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# Decision-making by bushveld gerbils (*Gerbilliscus leucogaster*)

Decision-making in gerbils. Cruise et al.

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Decision-making reflects an individual's behavioral motivation, shaped by intrinsic and extrinsic factors. We investigated the motivation and decision-making to forage in captive bushveld gerbils (*Gerbilliscus leucogaster*) using an individually-tailored experimental protocol. Individual gerbils were subjected to four experiments, where we assessed behavior and decision-making in response to: 1) food quality when resources were clumped (experiment 1); 2) food quality when resources were scattered (experiment 2); 3) changing food distribution (clumped vs. scattered; experiment 3); and 4) predation risk. Each experiment comprised of four treatments, where both cost (a weighted door) and incentive (preferred vs. non-preferred seeds; clumped vs. scattered seeds) varied according to the mass and personal preferences of individual gerbils. We counted the number of seeds eaten, assessed the frequency of door usage, and measured the duration of exploration, vigilance and foraging (as a proportion of total time) of gerbils in each experiment. Gerbils showed individual preferences for different seed types, although all preferred sunflower or sorghum seeds. Generally, gerbils ate more seeds, and used the door more frequently, when the costs were low. Similarly, gerbils tended to forage more when the costs were low, and predation risk was low. We also found that males, in general, were more vigilant than females in experiments 3 and 4, likely because of risk of intrasexual competition over a high-resource patch. There was considerable individual variation in behavior, but there was also consistency in most behaviors, indicating that individual gerbils perform consistently differently to other gerbils.

*Keywords:* consistency, decision-making, flexibility, foraging, motivation

Decision-making describes the cognitive processes of evaluating information and then choosing between alternate or competing behaviors (Blumstein & Bouskila, 1996; Lima & Dill, 1990). The decision to continue with an existing behavior, or change to another, reflects an animal's behavioral motivation (i.e., intrinsic cues, Kirkden & Pajor, 2006), which needs to complement extrinsic (e.g., environmental) stimuli. Changes in an animal's internal state can vary in magnitude, shaping whether it responds to, disregards, or avoids stimuli, and these changes can also influence the levels of responses displayed (Mason & Bateson, 2017). However, the interaction between internal and external drivers can also vary dynamically (Jensen & Toates, 1993), leading to trade-offs between competing behaviors (e.g., feeding vs avoiding predation). For example, in group-living species, such as degus (*Octodon degus*), several group members could take turns engaging in vigilance (e.g., act as sentinels), giving others the opportunity to increase their foraging effort (Vásquez, 1997). However, for solitary species, such as yellow mongoose (*Cynictis penicillata*), foraging effort may be hindered by a need to be vigilant, although this cost may be offset by adopting less costly foraging and vigilance behaviors compared to group-living species, such as meerkats (*Suricata suricatta*, le Roux, Cherry, Gygax, & Manser, 2009).

The final behavioral outcome is largely determined by the prevailing motivational state of highest demand, which is mechanistically interpreted by the brain (McFarland, 1977), and is also influenced by several extrinsic factors. These include the location (Lima, Valone, & Caraco, 1985), type (Muñoz & Bonal, 2008) and accessibility of resources (Atkinson, Buckingham, & Morris, 2004), and predation risk (Holmes, 1991). In addition, any behavior an animal performs has associated costs and benefits, which should be weighed up prior to making a decision (McFarland, 1989). Consequently, the final decision has to 1) satisfy the particular motivational need under a specified set of circumstances, resulting in an array of consequent behaviors (Albin et al., 2015), and 2) weigh up the costs and benefits of performing any one of those consequent behaviors. A hungry animal, for example, will usually display enhanced sensory awareness (Pager, Giachetti, Holley, & Le Magnen, 1972), and engage in a sequence of behaviors, such as increased locomotion (Pirke, Broocks, Wilckens, Marquard, & Schweiger, 1993), increased food hoarding (Buckley & Schneider, 2003) and/or increased food consumption (Albin et al., 2015), and it will concurrently weigh up risks, such as predation risk (i.e., the starvation-predation risk trade-off, Lima, 1986).

Decision-making is, at its core, a function of the individual, not the species, and the accuracy of decision-making thus depends on the ability of the individual animal to reliably assess the costs and benefits associated with performing a specific behavior (van den Bos, van der Harst, Jonkman, Schilders, & Spruijt, 2006; Walton, Kennerley, Bannerman, Phillips, & Rushworth, 2006). Consequently, an individual's decision-making ability is influenced by numerous individual-specific factors, including its genotype (e.g., fruit flies [*Drosophila melanogaster*]: Osborne et al., 1997), sex (e.g., guppies [*Poecilia reticulata*]: Abrahams & Dill, 1989), age (e.g., redshanks [*Tringa totanus*]: Cresswell, 1994), experience (e.g., nightingales [*Luscinia megarhynchos*]: Schmidt, Amrhein, Kunc, & Naguib, 2007), personality (e.g., great tits [*Parus major*]: Amy, Sprau, de Goede, & Naguib, 2010) and fundamental intrinsic motivational needs of an individual at a particular moment in time.

Thus, the individual must decide how much effort to expend in order to obtain a desired outcome that will satisfy its motivational needs (van den Bos et al., 2006). For most animals, acquiring food underlies most of their decisions. Interestingly, most studies have focused on the effects of different costs of foraging behavior at a species level (e.g., predation risk and resource abundance in black-tailed jackrabbits (*Lepus californicus*; Marín, Hernández, & Laundré, 2003), with the conclusion that some decisions may be "hard-wired" whereas others may be flexible (Dill, 1987). However, it is peculiar why studies focusing on decision-making do not generally consider individual variation, rather reporting population means and variances, which reflect a population average and the main outliers. Therefore, whereas assessing group-level responses can demonstrate a general population-level response, such assessments can mask underlying individual variation and could present an inaccurate view of foraging decisions at the individual level.

We investigated motivation and decision-making in the solitary-living bushveld gerbil (*Gerbilliscus leucogaster*) during foraging and under potential predation risk at both the population and individual levels. The bushveld gerbil is a suitable study animal for assessing individual differences in foraging behavior and decision-making. Although it is predominantly granivorous, consuming a wide range of seeds, it also consumes other plant material and insects (Perrin & Swanepoel, 1987; Skinner & Chimimba, 2005), indicating that it is unlikely to be limited by food availability, but will need to make appropriate decisions to maximize its energy intake from foods of differing quality. In addition, bushveld gerbils do not hoard or cache food (Pettifer & Nel, 1977), suggesting that they regularly make trade-offs between the quality of the food they find and the relative predation risk. Although they are solitary, bushveld gerbils adopt a vigilance stance standing up on the hind limbs (bipedal guarding; le Roux et al., 2009) typical of many social rodents (e.g., white-tailed prairie dogs [*Cynomys leucurus*]: Hoogland, Hale, Kirk, & Sui, 2013; Richardson's ground squirrels [*Spermophilus richardsonii*]: Sloan & Hare, 2006).

We adopted a unique approach by tailoring the experimental protocol to each individual gerbil. First, we conducted seed preference tests to establish which seeds were considered high and low incentives for each gerbil. This allowed us to avoid a 'one size fits all' approach of assuming similar food preferences by all individuals. Second, we required the gerbils to access the incentives through a weighted door that could be weight-matched to each gerbil, representing a high cost. By doing so, the cost was tailored to the individual gerbil, meaning that we could assume that the amount of energy required to move the door would be similar between gerbils, and not set to a population mean, which would have benefitted larger gerbils but not smaller ones. For example, if the population mean was 70 g and the door was weighted to the mean, a 35 g gerbil would have to exert enough force to push double its body weight, whereas a 140 g gerbil would only have to exert enough force to push half its body weight. Consequently, the smaller gerbil would experience a higher cost. Third, we tested gerbils under different cost-incentive scenarios, from least cost to greatest cost, to incorporate the dynamic nature of decision-making in our experiments.

Individual gerbils were subjected to four experiments, each comprising four treatments, in which costs and incentives were varied. The first experiment aimed to investigate how the value of the incentive (preferred vs. non-preferred seeds) affected decision-making under increasing cost. The second experiment built on the first and aimed to investigate how imposing multiple costs (weighted door and scattering resources) affected decision-making. In this second experiment, we expected that scattering of seeds would increase the energetic costs of obtaining them, as suggested for domestic chickens (*Gallus domesticus*; Aoki, Csillag, & Matsushima, 2006), thereby imposing an additional cost. We predicted that gerbils would spend more time foraging for, and eat a greater number of, preferred seeds when the costs were low (i.e., door not

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weighted and seeds clumped), because preferred seeds have the highest palatability (Johnson & Collier, 2001), nutritional value (Muñoz & Bonal, 2008) and/or energy content. However, when the cost was greater (i.e., a heavier door and/or scattering of seeds), we expected that the number of preferred vs. non-preferred seeds eaten would be similar since the value of the resource declines with increasing cost (Hanson & Green, 1989).

The third and fourth experiments built on the second experiment and aimed to investigate how changing resource distribution of seeds (clumped vs. scattered) affected decision-making first under low perceived predation risk and then under high perceived predation risk. In these experiments, gerbils had access to two different seed types they preferred. We predicted that the gerbils would prefer to forage for clumped seeds, regardless of the cost (i.e., whether or not the door was weighted), and that gerbils would alter their vigilance and foraging behavior in response to increased perceived predation risk. Finally, we predicted that the foraging efficiency of gerbils would reflect a trade-off between nutritional value of food, risk of predation and clumping of resources (Lima, 1985; Lima et al., 1985). In particular, we expected that gerbils would spend more time vigilant when the perceived risk of predation was high, as seen in bison (*Bison bison*; Fortin & Fortin, 2009) and mid-day gerbils (*Meriones meridianus*; Shuai & Song, 2011).

For all experiments, we investigated patterns at both the population and individual levels. We first explored the general pattern of decision-making and trade-offs made by the population. We then compared decision-making of males and females. Numerous studies have shown that males and females differ in their risk-taking behavior. Consequently, we expected that, as in wild rats (*Rattus norvegicus*; Inglis et al., 1996), male gerbils would engage in more risk-taking behavior than females. However, Ebensperger, Hurtado, & Ramos-Jiliberto (2006) found that, under high predation risk, male and female degus did not behave differently, suggesting context-specific effects. Consequently, we also expected that sex differences might not occur under increased predation risk. Finally, we explored patterns of individual variation in behaviors to assess the relative flexibility of decision-making under different contexts.

## General Methods

*Subjects*

Twenty adult bushveld gerbils (males: n = 10; females: n = 10), were trapped near Orkney (26°54'7.5228" S; 26°41'40.8012" E), North-West Province, South Africa, and acclimated to laboratory conditions for three months prior to testing. Study animals were housed in a room with partial environmental control (light regime of 14:10 light/dark cycle, lights on at 0500 h; 22 °C (± 2 °C); 30-60% relative humidity) at the Milner Park Animal Unit, University of the Witwatersrand. Gerbils were housed individually in large tanks (45 x 29 x 35 cm) provided with a layer of coarse wood shavings for bedding. Hay and a plastic nest box (15 x 15 cm) were provided for nesting. Water was available *ad libitum*. During the acclimation phase, each gerbil received 3 g of commercial rodent cubes (Epol, Westville, KwaZulu-Natal, South Africa), 3 g of mixed seeds (hamster food), and 2 g of fruits or vegetables (e.g., lettuce, apple) daily.

The gerbils were placed on a restricted diet two weeks before experiments began. Food restriction is commonly used to increase feeding motivation in behavioral experiments (Tucci, Hardy, & Nolan, 2006). For example, Archard, Cuthill, & Partridge (2006) showed that guppies that were only food restricted for a short period (one day before testing) were less motivated (took longer to start eating and spent less time eating) than guppies that were food restricted for longer periods. The diet consisted of 1.5 g rodent cubes, 1.5 g commercial rice cereal (Pick n Pay no-name brand; protein content: 6 g/100 g; fat content: 0.2 g/100 g; carbohydrate: 80 g/100 g) and 1-2 g lettuce. Cereal was provided in place of seeds to reduce the gerbils' protein and fat intake. During experiments, gerbils received only 1.5 g of rice cereal daily, apart from the seed incentives given during experiments (see below). Between experiments, gerbils received the restricted diet only (described above). Gerbils were weighed every third day to assess changes in their weights. None gained weight, and five lost 1-3% body weight over the study period. All food was removed from each gerbil's cage one hour before each treatment.

### *Test Apparatus*

For each gerbil, experiments were conducted in an experimental tank (identical in size to the home tank) connected to the home tank with a PVC pipe (30 cm long x 5 cm wide, with an internal diameter of 4.5 cm; Figure 1). This allowed the gerbil to move freely between the relative "safety" of the home tank with the refuge (nest box) and the open experimental tank with no refuge. The experimental tank was modified to include an immovable, opaque Perspex partition, 14 cm from the entrance, with a Perspex door (6 x 6 cm) fitted at the bottom center of the partition that moved in both directions, allowing the gerbil to move freely back and forth between the two parts of the experimental tank (Figure 1). Small holes were drilled in the Perspex partition, allowing the gerbil to smell seeds placed on the other side of the partition during experiments. The experimental tank was furnished with river sand 2 cm deep. Seed preference tests (below) allowed the gerbils to become familiar with the experimental tank and the action of the Perspex door and partition prior to experiments. During seed preference tests and main experiments, seeds were placed in the experimental tank on the other side of the door only, and gerbils did not receive food in the home tank. Consequently, during these periods,

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gerbils first had to move from the home tank to the experimental tank via the PVC pipe, and then they had to push through the door to access food on the other side of the partition.

*Protocol and Data Analysis*

We conducted four experiments to test foraging decisions made by gerbils (see below). The general protocol was to impose a cost for individual gerbils to access an incentive in an experimental tank. The Perspex door permitting access into the main part of the experimental tank (Figure 1) could be weighted with metal plates to create low (no plates; Lc) or high (equal to 100% mass of the gerbil; Hc) costs, respectively. In addition, we also imposed other costs on the gerbils (see below). The preference of each gerbil was taken into consideration in some experiments, such that the seeds it preferred the most represented high incentives (Hi), whereas seeds it preferred the least represented low incentives (Li). Consequently, both costs and incentives were individually tailored to each gerbil. Within each experiment, gerbils thus experienced four treatments (LcLi, LcHi, HcLi and HcHi) run over four consecutive days, the sequence of which was randomly assigned for each gerbil (see below).

The behaviors of the gerbils were video recorded (using Sony DCR SX 44E cameras) for one hour (1900-2000 h) under red light to facilitate recording in the dark. At the end of each hour of treatment within each experiment (see below), the remaining seeds were counted and weighed (to the nearest 0.1 g) to determine the quantity (as a proportion of the whole) and mass of seeds eaten during the treatments. Later, we used Observer XT 9™ (Noldus Information Technologies) to score the duration of time (as a proportion of total time) spent (a) exploring the experimental tank, (b) vigilant (raising the front paws off the ground, standing on the hind legs, with ears up

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and gerbil motionless), and (c) foraging (handling and consuming seeds). We also recorded the frequency of crosses from the home tank to the experimental tank through the door (door usage).

All analyses were performed using R studio (R version 3.5.1; http://www.R-project.org). All data were first examined for normality using Shapiro-Wilk tests, and were transformed where necessary (Supplementary Table S1). We used a Shapiro-Wilk test on model residuals, visually examined the boxplot model residuals and inspected Q-Q plots of the model residuals against fitted values after analyses to assess whether the model distribution was appropriate. We also used the descdist function (fitdistrplus package, Delignette-Muller, Dutang, Pouillot, Denis, & Siberchicot, 2020) to assess appropriate distributions (Supplementary Table S1).

Instead of analyzing experiments independently, we combined experiments 1 and 2 into a single model, and experiments 3 and 4 into a second model. This allowed us to compare how changing 1) resource distribution (experiments 1 and 2) and 2) perceived predation risk (experiments 3 and 4) impacted decision-making while maintaining similar imposed costs and benefits. For all experiments, we used either linear or generalized linear mixed effects models (LMER or GLMER) using the lmerTest package (Kuznetsova, Brockhoff, & Christensen, 2015) for number of seeds consumed, duration of time spent exploring the experimental tank, vigilant and foraging, and frequency of crosses between tanks (Supplementary Table S1). We excluded mass of seeds consumed in the final analyses since the mass of seeds eaten was always highly significantly positively correlated with number of seeds eaten (Supplementary Table S2). In all initial models, the number of seeds eaten, and duration and frequency of behaviors were the dependent variables, treatment, sex and experiment were included as fixed factors, body mass was included as a covariate, and individual identity was included as a random factor to account for the repeated measures obtained from individual gerbils. We also included the interaction between treatment and experiment. Body mass was not a significant predictor of behavior in any of the experiments ($p > .05$) and was consequently not considered in final models. For experiments 3 and 4, gerbils were presented simultaneously with two seed types that they preferred, which gave them a choice of which seeds to eat rather than just whether it was worth eating the seeds presented, as for experiments 1 and 2. However, gerbils always preferred sunflower seeds over sorghum seeds (Supplementary Table S2), so we did not include the variable "seed type" in final models. $\chi^2$ statistics are reported (car package, Fox et al., 2012). Tukey's *post hoc* tests were used to obtain pairwise comparisons of levels for significant categorical predictors (emmeans package, Lenth, Singmann, Love, Buerkner, & Herve, 2020).

To analyze whether there was an effect of individual identity on behavior, we used the ranova function (lmerTest package) when we used an LMER. However, if we used a GLMER, we ran likelihood ratio tests to determine the significance of the random factor (since the ranova function cannot be used with a GLMER). Then, to analyze specific differences between individuals, we ran the main model again, but this time using individual identity as a fixed factor. Tukey's *post hoc* tests were then used to obtain pairwise comparisons between individuals (emmeans package). We also calculated the coefficient of repeatability (R; rptR package, Stoffel, Nakagawa, & Schielzeth, 2019) and estimated the 95 % confidence intervals (CI) around the repeatability estimates for each behavior in each experimental group (experiments 1 and 2, experiments 3 and 4) to assess the proportion of phenotypic variation attributable to between-individual variation. Adjusted repeatabilities were calculated for each model as the between-individual variance divided by the sum of the between-individual and the residual variance (Nakagawa & Schielzeth, 2010).

For all models, we present means, standard errors, confidence intervals and Cliff's delta effect sizes (effectsize package, Makowski, Lüdecke, Ben-Shacha, Kelley, & Stanley, 2020; Table 1). Figures were generated using the calculated emmeans means and standard errors.

## Experiments: Methods and Results

*Seed preference experiment*

Methods

Each gerbil underwent a seed preference test one month before experiments commenced, during which each animal was provided with five types of commercial seeds (sunflower, dried maize, sorghum, wild oats, wild rice; Supplementary Table S3). All five seed types were presented simultaneously in the experimental tank in a cafeteria-style choice test (Murray & Dickman, 1997). 50 seeds of each seed type (total seeds = 250) were weighed, then placed into the experimental tank at approximately 1300 h, and left overnight until approximately 1000 h the next day on three separate occasions for each gerbil. Any seeds remaining were counted and weighed to the nearest 0.1 g. These data were used to determine the most preferred (greatest number of seeds consumed) and least preferred (smallest number of seeds consumed) seeds for each gerbil.

Results

Individual gerbils showed different seed preferences (Supplementary Table S4), and there was no ambiguity in preference (i.e., each individual made a distinct choice for a particular seed type). 65% (13/20) preferred sunflower seeds (ranked 1), whereas maize was the least preferred for 75% (15/20) of gerbils (ranked 5). Wild rice was not preferred by any individual (i.e., never ranked 1), while sunflower seeds never ranked 5 for any individual (Supplementary Table S4). These preferences were used in experiments to create low and high incentives (see below).

## Discussion

Seed preference is based on many factors, including palatability, size, nutrition and ease of consumption (Johnson & Collier, 2001; Kelrick, MacMahon, Parmenter, & Sisson, 1986; Muñoz & Bonal, 2008; Murray & Dickman, 1997; Parshad & Jindal, 1991). Whereas the gerbils showed clear individual preferences, most favored sunflower seeds, which had the highest nutritional value (energy, protein and carbohydrate), suggesting they were selecting for seed quality, common to shrub-steppe granivores (Kelrick et al., 1986). Despite its high energy and protein value, maize was the least preferred seed generally, most likely because its hardness made it difficult to ingest (Parshad & Jindal, 1991) or because its size resulted in increased handling time and difficulty with transportation (Muñoz & Bonal, 2008).

### *Experiments 1 and 2: preferred vs. non-preferred seeds (clumped vs. scattered)*

## Methods

In these experiments, gerbils had access to seeds they preferred the most (high incentive: Hi) and least (low incentive: Li) as the cost changed by adding weights to the door (low vs. high cost: Lc or Hc). For each gerbil, 2 g of each seed type was weighed and counted. In the first experiment, the seeds were presented in a pile in the center of the experimental tank. In contrast, in the second experiment, the seeds were scattered (randomly sprinkled over the surface) and tossed in the sand (mixed in the sand with a shaking motion of the hand) to a depth of approximately 0.5 cm in the experimental tank. Gerbils had to actively search and dig for seeds when they were scattered. In these experiments, gerbils were not given a choice between alternative seed types within treatments and were presented with only one seed type at a time within treatments.

## Results

### *Number of Seeds Eaten and Frequency of Door Usage*

Treatment affected the number of seeds eaten (Table 1; Figure 2a) and the frequency of door usage (Table 1; Figure 3a). Gerbils ate significantly more seeds when they were presented with their preferred seeds and the door was not weighted (LcHi: 77.16 ± 3.40%) than when the door was weighted (HcLi: 45.63 ± 3.81%; HcHi: 53.69 ± 4.27%; Figure 2a). Gerbils also ate significantly more of their least preferred seeds when the door was not weighted (LcLi: 63.14 ± 4.38%) than when it was weighted (HcLi; Figure 2a). Similarly, gerbils used the door significantly more when it was not weighted (LcLi: 12.95 ± 1.36 times; LcHi: 15.18 ± 1.55 times) than when it was weighted (HcLi: 4.00 ± 0.65 times; HcHi: 3.33 ± 0.46 times; Figure 3a). Sex, experiment and the interaction between treatment and experiment had no significant effects on the number of seeds consumed or the frequency of door usage (Table 1). There was no significant individual variation in the number of seeds eaten between gerbils (Table 1), with no significant repeatability (R = 0.06; SE = 0.05; CI [0.000, 0.182]; $p = .151$; Supplementary Figure S1). There was, however, significant individual variation in the frequency of door usage (Table 1), and this was significantly repeatable (R = 0.53; SE = 0.10; CI [0.304, 0.706; $p < .001$); for specific patterns, see Supplementary Figure S2).

*Duration of Behaviors*

Treatment, sex, experiment and the interaction between treatment and experiment were not significant predictors of the duration of exploration (Table 1; Figure 4a). However, treatment was a significant predictor of the duration of vigilance and foraging (Table 1). Gerbils spent significantly more time being vigilant in the HcLi treatment (15.73 ± 1.60%) than in any other treatment (Figure 5a), and spent significantly more time foraging in the low cost treatments (LcLi: 22.63 ± 2.16%; LcHi: 17.10 ± 1.20%) than the HcLi treatment (13.72 ±2.03%, Figure 6a).

Neither sex nor experiment were significant predictors of the duration of vigilance or foraging (Table 1). However, there was a significant effect of the interaction between treatment and experiment on duration of vigilance (Table 1). Gerbils in the HcLi treatment in experiment 1 were significantly more vigilant than in any other treatment or experiment 2 (Figure 5a). There was no significant interaction effect between treatment and experiment on the duration of foraging (Table 1). There was significant individual variation in duration of exploration and foraging between gerbils (Table 1), which was significantly repeatable (exploration: R = 0.44; SE = 0.10; CI [0.248, 0.623; $p < .001$; for specific patterns, see Supplementary Figure S3; foraging: R = 0.23; SE = 0.09; CI [0.074, 0.402; $p < .001$; for specific patterns, see Supplementary Figure S5). However, there was no significant individual variation in duration of vigilance, with no repeatability (R = 0.02; SE = 0.04; CI [0.000, 0.120]; $p = .365$ (Supplementary Figure S4).

## Discussion

When foraging, animals pay costs to obtain food, and must balance out these costs against the benefits obtained from food (Abrams, 1991; Ackroff, Schwartz, & Collier, 1986). We first

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explored how the value of an incentive and imposing multiple costs affected decision-making. A major cost of foraging is the time needed to locate resources (search time, Murphy & Kelly, 2001). Consequently, when resources are scattered, both the energetic and time costs to obtain them should increase. We expected that scattering seeds would increase the energetic costs of obtaining them, as suggested by Aoki et al. (2006) for domestic chickens, but there was no effect of experiment on any behavior, suggesting that scattering seeds did not impose an additional cost compared to clumping seeds. Rather, the gerbils behaved similarly when offered a single seed type, regardless of whether the seeds were clumped or scattered. Whereas the spacing of seeds might not have been sufficient to generate an additional cost to foraging compared to the clumped condition (i.e., a threshold limitation of spacing was not reached), we suggest that this lack of difference indicates that the gerbils were making the best of a bad job when the seeds were scattered (i.e., they have a cognitive bias that minimizes mistakes that incur a greater cost; Johnson, Blumstein, Fowler, & Haselton, 2013), and that they continued to feed, even on non-preferred food, to avoid incurring costs of not feeding at all.

We predicted that gerbils would spend more time foraging for, and eat a greater number of, preferred seeds when the cost was low (Johnson & Collier, 2001; Muñoz & Bonal, 2008) but that there would be no difference in the number of preferred vs. non-preferred seeds eaten as the cost increased (Hanson & Green, 1989). When the cost was low (i.e., door unweighted) and the incentive was high (i.e., preferred seeds offered), gerbils ate more seeds, used the door more, were less vigilant and spent more time foraging than when the cost was high and the incentive was low. Conventional models of foraging suggest that the net rate of energy intake is influenced by the time and energy costs incurred from accessing and handling food (Stephen & Krebs, 1986). Preferred seeds had the highest energy, palatability and/or nutritional value, making them a more attractive resource (Johnson, Ackroff, Collier, & Plescia, 1984; Johnson, Ackroff, Peters, & Collier, 1986; Muñoz & Bonal, 2008; Sunday, Sanders, & Collier, 1983) than non-preferred seeds. Similarly, an unweighted door is less costly to use than a weighted door, and individuals are likely to be more motivated to access a resource when the cost to access it is low. Similar to our findings, American minks (*Mustela vison*) increased their number of uses of a weighted door as the weight of the door decreased (Cooper & Mason, 2000).

Collectively, our findings suggest that gerbils decrease their motivation to work to access a reward as the cost increases. As expected, when the cost to access the reward increased (i.e., door was weighted), we saw no difference in the number of seeds eaten for preferred or non-preferred seeds, suggesting that the value of the resource (preferred seeds) declined with increasing cost (Hanson & Green, 1989). Our results also suggest a trade-off between vigilance and foraging behavior, since gerbils spent significantly less time foraging for seeds, and more time being vigilant, when the cost was high and they had access to their least preferred seeds. Patch quality can affect feeding rate and vigilance in herbivores (Underwood, 1982) and birds (Elgar, 1989). We suggest three reasons why gerbils reduce foraging and increase vigilance when presented with their least preferred seeds. 1) Foraging in a poor patch necessitates a longer period of foraging to meet energetic demands, which could increase the possibility of predation. Thus, vigilance could increase because gerbils scan to avoid predators. 2) Gerbils may increase vigilance, not to search for predators, but rather because they are scanning for a potential new patch, as suggested for herbivores (Underwood, 1982). 3) When the rate of return from food is low, gerbils might be less willing to sacrifice vigilance (Beauchamp, 2015).

We found significant individual variation in frequency of door use, duration of exploration and duration of foraging, that is, some gerbils used the door significantly more, explored more and foraged more than other gerbils. Furthermore, these were repeatable across contexts, indicating that gerbils generally performed consistently in relation to each other. In contrast, although there was individual variation in the number of seeds eaten and the duration of vigilance, this was not significantly different between individuals (e.g., Gerbil 6 ate more seeds than Gerbil 4 but this was not significantly different), and there was no significant repeatability, indicating that gerbils did not behave consistently over experiments. These findings suggest that vigilance behavior and amount of food eaten are fairly flexible, with other intrinsic factors, such as personality (Aplin, Farine, Mann, & Sheldon, 2014) and hunger state, potentially influencing their decision making.

### *Experiments 3 and 4: clumped vs. scattered resources under low and high predation risk*

#### Methods

In these experiments, gerbils had access to two seed types that they preferred, namely sunflower and sorghum. Presenting the gerbils simultaneously with two preferred seed types gave the gerbils a choice of which seeds to eat rather than just whether it was worth eating the seeds presented, as in experiment 1 and 2. For each gerbil, seeds were mixed, and 2 g of the combined seed mix was presented either in a pile in the center (high incentive: Hi) or scattered and tossed in the sand to a depth of approximately 0.5 cm (low incentive: Li) in the experimental tank. Gerbils had to actively search and dig for seeds when they were scattered. In addition, we changed the cost by adding weights to the door (low vs. high cost: Lc or Hc; as for experiments 1 and 2). For experiment 4, because animals, in general, use both illumination level (e.g., moonlight; Alleby's gerbil [*Gerbilus andersoni allenbyi*]: Kotler, Brown, Mukherjee, Berger-Tal, & Bouskila, 2010; Darwin's leaf-eared mouse [*Phyllotis darwini*]: Vásquez, 1994) and predator olfactory cues (e.g., fawn-footed mosaic-tailed rat [*Melomys cervinipes*]: Paulling, Wilson, & Rymer, 2019; African striped mouse [*Rhabdomys pumilio*]: Pillay, Alexander, & Lazenby, 2003) to assess the risk of predation, we placed a white light above the experimental tank to simulate a full moon, and placed ± 5 ml of fresh honey badger (*Mellivora capensis*) urine (collected from the Johannesburg Zoo on the morning of the experiment) into the experimental tank. Honey badgers are known predators of a variety of gerbil species (e.g., Begg, Begg, Du Toit, & Mills, 2003; Kruuk, & Mills, 1983). In pilot studies, gerbils responded to these stimuli by reducing activity, suggesting increased perceived predation risk (Lima, 1998). We acknowledge that the use of the term "incentive" to represent the distribution of resources in this situation does not adequately describe a benefit for the gerbils. However, to distinguish between the multiple costs imposed in this experiment (i.e., weighted door is a high cost, but scattered seed is also a high cost), we use the same abbreviations as for other treatments/experiments in our study for simplicity and convenience.

## Results

### *Number of Seeds Eaten and Frequency of Door Usage*

Treatment, sex, experiment and the interaction between treatment and experiment did not affect the number of seeds eaten (Table 1; Figure 2b). However, there was a significant effect of treatment on the frequency of door usage (Table 1; Figure 3b). Gerbils used the door significantly more when the door was unweighted and the seeds were clumped (LcHi: 9.95 ± 1.00 times) than when the door was weighted (HcLi: 2.43 ± 0.32 times; HcHi: 2.58 ± 0.38 times) or the seeds were scattered (LcLi: 7.25 ± 0.85 times; Figure 3b). Sex, experiment and the interaction between treatment and experiment did not affect the frequency of door usage (Table

1). There was significant individual variation in the number of seeds eaten and the frequency of door usage (Table 1), with significant repeatability for both number of seeds consumed (R = 0.44; SE = 0.10; CI [0.248, 0.613]; $p < .001$; for specific patterns, see Supplementary Figure S1) and door usage (R = 0.49; SE = 0.10; CI [0.285, 0.672]; $p < .001$; for specific patterns see Supplementary Figure S2).

### *Duration of Behaviors*

Treatment and experiment were both significant predictors of the duration of exploration (Table 1). Gerbils explored for significantly longer when the door was unweighted and the seeds were clumped (LcHi) than when they were scattered (LcLi) or the door was weighted (HcLi and HcHi; Figure 4b). In addition, gerbils explored 1.3 times longer in experiment 3 than in experiment 4. Sex and the interaction between treatment and experiment were not significant predictors of the duration of exploration (Table 1). Although treatment, experiment and the interaction between treatment and experiment were not significant predictors of the duration of vigilance (Table 1), sex was a significant predictor of duration of vigilance, with males being 2.3 times more vigilant than females (Table 1; Figure 5b). Experiment was a significant predictor of duration of foraging, with gerbils foraging for 1.3 times longer in experiment 3 than experiment 4 (Table 1; Figure 6b). There was no effect of sex, treatment or the interaction between treatment and experiment on duration of foraging (Table 1). There was significant individual variation in duration of exploration between gerbils (Table 1), with significant repeatability (R = 0.59; SE = 0.10; CI [0.390, 0.755]; $p < .001$; for specific patterns see Supplementary Figure S3). Similarly, there was also significant individual variation in duration of vigilance and foraging (Table 1), with significant repeatability (vigilance: R = 0.35; SE = 0.10; CI [0.163, 0.531]; $p < .001$; for specific patterns see Supplementary Figure S4; foraging: R = 0.18; SE = 0.08; CI [0.041, 0.339]; *p* < .001; for specific patterns see Supplementary Figure S5).

## Discussion

Animals should evaluate the costs and benefits associated with particular behaviors, and then choose between alternate or competing behaviors (Lima & Dill, 1990). Their decision will be affected by their current internal body state (McFarland, 1977) as well as other extrinsic factors, including accessibility of resources (Atkinson, Buckingham, & Morris, 2004) and predation risk (Holmes, 1991). Consequently, we explored how changing the distribution of resources under low and high perceived predation risk affected decision making. We predicted that the gerbils would eat more seeds, use the door more, explore and forage more and be less vigilant when resources were clumped and perceived predation risk was low.

Animals should trade off energy gain against the risk of predation. Interestingly, we found no difference in the number of seeds eaten between the different treatments or experiments. This is contrary to Kotler, Brown, & Mitchell (1993) for Allenby's and greater Egyptian sand gerbils, but similar to Pastro & Banks (2006) for wild house mice (*Mus musculus*). However, gerbils did use the door significantly less when it was weighted. Furthermore, resource distribution affected the frequency of door use, since gerbils used the door significantly more, and also spent more time exploring, when resources were clumped. These results demonstrate that physical costs affect motivation to access resources, and the energy obtained from staying in a patch with scattered resources likely outweighs the time spent searching for a new patch (Holbrook & Schmitt, 1988).

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We expected that the foraging efficiency of gerbils would reflect a trade-off between foraging, risk of predation and clumping of resources under increased perceived predation risk (Lima, 1985; Lima et al., 1985), with increased vigilance under higher perceived risk of predation (Fortin & Fortin, 2009; Shuai & Song, 2011), and a reduction in foraging (Bengsen, Leung, Lapidge, & Gordon, 2010; Krivan & Vrkoc, 2000; Lima, 1985), as for other species. Both indirect (Hughes, Ward, Perrin, 1995; Jacquot & Baudoin, 2002) and direct cues of predation can cause considerable changes in foraging behavior (Bengsen et al., 2010; Krivan & Vrkoc, 2000; Lima, 1985). Interestingly, we found no change in vigilance behavior across treatments or experiments. However, we did find a reduction in foraging behavior, regardless of treatment, under increased predation risk, although this did not affect their overall consumption of seeds. Gerbils always ate more sunflower seeds than sorghum seeds, suggesting a preference when provided with a choice. The gerbils were placed on a nutritionally restricted diet prior to experiments, were food deprived for an hour before experiments, and only had one hour to obtain and consume the seeds during experiments. Thus, they might have been more selective for seeds with a higher nutritional value (Moon & Zeigler, 1979). It is equally possible that they had a greater encounter rate with the larger, more conspicuous sunflower seeds, leading to their higher consumption, as occurred in Allenby's and Egyptian sand gerbils (Garb, Kotler, & Brown, 2000).

A reduction in foraging suggests that gerbils might have potentially reduced initial risk by reducing movement (Diaz, Torre, Peris, & Tena, 2005). Furthermore, it is possible that we observed no change in vigilance behavior overall because of subtle differences in behavior over time. Many animals use vigilance, such as pauses and head raising, to increase their chances of detecting a predator's presence (Embar, Kotler, & Mukherjee, 2011; McAdam & Kramer, 1998;

Trouilloud, Delisle, & Kramer, 2004). If no predator is detected initially, the perceived risk of predation may decline over time within a foraging bout, with a concomitant reduction in vigilance. However, it is also possible that we observed no change in vigilance behavior overall because gerbils may not respond to direct cues of predation risk. Oldfield mice (*Peromyscus polionotus*, Orrock, Danielson, & Brinkerhoff, 2004) and fox squirrels (*Sciurus niger*, Thorson, Morgan, Brown, & Norman, 1998) do not adjust foraging behavior when presented with direct cues of predators (e.g., urine or plastic models of predators), whereas both species respond strongly to changes in microhabitat (e.g., distance from a refuge, amount of cover). Our results suggest that gerbils may also rely more on indirect cues, although this will require further testing in the future.

We expected that male gerbils would engage in more risk-taking behavior than females (Inglis et al., 1996), but males were actually more vigilant, suggesting perhaps that males were more risk-averse in particular contexts (Ebensperger et al. 2006). Since there was no experiment effect, it is unlikely that perceived predation risk was the underlying cause. Moreover, there was no treatment effect, suggesting that differences in costs and incentives are unlikely to affect differences in behavior. Bushveld gerbils can be aggressive towards conspecifics (Lötter, 2010), so it is possible that males increase vigilance when foraging in a high quality patch to defend patches against conspecifics. However, since little is known about the general behavior of bushveld gerbils, this assumption would require additional testing.

We found significant individual variation for most behaviors, and significant repeatability (albeit low for foraging behavior). These results again indicate that gerbils generally performed consistently in relation to each other. In contrast to the first two experiments, we found repeatability for both the number of seeds eaten and duration of vigilance. We presented the

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gerbils with two seed types (experiments 3 and 4) and introduced predation risk into the design (experiment 4). Flexibility in behavioral responses may decrease under increasing risk, indicating context-specific effects. For example, Bell & Sih (2007) found that threespined sticklebacks (*Gasterosteus aculeatus*) only showed personality (i.e., a correlation between boldness and aggression) under increased predation risk. Alternatively, or in addition, environmental variation may affect repeatability of behavior, either increasing or decreasing repeatability estimates, often in a sex-dependent manner (e.g., stitchbirds [*Notiomystis cincta*]: Low, Makan, & Castro, 2012).

## General Discussion

We investigated the motivation and decision-making of individual bushveld gerbils during foraging to understand whether decision-making is consistent for individuals under different cost-incentive decision scenarios. Our study was unique because we tailored the protocol to each gerbil. Prior to testing, we assessed each gerbil's preferences for different seed types. Gerbils showed clear individual preferences for seeds with high nutritional value. In experiments 1 and 2, we investigated how the value of the incentive and imposing multiple costs affected decision-making. Physical costs and incentives resulted in changes in behavior, whereas gerbils did not adjust their behavior in response to patchiness of resources, suggesting a cognitive bias to respond consistently when no alternatives are present. In experiments 1 and 2, some behaviors were flexible (vigilance and number of seeds eaten). However, this flexibility in behavioral response decreased under increasing risk, indicating context-specific effects. In experiments 3 and 4, we investigated how changing the distribution of the resource and altering perceived predation risk affected decision-making. We did not find an expected trade-off between vigilance and foraging behavior, most likely because gerbils initially responded to the predation threat, but then adjusted (habituated) their behavior when a threat did not materialize. Gerbils reduced foraging overall, which did not affect their seed consumption. Interestingly, gerbils were selective of seed type when given a choice, always choosing food of higher nutritional value.

Individual gerbils showed different seed preferences, and showed significant individual variation in the number of seeds eaten, frequency of door usage, and duration of exploration, vigilance and foraging. There was also significant repeatability of behaviors across tests. For example, some gerbils (e.g., G5) consistently ate more seeds than other gerbils (e.g., G4 and G9), whereas some other gerbils (e.g., G11) consistently used the door more than other gerbils (e.g., G8 and G9). Although it is known that individuals vary in behavior and decision-making (e.g., Mazza, Jacob, Dammhahn, Zaccaroni, & Eccard, 2019; Sih, Sinn, & Patricelli, 2019), individual variation in behavior and decision-making under different cost-incentive scenarios is often glossed over in the literature in favor of presentation of generalized patterns (means and standard errors/deviations) of populations. We suggest that simply presenting a population mean, and even taking standard errors or deviations into account, is not sufficient for capturing the variability in consistency and flexibility of individual decision-making. Consequently, traditional presentation of data as means and standard errors masks individual variation in trade-offs and fails to account for different tactics of individuals in different contexts. Therefore, we recommend that, even if generalized patterns are of principal interest, studies should also consider how individual tactics may be shaping these more generalized patterns, remembering that the population average is unlikely to accurately reflect how any specific individual responds.

We considered several intrinsic (hunger, fear) and extrinsic (door weight, seed type, seed presentation) drivers of seed consumption in our study. Our study is unique in that we took an

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individual-centric approach to the experimental design. Although our experimental design does not allow us to isolate the individual effects of these intrinsic and extrinsic drivers on decisions made, the outcome of the different experiments indicate that the final behavioral outcome is not necessarily primarily determined by the prevailing motivational state of highest demand.

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## Ethical approval

The research adhered to the ABS/ASAB guidelines for the ethical treatment of animals (Bee et al., 2020). The experiments were approved by the Animal Ethics and Screening Committee of the University of the Witwatersrand (AESC number: 2010/15/2A) and complied with the laws and regulations of South Africa.

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*Table 1***.** Statistical outputs for model analyses of behavior of bushveld gerbils (*Gerbilliscus leucogaster*) in four different experiments: Experiment 1: preferred vs. non-preferred seeds (clumped); Experiment 2: preferred vs. non-preferred seeds (scattered); Experiment 3: clumped vs. scattered (mixed); Experiment 4: predation risk. Significant values indicated in bold.

| **Experiment** | **Factor** | **Mean (±SE); CIs** | **Predictor** | **Effect Size (+ CIs)** | **Statistics** |
|---|---|---|---|---|---|
| ***Experiments 1 and 2 combined*** | Number of seeds eaten | 60.20 (2.19); 55.87-64.52 | Individual | 0.02 (-0.52; 0.55) | $\chi^2_1 = 1.32$, $p = .251$ |
| | | | Sex | 0.15 (-0.03; 0.32) | $\chi^2_1 = 2.23$, $p = .136$ |
| | | | Treatment | 0.21 (-0.05; 0.44) | **$\chi^2_3 = 30.50$, $p < .001$** |
| | | | Experiment | -0.11 (-0.28; 0.08) | $\chi^2_1 = 2.528$, $p = .112$ |
| | | | Treatment x Experiment* | - | $\chi^2_1 = 4.49$, $p = .213$ |
| | Frequency of door usage | 8.86 (0.69); 7.50-10.22 | Individual | 0.03 (-0.53; 0.57) | **$\chi^2_2 = 8.48$, $p = .014$** |
| | | | Sex | 0.07 (-0.11; 0.24) | $\chi^2_1 = 0.04$, $p = .845$ |
| | | | Treatment | -0.09 (-0.33; 0.16) | **$\chi^2_1 = 30.05$, $p < .001$** |
| | | | Experiment | 0.03 (-0.15; 0.21) | $\chi^2_1 = 2.59$, $p = .108$ |
| | | | Treatment x Experiment* | - | $\chi^2_3 = 2.24$, $p = .524$ |
| | Duration of exploration | 37.30 (1.28); 34.77-39.82 | Individual | -0.52 (-0.84; 0.08) | **$\chi^2_1 = 49.47$, $p < .001$** |
| | | | Sex | -0.32 (-0.48; -0.15) | $\chi^2_1 = 2.65$, $p = .104$ |

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|  |  |  |  |  |  |
|---|---|---|---|---|---|
|  |  |  | Treatment | -0.05 (-0.29; 0.21) | $\chi^2_3 = 4.37, p = .225$ |
|  |  |  | Experiment | -0.02 (-0.20; 0.16) | $\chi^2_1 = 0.15, p = .701$ |
|  |  |  | Treatment x Experiment* | - | $\chi^2_3 = 1.68, p = .641$ |
|  | Duration of vigilance | 8.60 (0.58); 7.46-9.74 | Individual | 0.36 (-0.27; 0.77) | $\chi^2_2 = 3.90, p = .143$ |
|  |  |  | Sex | -0.14 (-0.31; 0.04) | $\chi^2_1 = 0.83, p = .363$ |
|  |  |  | Treatment | -0.55 (-0.73; -0.30) | **$\chi^2_3 = 57.29, p < .001$** |
|  |  |  | Experiment | 0.02 (-0.16; 0.20) | $\chi^2_1 = 1.81, p = .179$ |
|  |  |  | Treatment x Experiment* | - | **$\chi^2_3 = 23.59, p < .001$** |
|  | Duration of foraging | 17.31 (0.91); 15.51-19.10 | Individual | -0.09 (-0.61; 0.48) | **$\chi^2_1 = 15.93, p < .001$** |
|  |  |  | Sex | 0.02 (-0.16; 0.20) | $\chi^2_1 = 0.06, p = .804$ |
|  |  |  | Treatment | 0.19 (-0.05; 0.41) | **$\chi^2_3 = 19.99, p < .001$** |
|  |  |  | Experiment | 0.02 (-0.15; 0.20) | $\chi^2_1 = 0.41, p = .520$ |
|  |  |  | Treatment x Experiment* | - | $\chi^2_3 = 6.55, p = .088$ |
| ***Experiments 3 and 4 combined*** | Number of seeds eaten | 38.63 (1.69); 35.30-41.97 | Individual | -0.28 (-0.75; 0.38) | **$\chi^2_1 = 48.48, p < .001$** |
|  |  |  | Sex | -0.03 (-0.21; 0.15) | $\chi^2_1 = 0.02, p = .897$ |
|  |  |  | Treatment | 0.06 (-0.18; 0.29) | $\chi^2_3 = 3.97, p = .264$ |

| | | | |
|---|---|---|---|
| | | Experiment | -0.01 (-0.19; 0.17) | $\chi^2_1 = 0.13$, $p = .713$ |
| | | Treatment x Experiment[*] | - | $\chi^2_3 = 1.87$, $p = .600$ |
| Frequency of door usage | 5.55 (0.43); 4.70-6.40 | Individual | 0.14 (-0.44; 0.64) | **$\chi^2_1 = 58.20$, $p < .001$** |
| | | Sex | 0.04 (-0.14; 0.21) | $\chi^2_1 = 0.05$, $p = .821$ |
| | | Treatment | 0.02 (-0.22; 0.27) | **$\chi^2_1 = 81.56$, $p < .001$** |
| | | Experiment | -0.13 (-0.30; 0.05) | $\chi^2_1 = 3.26$, $p = .071$ |
| | | Treatment x Experiment[*] | - | $\chi^2_3 = 0.76$, $p = .858$ |
| Duration of exploration | 27.77 (1.26); 25.29-30.25 | Individual | 0.27 (-0.34; 0.71) | **$\chi^2_1 = 85.64$, $p < .001$** |
| | | Sex | -0.31 (-0.47; -0.13) | $\chi^2_1 = 2.33$, $p = .127$ |
| | | Treatment | 0.00 (-0.25; 0.25) | **$\chi^2_3 = 13.15$, $p = .004$** |
| | | Experiment | -0.31 (-0.46; -0.14) | **$\chi^2_1 = 12.28$, $p < .001$** |
| | | Treatment x Experiment[*] | - | $\chi^2_3 = 5.40$, $p = .145$ |
| Duration of vigilance | 6.37 (0.71); 4.96-7.78 | Individual | 0.64 (-0.06; 0.92) | **$\chi^2_2 = 29.18$, $p < .001$** |
| | | Sex | -0.47 (-0.61; -0.30 | **$\chi^2_1 = 6.05$, $p = .014$** |
| | | Treatment | 0.17 (-0.08; 0.41) | $\chi^2_3 = 1.67$, $p = .643$ |
| | | Experiment | -0.05 (-0.22; 0.12) | $\chi^2_1 = 0.17$, $p = .684$ |

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|  |  |  |  |  |  |
|---|---|---|---|---|---|
|  |  |  | Treatment x Experiment* | - | $\chi^2_3 = 0.22$, $p = .974$ |
|  | Duration of foraging | 15.13 (0.96); 13.23-17.04 | Individual | -0.41 (-0.83; 0.30) | **$\chi^2_1 = 10.60$, $p = .001$** |
|  |  |  | Sex | -0.11 (-0.28; 0.07) | $\chi^2_1 = 0.49$, $p = .486$ |
|  |  |  | Treatment | 0.05 (-0.19; 0.28) | $\chi^2_3 = 7.25$, $p = .064$ |
|  |  |  | Experiment | -0.21 (-0.38; 0.03) | **$\chi^2_1 = 4.91$, $p = .027$** |
|  |  |  | Treatment x Experiment* | - | $\chi^2_3 = 0.94$, $p = .817$ |

* Effect sizes could not be calculated for interactions as this variable is not a factor.

## List of Figures

*Figure 1.* Top view of the experimental set up with the home tank containing a nest box (left side) connected to the experimental tank (right side) via a plastic tube. The pipe allowed free access between the tanks. The partition and door are shown.

*Figure 2.* Mean ± SE number of seeds eaten (%) by bushveld gerbils (*Gerbilliscus leucogaster*) in four treatments. LcLi = low cost and low incentive; LcHi = low cost and high incentive; HcLi = high cost and low incentive; HcHi = high cost and high incentive. The cost refers to the weight of the Perspex door and the incentive refers either to the preference of seeds presented or the presentation of seeds. (a) Experiments 1 and 2 = least preferred seeds vs. most preferred seeds in either clumped or scattered arrangement and (b) Experiments 3 and 4 = scattered seeds vs. piled seeds under either low or high predation risk. Treatments with different letters within experiments indicate significant differences (Tukey's *post hoc* tests).

*Figure 3.* Mean ± SE frequency of door usage by bushveld gerbils (*Gerbilliscus leucogaster*) in four treatments. LcLi = low cost and low incentive; LcHi = low cost and high incentive; HcLi = high cost and low incentive; HcHi = high cost and high incentive. The cost refers to the weight of the Perspex door and the incentive refers either to the preference of seeds presented or the presentation of seeds. (a) Experiments 1 and 2 = least preferred seeds vs. most preferred seeds in either clumped or scattered arrangement and (b) Experiments 3 and 4 = scattered seeds vs. piled seeds under either low or high predation risk. Treatments with different letters within experiments indicate significant differences (Tukey's *post hoc* tests).

*Figure 4.* Mean ± SE duration (s) of exploration by bushveld gerbils (*Gerbilliscus leucogaster*) in four treatments. LcLi = low cost and low incentive; LcHi = low cost and high incentive; HcLi = high cost and low incentive; HcHi = high cost and high incentive. The cost refers to the weight of the Perspex door and the incentive refers either to the preference of seeds presented or the presentation of seeds. (a) Experiments 1 and 2 = least preferred seeds vs. most preferred seeds in either clumped or scattered arrangement and (b) Experiments 3 and 4 = scattered seeds vs. piled seeds under either low or high predation risk. Treatments with different letters within experiments indicate significant differences (Tukey's *post hoc* tests).

*Figure 5.* Mean ± SE duration (s) of vigilance by bushveld gerbils (*Gerbilliscus leucogaster*) and in (a) four treatments (LcLi = low cost and low incentive; LcHi = low cost and high incentive; HcLi = high cost and low incentive; HcHi = high cost and high incentive, where the cost refers to the weight of the Perspex door and the incentive refers either to the preference of seeds presented or the presentation of seeds) in two experiments (Experiment 1 = least preferred seeds vs. most preferred seeds in clumped arrangement and Experiment 2 = least preferred seeds vs. most preferred seeds in scattered arrangement) and (b) separated by sex for two experiments (Experiments 3 and 4 = scattered seeds vs. piled seeds under either low or high predation risk). Bars with different letters indicate significant differences (Tukey's *post hoc* tests).

*Figure 6.* Mean ± SE duration (s) of foraging by bushveld gerbils (*Gerbilliscus leucogaster*) in (a) four treatments (LcLi = low cost and low incentive; LcHi = low cost and high incentive; HcLi = high cost and low incentive; HcHi = high cost and high incentive) for experiments 1 and

2, and (b) two experiments (Experiment 3 = scattered seeds vs. piled seeds under low predation risk; Experiment 4 = scattered seeds vs. piled seeds under high predation risk). The cost refers to the weight of the Perspex door and the incentive refers either to the preference of seeds presented or the presentation of seeds. Bars with different letters indicate significant differences (Tukey's *post hoc* tests).

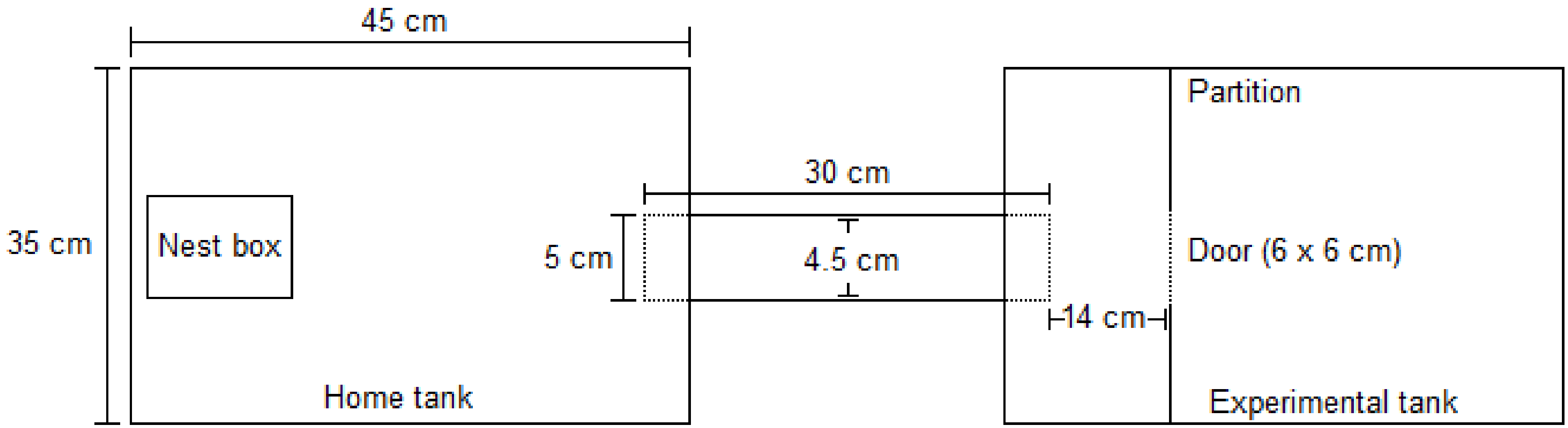
45 cm
35 cm
Nest box
Home tank
30 cm
5 cm
4.5 cm
14 cm
Partition
Door (6 x 6 cm)
Experimental tank

*Figure 1.*

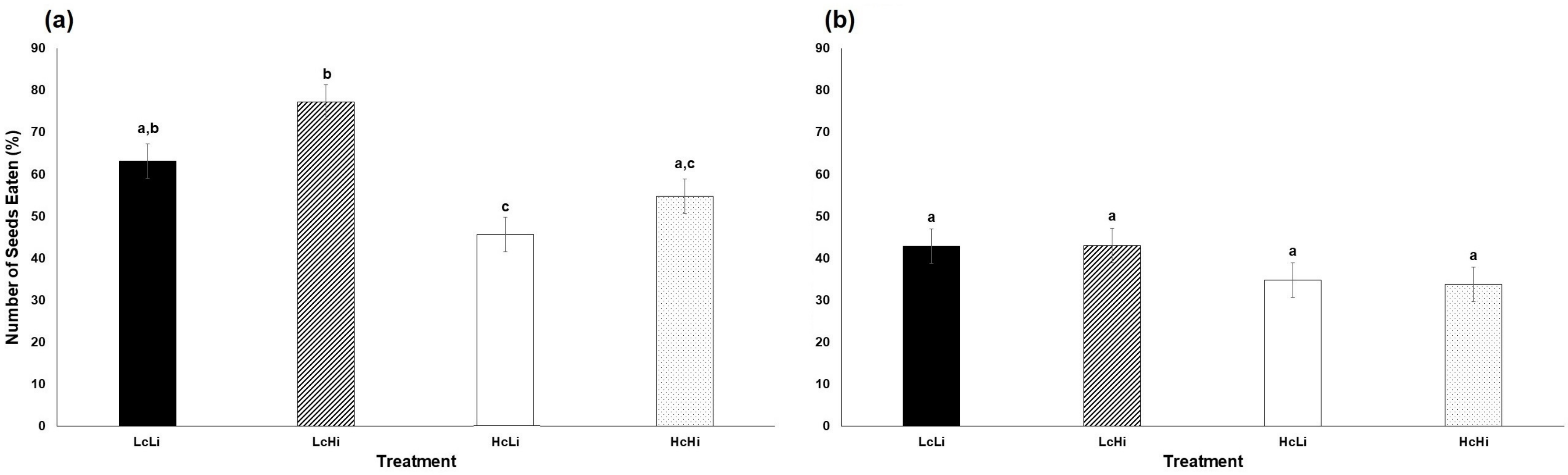
(a)
Number of Seeds Eaten (%)
0
10
20
30
40
50
60
70
80
90
a,b
b
c
a,c
LcLi
LcHi
HcLi
HcHi
Treatment
(b)
0
10
20
30
40
50
60
70
80
90
a
a
a
a
LcLi
LcHi
HcLi
HcHi
Treatment

*Figure 2.*

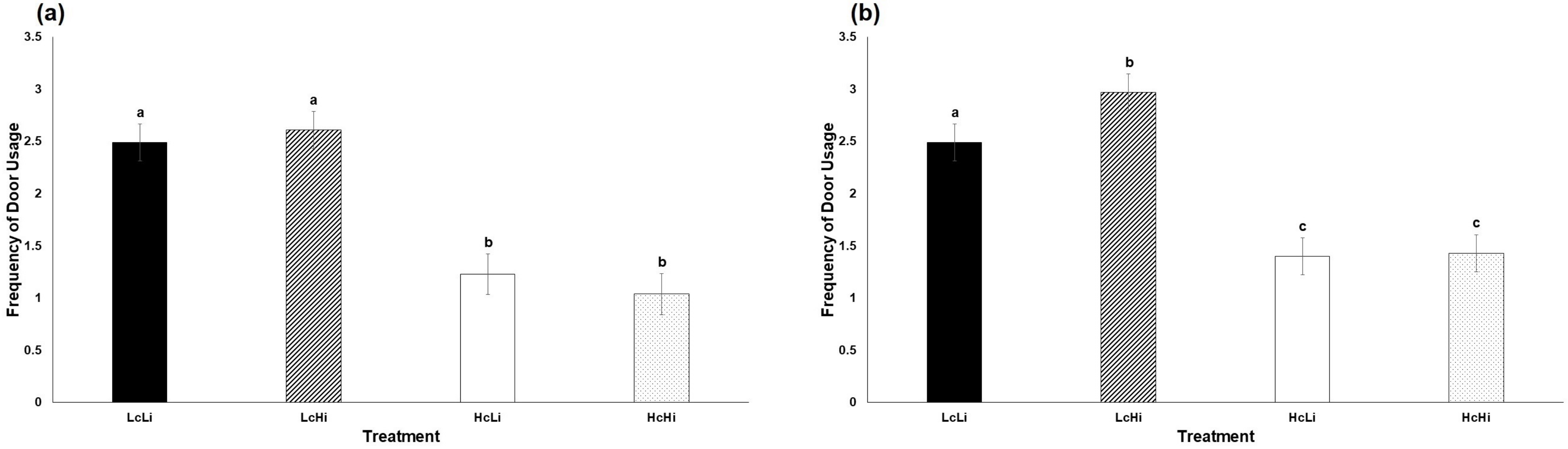
(a)
3.5
3
2.5
2
1.5
1
0.5
0
Frequency of Door Usage
a
a
b
b
LcLi
LcHi
HcLi
HcHi
Treatment
(b)
3.5
3
2.5
2
1.5
1
0.5
0
Frequency of Door Usage
a
b
c
c
LcLi
LcHi
HcLi
HcHi
Treatment

*Figure 3.*

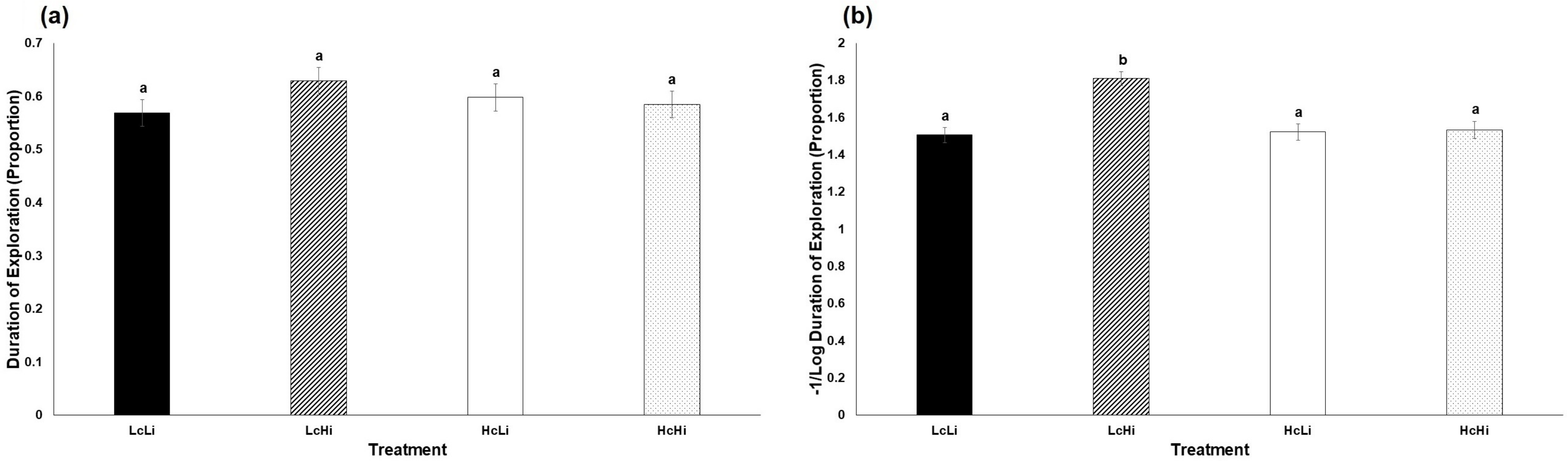

*Figure 4.*

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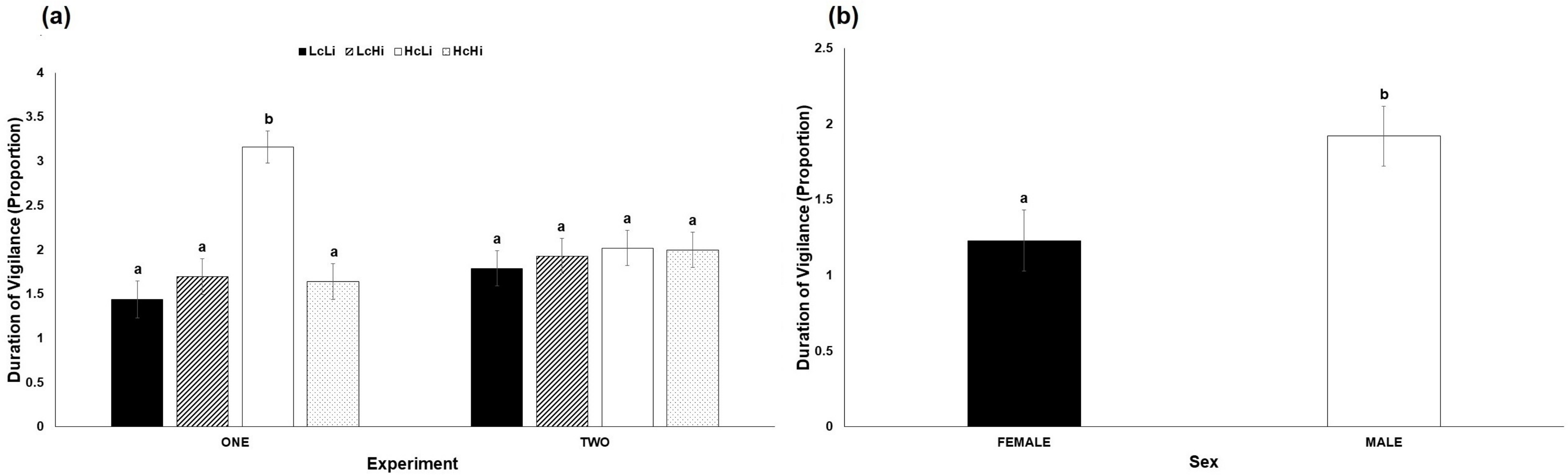
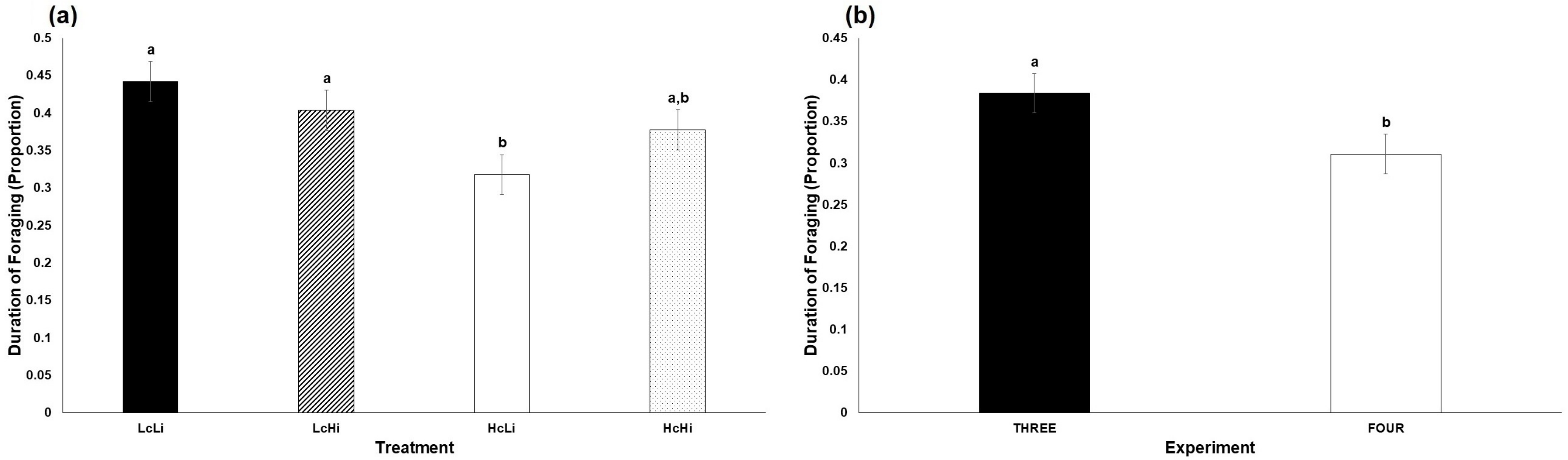

(a)
■ LcLi ▨ LcHi □ HcLi □ HcHi
Duration of Vigilance (Proportion)
0
0.5
1
1.5
2
2.5
3
3.5
4
a
a
b
a
a
a
a
a
ONE
TWO
Experiment
(b)
Duration of Vigilance (Proportion)
0
0.5
1
1.5
2
2.5
a
b
FEMALE
MALE
Sex

*Figure 5.*


(a)
0.5
0.45
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
Duration of Foraging (Proportion)
a
a
b
a,b
LcLi
LcHi
HcLi
HcHi
Treatment
(b)
0.45
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
Duration of Foraging (Proportion)
a
b
THREE
FOUR
Experiment

*Figure*