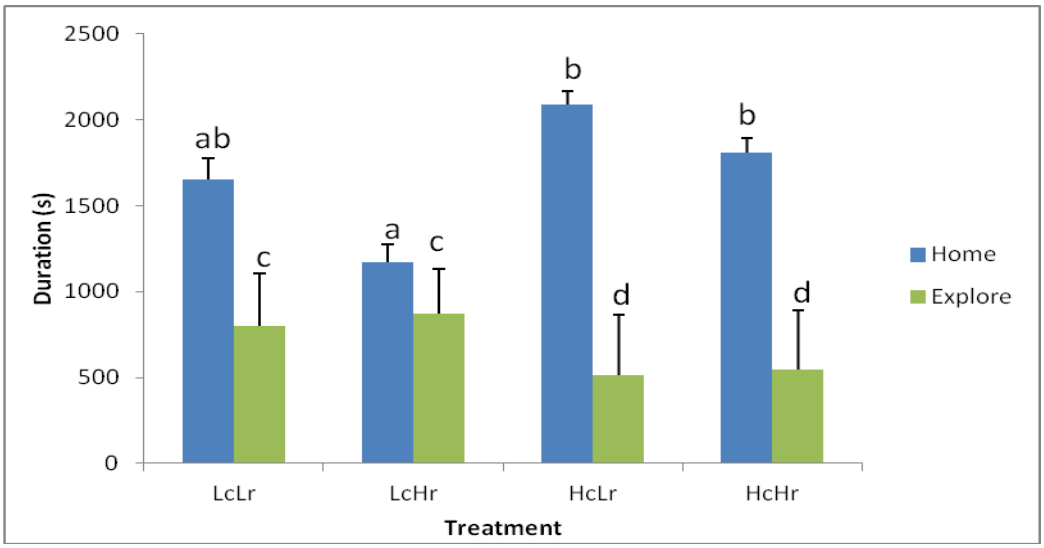

Figure 23. Mean (+SE) duration of home and explore behaviour in 4 treatments. LcLr = Low cost Low reward, LcHr = Low cost High reward, HcLr = High cost Low reward and HcHr = High cost High reward. The highest duration of home behaviour occurred in HcLr treatment and the least in the LcHr treatment, whereas the highest duration of explore behaviour occurred in LcHr treatment and the least in the HcLr treatment. Bars sharing the same letters indicate non-significant differences (Fisher's post hoc tests).

For the frequency of behaviours, treatment was a significant predictor of door usage, attentive and home ($F_{3,27} = 12.08$, $P < 0.001$; $F_{3,27} = 3.01$, $P = 0.049$; $F_{3,27} = 3.02$, $P = 0.047$, respectively). Frequency of door usage occurred significantly more in low cost treatments than in high cost treatments, whereas the frequency of home and attentive behaviour occurred significantly more in high reward treatments than in low reward treatments, with HcHr having the most home and attentive frequency and HcLr the least (Figure 25). There was no significant sex ($F_{1,9} = 0.12$, $P = 0.739$; $F_{1,9} = 0.07$, $P = 0.798$; $F_{1,9} = 0.64$, $P = 0.444$) and treatment*sex ($F_{3,27} = 0.19$, $P = 0.900$; $F_{3,27} = 0.97$, $P = 0.422$; $F_{3,27} = 2.31$, $P = 0.100$) effects for door, attentive and home frequency, respectively. Frequency for enter was not affected by treatment ($F_{3,27} = 1.91$, $P = 0.152$), sex ($F_{1,9} = 0.56$, $P = 0.475$) and treatment*sex ($F_{3,27} = 2.81$, $P = 0.058$); data provided in Appendix 4.

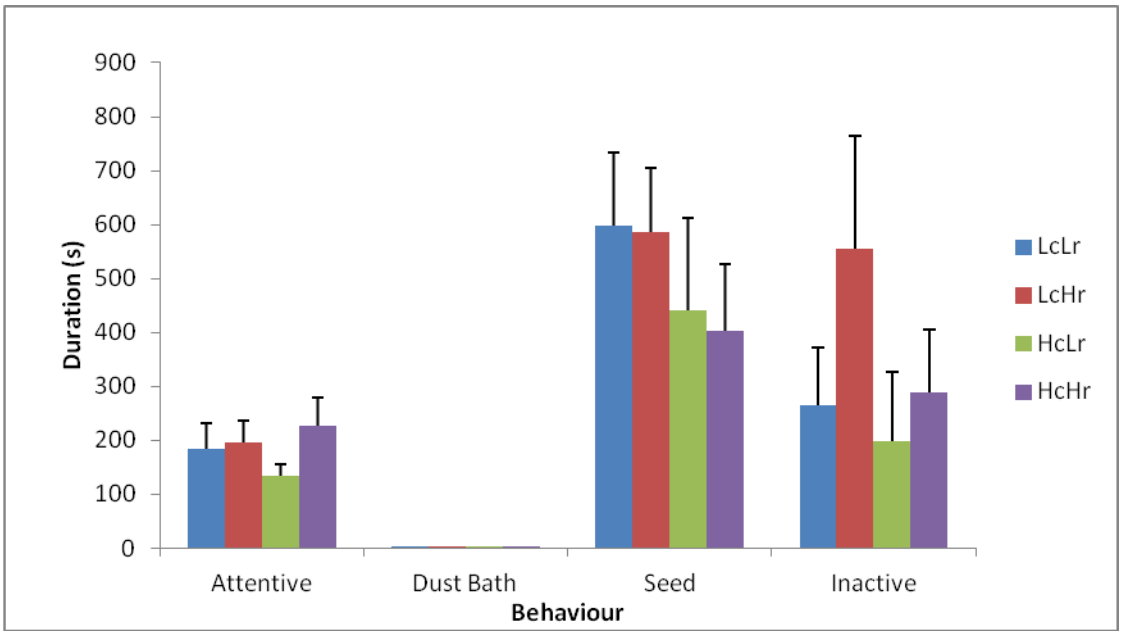

Figure 24. Mean (+SE) duration of non-significant behaviours in 4 treatments. LcLr = Low cost Low reward, LcHr = Low cost High reward, HcLr = High cost Low reward and HcHr = High cost High reward.

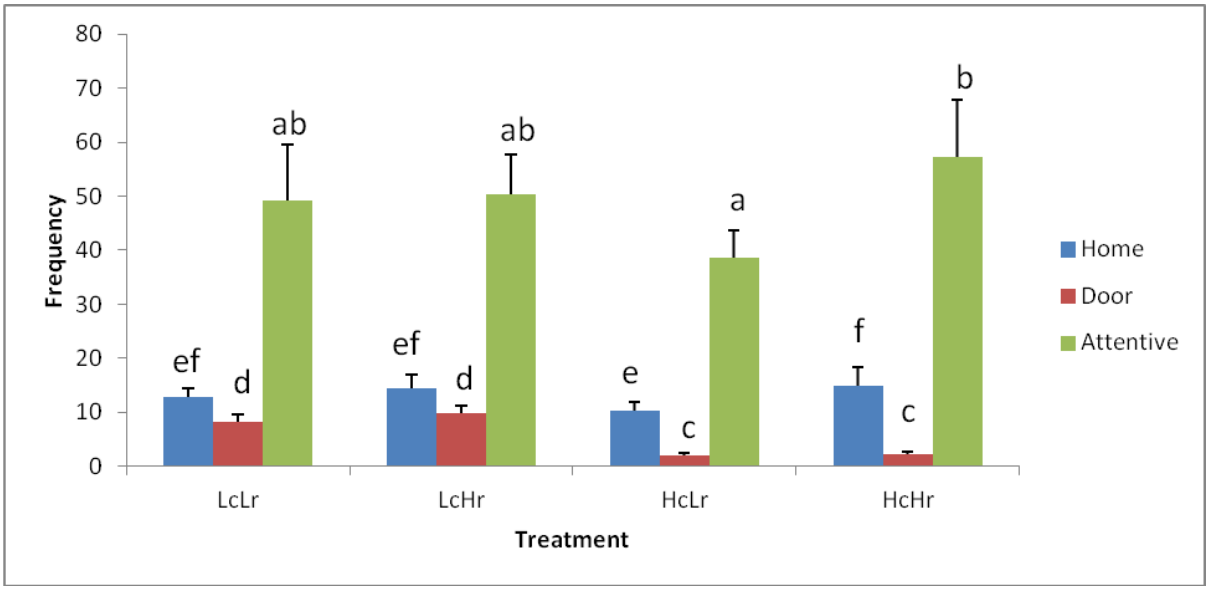

Figure 25. Mean (+SE) frequency of home, door and attentive behaviour in 4 treatments. LcLr = Low cost Low reward, LcHr = Low cost High reward, HcLr = High cost Low reward and HcHr = High cost High reward. The highest frequency of home and attentive behaviour occurred in the HcHr treatment, while the lowest occurred in the HcLr treatment. The highest frequency of door use occurred in the LcHr treatment, while the lowest in the HcLr treatment. Bars sharing the same letters indicate non-significant differences (Fisher's post hoc tests).

Chapter 4: Discussion and conclusions

My study aimed to provide insight into motivation and decision making in Bushveld gerbils. I investigated willingness of Bushveld gerbils to work for seeds they preferred the most and least, their foraging decisions under different cost/benefit scenarios and how predation risk affects these decisions. I also ascertained whether gerbils show individual preference for different seeds.

4.1 Seed preference

The primary aim of the seed preference tests was to assess whether gerbils displayed individual preferences in seed choice, and these data were then used to individually tailor the cost/benefit experiments for each gerbil. The inclusion of food items in an animal's diet are based on the cost in obtaining the item and the relative benefits received from it (Mac Arthur and Pianka, 1966; Ackroff *et al.*, 1986), such as nutritional content (Johnson *et al.*, 1984), palatability (Johnson and Collier, 2001) and possibly presentation and quantity (Moon and Ziegler, 1979). Therefore, I presented 5 different commercial seeds in the same quantity and presentation, as well as minimizing the effect of cost by allowing the gerbils free access to the seeds overnight. I then assessed the selection and consumption of these seeds to assign preferences for each gerbil, as recommend by Taghon (1981).

The gerbils not only differed in the seeds they preferred the most but also in the foods they preferred the least, showing clear individual preferences for foods. The literature does indicate that individual animals differ in behavioural traits and personalities (Wilson, 1998; Carere *et al*., 2005; Van Oers *et al*., 2008). Yet, studies usually focus on the group or species as the measurable units, and the individual animals preferences are overlooked (Moon and Zeigler, 1979). Very few studies have investigated individual variation in food preference, with pigeons being one of few species that have been shown to display individual preference when given a choice of different kinds of grain (Brown, 1969; Moon and Zeigler, 1979; Shettleworth, 1987). I conducted the preference test only once for each gerbil, but it has been shown in pigeons that a single test of their preference behaviour is a good predictor of future preference (Moon and Zeigler, 1979).

Preference tests showed that six gerbils preferred sunflower seeds, three preferred oats and two preferred sorghum. These three seeds varied in their nutritional content, with sunflower seeds having the greatest energy, fat and carbohydrate content and wild oats having the highest protein and fibre content. Sorghum has greater energy, carbohydrates and less fat than wild oats as well as having the same protein content as sunflower and little fibre content. The gerbils also differed in the seeds they least preferred, with eight not preferring maize, two not preferring wild rice, and one not preferring oats; it is interesting that three gerbils preferred oats most and one the least.

Seed preference is based on many factors such as palatability, size, nutrition and ease of consumption (Parshad and Jindal, 1991; Murray and Dickman, 1997; Johnson and Collier; 2001; Munoz and Bonal, 2008). Therefore, the most preferred foods are highly palatable and have nutritional value particular to an individual's needs. Most gerbils selected sunflower seeds, which had the highest nutritional value, so it can be assumed the gerbils were selecting for seed quality. Even though sorghum and oats have a lesser nutritional quality than maize, these seeds were preferred, possibly because other aspects of the seeds (such as small size, soft coat) make them more profitable and of good quality to the gerbils. Despite its nutritional value, the hardness of the maize possibly makes it the least profitable and consequently the least preferred (Parshad and Jindal, 1991) for most gerbils, suggesting it is of a lesser quality. Similarly, palatability and hardness could have played a large role to why wild rice was least preferred.

Differences in individual metabolic rates may be a reason for the gerbils having preferences for seeds that differ quite widely in nutritional content, as suggested by studies on pigeons (Brown, 1969; Moon and Zeigler, 1979). It is also suggested that the inherited effects and experience may influence seed preference as well as seed size, colour and shape (Brown, 1969). The gerbils received sunflower seeds in the period of acclimatisation to captivity (i.e. 3 months before seed preference tests), and it possible that the eight gerbils that preferred sunflower seeds developed this preference prior to tests, yet not all gerbils showed a preference for sunflower seeds later, indicating that past experiences do not always predict seed preferences in Bushveld gerbils.

Brown (1969) showed that preferences are quite stable and are not affected by the presentation (e.g. piled) and amount of seeds provided, because the proportions of seeds eaten (when given a choice) remain constant and only amount of seeds eaten may change. Therefore, it can be inferred that preference during experiments did not change and seed consumption was influenced by the cost/reward protocol used during experiments.

4.2 Foraging decisions

In experiments 1 and 2, the aim was to assess the costs gerbils were willing to pay to access seeds they most and least preferred. In experiment 1, seeds were presented in piles and in experiment 2, the seeds were scattered. Both piled and scattered presentations were tested to ensure that all possibilities of presentation were explored in case presentation affected seed consumption under the different cost-reward scenarios. I predicted that gerbils would work harder to access seeds they most preferred than seeds they least preferred.

4.2.1 Experiment 1 - piled seeds

There was no cost for searching for food in this experiment, and therefore the only cost for obtaining the food was the weight of the doors. Overall, the gerbils ate more in the low cost treatments than in the high cost treatments, regardless of the reward. However, when looking at low cost and high cost treatments separately, the gerbils ate more in high reward treatments (most preferred seeds) compared to the low reward treatments, consistent with literature that an animal will remove more food from ‘rich patches’ (Hanson and Green, 1989). However, in low cost treatments, the gerbils used the door more frequently and explored the experimental tank for longer in high reward treatments whereas in high cost treatments, the gerbils explored and used the door more in low reward treatments (least preferred seeds), contradicting my prediction that gerbils would work harder for their most preferred seed. These data support the hypothesis of Kramer and Weary (1991) that animals are willing to spend more time exploring when the quality of a patch decreases, because when they are in a high quality patch, exploring would result in giving up a high rate of gain for a low chance of finding a better patch but when they are in a low quality patch they are sacrificing a low rate of gain for a higher chance of finding a better patch. These results indicate that when gerbils pay minimal cost in obtaining food, they spent more time exploiting preferred food (good

quality patches) whereas when they did pay a cost, they offset the cost in low reward (least preferred food) treatments by exploring more.

4.2.2 Experiment 2 - scattered seeds

When food was scattered, it was not only the cost of obtaining the food (doors) but also a cost in searching for the food that influenced the gerbil's behaviour. In the scattered food experiments, the gerbils ate more in high reward treatments than in low reward treatments, regardless of the cost, indicating that they removed more prey from 'rich patches' than 'poor' ones (Hanson and Green, 1989). Hanson and Green (1989) also showed that when animals search for food and the encounter rate with low quality food increases, they tend to reject low quality food, and therefore in the low reward treatments in which the gerbils only encountered less preferred food, they might have just rejected it, leading to lower consumption. Again, however, the gerbils ate less in high cost treatments than in low cost treatments. When food was scattered, the gerbils needed to spend extra energy to search for their food and they would have had less information about the abundance and types (good/poor quality) of food available. The gerbils explored for longer and used the door more frequently in low cost treatments than in high cost treatments. Looking within the low cost treatments, the gerbils explored more and used the door more in high reward treatment, consistent with their consumption of seeds. This indicates that when faced with the extra cost of searching for seeds, the gerbils explored more in the high reward treatment to enhance encounter rates with high quality seeds, whereas in the low reward treatment, the gerbils encountered less preferred food and therefore the energy spent exploring would not have increased the payoff. Similarly, in high cost treatments, the gerbils explored longer in high reward treatment but used the door more often in low reward treatment, but the difference between the low reward and high reward door usage was minimal.

When foraging, animals pay costs to obtain food and balancing out these costs with the benefits obtained from these food shapes how animals forage (Ackroff *et al*., 1986; Abrams, 1991). In my experiments, the gerbils had to balance out the costs of searching for food and obtaining the food. The amount Bushveld gerbils were willing to work (door usage) is independent of seed presentation but influenced by the types of seeds available (reward). In both experiments 1 and 2, the door usage by the gerbils was the same, revealing that when

they did not have to work as hard (i.e. low cost) the gerbils used the door more. This result has been similarly shown before with American mink (*Mustela vison*), when they too had to experience a cost of a weighted door to access a resource (Cooper and Mason, 2000). However, in the treatments where they did not have to work hard (low cost), the gerbils used the door more in the high reward treatment than in the low reward treatment, indicating they returned more often to a patch of food they preferred than to that which they did not prefer. When the gerbils then paid a price (high cost), they used the door more in low reward treatments, indicating that they were possibly willing to work more to increase their chances of finding better food (Kramer and Weary, 1991). Their exploratory behaviour showed a similar pattern to door usage; they explored more in the low cost treatments than in high cost treatments in both experiments 1 and 2. When they incurred no cost to searching for food (piled experiments) the gerbils exploratory behaviour mimicked their door usage (as above) but when they experienced a cost of searching for food (scattered experiments) the gerbils explored more in the high reward treatments, linking with their consumption. This suggests that the gerbils offset the extra cost they pay in the scattered situations by exploring more in high reward treatments in order to increase their chances of obtaining preferred foods (as explained above).

Many factors influence the consumption behaviour of animals, including the nutrient quality and palatability of the food (Sunday *et al*., 1983; Johnson *et al*., 1984; Johnson *et al*., 1986), environmental structure (such as cover, distance to cover and physical structure of habitat and patches; Arcis and Desor, 2003) as well as the various costs in procuring the food. Seed consumption of Bushveld gerbils in my study was affected by the presentation of the seeds (piled/scattered). In a piled situation where the gerbils did not have to search for their food, I found that they responded to cost more than reward. While in a scattered situation where there was an extra cost placed on the gerbils to search for their food, the gerbils seem to respond more to the reward. In both experiments, though, the gerbils ate more seeds in the high reward treatment than in a low reward treatment, indicating that they will consume more seeds of higher profitability (possibly due to nutrient content); it is also possible that the quality and palatability of the least preferred food lead to consuming less of these seeds (Johnson and Collier, 1987; Warwick *et al*., 2003).This could also be partly why, even though the consumption of seeds by gerbils was different in experiment 1 than in experiment 2, in both experiments, the gerbils obtained similar amounts of energy from the treatments,

with the most energy being obtained from high reward treatments. The demand curves for both experiments revealed that the gerbils mostly make uniform decisions as most of their decisions are inelastic. However, under certain circumstances, some individuals change their decision-making, such as in the case where both cost and reward are increased (i.e. LcLr - HcHr). These elastic responses reveal that the gerbils consider consumption under these changes as a luxury, which is further shown by their lack of compensation in HcHr treatments.

4.3 Experiment 3 - mixed seeds

Experiment 3 involved offering Bushveld gerbils sunflower and sorghum seeds at the same time, which consequently gave them a choice of two preferred seeds (see seed preference experiment) compared to experiments 1 and 2 where only one seed (preferred or non-preferred) was offered at a time. The two types of seeds were of different size, shape and nutritional content, allowing me to assess seed choice and consumption for seeds of different qualities. In experiment 3, I predicted that when the cost was high, the gerbils would choose a seed with greater energy content to offset the cost experienced to obtain the seeds. Whereas, when the cost was low, the gerbils would be less selective in their seed choice. Experiment 3 represented a combination of experiment 1 and 2, with low cost and high cost in obtaining the food (doors) as well as no cost in searching for food (high reward- piled) and high cost in searching for food (low reward- scattered).

In contrast to my predictions, the gerbils ate more sunflower than sorghum seeds regardless of the cost or presentation, possibly because the sunflower seeds had greater nutritional content than sorghum. However, even the gerbils that showed a preference for the sorghum in the seed preference tests ate more sunflower seeds (although only marginally). This could possibly be because under experimental situations, the encounter rate was greater with the larger, more conspicuous sunflower seeds. The fact that the gerbils were also under food deprivation and only had one hour to obtain and eat the seeds could also have contributed to their seed selection (Moon and Zeigler, 1979). In this experiment, cost again seemed to drive seed consumption since more seeds were consumed in low cost treatments than in high cost treatments, regardless of the presentation of the seeds. Considering the low cost and high cost treatments separately, the gerbils ate more seeds when they were piled under low cost, opting

for the route that incurs the least cost but ate more seeds that were scattered under high cost, possibly to offset the extra costs of searching for the food. The only significant difference in energy consumption within the treatments was with sunflower seeds, and this mimicked their seed consumption, with the most energy obtained from low cost treatments.

The duration of exploratory behaviour mirrored consumption, with exploring occurring longer in low cost than high cost treatments. Furthermore, in the low cost treatments, gerbils explored for longer when seeds were piled, whereas in the high cost treatment, they explored more when the seeds were scattered. These findings indicate that when they did not have to pay a price to obtain seeds, the gerbils adopted a "greater return for lower cost" strategy by eating more and exploring more when seeds were piled and there was no cost to searching for the food. However, when they paid a high cost to obtain the seeds, the extra cost of searching for the food lead the gerbils to explore for longer and eat more when the seeds were scattered, as shown by previous studies where animals will compensate for high costs by increasing consumption, possibly to balance out energy expended with energy gained (Kaufman, 1980; Collier, 1983; Gannon *et al*., 1983). The data from the door usage by the gerbils showed that they selected the option that lead to the lower cost because they used the door more frequently in the low cost treatments and when the seeds were piled, showing similar results to that of American mink (Cooper and Mason, 2000). The demand curves reveal that the gerbils were predominantly making uniform inelastic decisions in their food consumption, finding food consumption to be a necessity, except for a few individuals in certain circumstances.

Bushveld gerbils ate more in the low cost than high cost treatments in all experiments (except for one treatment; 6.25% of total treatments) which contradicts some previous literature that found that as cost to procure food increases, animals will compensate for the high cost by increasing their meal size (Collier and Collier, 1980; Collier, 1983; Ackroff *et al*., 1986). This hypothesis is based on a local effect of cost, suggesting that the cost just paid directly affects the meal patterning of animals (Johnson and Collier, 1994). However, there is a body of literature that supports many different reasons for the decrease in consumption as cost increases (as occurred in my study). Johnson and Collier (1987) found that in rats, low cost items were usually consumed when encountered and the probability of consuming a high cost item decreased with an increase in cost. Morato *et al*., (1995) and Johnson and Collier (1994)

both postulated that rats can integrate information from the past and present to predict future food outcomes, which possibly leads to rats using a cost minimizing strategy, where the animals consume most of their food when the cost is low. This strategy is usually employed when there is variability in cost to access food (Johnson and Collier, 1994; Morato *et al.*, 1995), as in my study where there was low and high costs as well as low/high searching costs that was varied randomly from one treatment to the next.

When procurement price changes frequently (as is the case in my study), food consumption can be greater than expected in low cost situations and lower than expected in high cost situations (Johnson *et al.*, 1985; Morato *et al.*, 1995). Two hypotheses are offered as explanations for this outcome. Firstly, it is suggested that there might not be enough time for the compensatory increase in meal size to occur and secondly, animals adopt a cost minimising strategy (Morato *et al.*, 1995). It is suggested that it takes some time (at least three days) at a stable cost for the compensatory increase in meal consumption to occur (Kanarek *et al.*, 1977; Johnson *et al.*, 1986; Morato *et al.*, 1995). Another factor that may play a part in the low consumption in high cost treatments may be the design of my experiment. The gerbils had to pay the same high cost when leaving the seed area as when entering, increasing the cost of using the door two-fold. With this extra cost to exiting, the gerbils used the door less often (as shown by the door usage data), and therefore they entered the 'food' area less and consequently ate less. The seeds can also possibly be perceived as being in the 'open' without available cover in the seed area (in all four experiments) and therefore relatively more risky (Arcis and Desor, 2003), which coupled with the hindrance of the high cost door, might possibly influence the foraging strategy that leads to the least amount of cost (such as cost of the door and searching cost).

4.4 Experiment 4 – predation risk

The aim of experiment 4 was to investigate how the perceived cost of predation would affect the gerbils foraging behaviour. I predicted that the gerbils would spend less time foraging, reducing their time 'in the open' and decreasing their predation risk under a high perceived predation-risk setting relative to a low risk setting. Animals will trade off energy gain against the risk of being preyed upon, where indirect and direct cues of predation can cause drastic changes in foraging behaviour (Lima, 1985; Krivan and Vrkoc, 2000; Bengsen *et al.*, 2010).

The indirect cues of predation used in my study were a white light source (mimicking moonlight) and odour of a possible predator (Hughes *et al*., 1995; Jacquot and Baudoin, 2002). Predation risk affects foraging in many ways, such as reduction in food consumption, changes in feeding rate and use of cover (Kotler *et al*., 1993; Abrams, 2000; Pastro and Banks, 2006). Bushveld gerbils appeared to have organised their foraging behaviour in such a way that led to least amount of energy expenditure and minimum exposure to predation risk, as similarly seen with the midday gerbil (*Meriones meridianus*) where energy expenditure and predator avoidance are important factors in their foraging strategies (Shuai and Song, 2011). In my study, the gerbils used the door and explored more in low cost treatments and when seeds were piled, minimising cost and consequently energy expended in obtaining the seeds. The reduction in door usage in high cost treatments suggests the gerbils respond to an increased potential predation risk through the high cost doors hindering the gerbil's escape. Food consumption was not affected by cost or reward, possibly because the gerbils reduced the amount they ate due to the perceived cost of predation (Kotler *et al*., 1993; Abrams, 2000), to the extent that their consumption did not vary across the treatments. As their seed consumption did not differ across treatments, the energy values from the seeds consumed also did not vary as well. As with experiment 3, the gerbils ate more sunflower seeds than sorghum, and possibly for the same reasons.

As predicted, the gerbils did indeed spend less time exploring and spent quite a large amount of their time in the home tank, making more use of cover (Diaz *et al*., 2005). However, the duration the gerbils spent in their home tank seemed to be dependent on the cost: they spent more time in the home tank in the high cost treatments than the low cost treatments. Considering the costs separately, the gerbils spent more time in their home cage when the seeds were scattered (the opposite pattern to their explore behaviour). The frequency with which the gerbils travelled to their home cage, however, was dependent on the reward because when the seeds were piled, the gerbils travelled to their home tank more frequently. I deduced that the gerbils explored more when seeds were piled and due to the perceived cost of predation, the gerbils possibly did their exploring in small bouts returning home every so often.

Many animals use vigilance (such as pauses and head raising) during foraging to increase their chances of predator detection (McAdam and Kramer, 1998; Trouilloud *et al*., 2004;

Embar *et al*., 2011). Under perceived cost of predation, the gerbils in my study displayed a significant difference in frequency of attentiveness across the treatments, based on reward. Overall, the frequency of the gerbils attentive behaviour was greater when the seeds were piled, possibly due to the fact that they explored more in these situations and therefore at a greater predation risk. When seeds were piled, the gerbils were more attentive in high cost treatments, which could have increased predation risk (as explained above) and when seeds were scattered, the gerbils were more attentive in low cost treatments as they explored more in these treatments and again were under greater perceived predation risk. These data provide evidence for the attentiveness of the gerbils being associated with increasing predation risk.

The demand curves in experiment 4 are similar to those in experiment 3. The gerbils predominantly made uniform inelastic decisions in their food consumption, except for the occasional individual under certain circumstances.

4.5 Conclusions and recommendations

Bushveld gerbils in my study appeared to be employing a cost minimizing strategy (Morato *et al*., 1995), making decisions that lead to the least amount of energy expenditure because in most cases the gerbils foraged more in low cost and high reward treatments. Therefore, they were foraging efficiently, because they were minimizing costs and maximizing benefits (Kaufman and Collier, 1981; Kaufman and Collier, 1983). However, whether these decisions are influenced by procurement cost (cost of the doors) or consumption cost (cost in consuming the seeds, i.e. search cost) is not entirely clear, and from the data it can be inferred that there may be a combination of the two. My study also revealed that the motivation of the gerbils to forage differed between individuals, and in all the experiments, there were differences between demand curves for gerbils for the various treatment comparisons within experiments. The demand curves show that the gerbils were generally making consistent inelastic decisions except for a few gerbils under certain conditions. The differences in the demand curves for experiments 1 and 2 compared to experiment 3 and 4, especially the number of elastic responses for the LcLr and HcHr comparison, can possibly be due to the difference in the quality of the seeds presented. In other words, in experiments 1 and 2, there was a larger discrepancy between the quality of seed in low reward (least preferred) and high (most preferred) reward treatments, whereas in experiments 3 and 4, the gerbils received the

same quality of seed in all treatments. The decrease in these elastic responses from experiments 1 and 2 to mostly inelastic responses in experiments 3 and 4 can be attributed to the complexity of the design of the experiments, with the simple design of experiments 1 and 2 creating more elastic responses because the gerbils were making relatively simple decisions, merely choosing between seeds of different preference.

In comparison, the decisions in experiments 3 and 4 may have been different (choosing between piled and scattered seeds). These data reveal how the gerbils are varying their decision making depending on the situation at hand. When the demand curves were evaluated for all gerbils combined however, the responses were always inelastic. It is therefore clear that even though the gerbils are making different foraging decisions, in these kinds of analyses (i.e. pooled data) the differences were masked and present an inaccurate view of foraging decisions at the individual level, highlighting the need to assess individual decisions rather than those of groups/species. The seed preference tests also revealed the importance of considering individuality, especially when using most and least preferred foods. Amongst the gerbils in my study, there was one that preferred oats the most and another which preferred oats the least, therefore making assumptions on whether a species will prefer a particular food the most or least can again lead to discrepancies (Moon and Zeigler, 1979). My study also revealed that the presentation of the seeds might affect how gerbils forage (Moon and Zeigler, 1979) by increasing or decreasing the cost through how long they have to search for the seeds. Behavioural motivation to forage and the level of foraging are clearly influenced by the presentation of the seeds and the cost the gerbils experience in obtaining them.

Future studies could look more closely at the individual's motivation and decision making, where inferences can be made about the group or species based on commonalities among the individuals, instead of pooling data together. It would also be necessary to possibly investigate the differences/similarities in decision-making using naturally occurring seeds and compare the results to what was found in my study. Therefore we could establish whether the gerbils are basing their decisions purely on what seeds are available or if there is some common attribute in their seed selection (such as nutrition, water, energy etc.). These studies should also consider examining whether gerbils learn to anticipate cost and reward. Recreating these studies in both lab (such as mine) and possibly in natural conditions, such as

offering different presentation of seeds in a seed tray that requires low/high cost to access, could also offer some valuable insight into the decision making process and its parameters.

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Appendices

Appendix 1. Frequency data for non-significant behaviours in experiment 1

	Enter		Home		Attentive	
	Mean	**SE**	**Mean**	**SE**	**Mean**	**SE**
LcLr	13.18182	3.062436	13.45455	3.069983	44.18182	10.44798
LcHr	14.18182	3.155999	14.27273	3.130759	59.45455	10.29683
HcLr	17.54545	3.317621	17.90909	3.369528	63.45455	9.604321
HcHr	13.72727	2.93905	14.09091	2.955594	56.63636	12.61909

Appendix 2. Frequency data for non-significant behaviours in experiment 2

	Enter		Home		Attentive	
	Mean	**SE**	**Mean**	**SE**	**Mean**	**SE**
LcLr	13.90909	2.664427	14.18182	2.665668	53.81818	7.607195
LcHr	16.18182	3.402721	16.54545	3.420164	69.36364	11.55561
HcLr	15.45455	3.488588	15.63636	3.446402	74.00000	16.31397
HcHr	18.90909	5.221380	19.27273	5.217263	76.45455	10.57730

Appendix 3. Frequency data for non-significant behaviours in experiment 3

	Enter		Home		Attentive	
	Mean	**SE**	**Mean**	**SE**	**Mean**	**SE**
LcLr	15.45455	4.154655	15.72727	4.193265	51.18182	9.284217
LcHr	16.90909	4.275628	17.27273	4.217045	50.18182	9.403885
HcLr	17.63636	4.744897	17.27273	4.118894	46.72727	11.09225
HcHr	14.18182	4.153461	14.54545	4.132716	53.00000	13.32325

Appendix 4. Frequency data for non-significant behaviours in experiment 4

	Enter	
	Mean	**SE**
LcLr	12.18182	1.715269
LcHr	13.81818	2.543506
HcLr	9.909091	1.423533
HcHr	13.90909	3.563590