The effects of predator scent and varying food amount on the foraging behavior of *Peromyscus maniculatus*

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ABSTRACT

Small mammalian prey species have been shown to decrease their foraging activity in times of predation risk and high resource availability in order to successfully balance survival and good physical conditions. Mammalian predator odors have the ability to elicit an avoidance response in small rodent species. Deer mice (*Peromyscus maniculatus*) are vulnerable to terrestrial predators when foraging for food. I observed the foraging behavior of deer mice populations by live trapping in grasslands in western Montana. Urine of two mammalian predator species – coyote (*Canis latrans*) and mink (*Neovison vison*) – was used to simulate predation risk, and traps were baited with varying amounts of food. I predicted that trapping success rates would be highest in traps that did not simulate predation risk and held higher amounts of food, and that mice of lower body mass would forage for high amounts of food. I found that predator scent did not have an effect on the foraging behavior of the mice, but that more mice were caught in traps with higher amounts of food. I believe that food limitation causing starvation pressure, as well as concern for avian predation and focus on habitat structure when foraging, determine the feeding strategy of deer mice when considering predation risk. Observing the direct and indirect cues that prey consider in their "landscape of fear" is an important part of studying mammalian predator-prey dynamics.

INTRODUCTION

A foraging-predation trade-off is often used to describe the strategy used by individuals that risk predation while acquiring food (Verdolin 2006). Animals that maximize their anti-predatory behavior will have a higher rate of survival, but may lower their fitness due to poorer physical conditions caused by reduced foraging (Trebaticka

2008). In variable conditions, the amount of predation risk, the amount of competition, and the availability of resources have been shown to influence the foraging behavior of prey species. The risk allocation hypothesis predicts that species will increase their foraging during periods of low resources and also during periods of low risk (Sundell, et al. 2004). In a similar way, species are expected to decrease their foraging during periods of high risk or in habitats that increase their vulnerability to predators.

Studies have shown that mammalian prey species show adaptations for the recognition and avoidance of mammalian terrestrial predators (Apfelbach, et al. 2005). Specifically, prey can decode the carnivore scents that are used for territory marking (Jedrzejwski, et al. 2003). Multiple studies have used small mammals as prey species to study behavioral and foraging response to predator olfactory cues. A combination of avoidance behaviors, such as freezing and a fast straight run to a refuge site, was seen in multiple types of voles in response to the odors of a *Mustela* predator (Sundell & Ylonen 2004). These studies are observed in context of the foraging of small mammals as well; for example, hares and porcupines foraged less in the presence of fisher and coyote urine (Osburn and Cramer 2013). In this study, deer mice were used as a prey species, and coyote and mink were used as predator species. Deer mice make up a portion of the diet of the coyote (*Canis latrans*) (Osburn and Cramer 2013). Deer mice and voles also make up a significant portion of the diet of mink (*Neovison vison*) (Cushing 1985). Coyote is considered a generalized predator, while mink is considered a specialized predator (Osburn & Cramer 2013).

Based on the risk allocation hypothesis, it can be predicted that mice will respond with increased foraging in low risk situations (Sundell, et al. 2004). This study looked at

the behavioral responses of deer mice to treatments that simulate high or low predation risk. Further, because the risk allocation hypothesis predicts that species will forage during periods of high need (Lima & Bednekoff 1999), this study also observed the response of mice to treatments of high and low food reward. The physical characteristics of deer mice and the vegetation surrounding the observed mouse populations were also observed.

Hypotheses

This study examined deer mice in western Montana, seeking to characterize the effects of predation risk on the foraging of mouse populations, and whether there is a difference in populations of mice who display differences in foraging behavior. I hypothesized that (1) There will be more mice foraging where predation risk is absent. (2) In the presence of high predation risk, perceived through coyote urine and mink urine, I predict that the majority of mice will forage where reward is higher (i.e., bait is larger). (3) Mice that forage where predation risk is present and mice that forage where higher food amounts are present will have lower body mass than mice foraging in areas with no predation risk treatment and lower food amounts.

METHODS

Study Organisms – Deer mice (*Peromyscus maniculatus*) were used for this study. *Peromyscus maniculatus* are found throughout North America and are abundant in wooded areas and grasslands of the western mountains. The diet of deer mice is diverse, including seeds, grains, forb parts, fruits, and insects, and the diet varies by season (Jameson 1952). In areas where deer mice share habitat with meadow voles (*Microtus*

pennsylvanicus), they typically share usage of communal runs and tunnels (Jameson 1952).

Study Sites and Survey – The study took place on three sites of cattle-grazed land south of St. Ignatius in western Montana, USA (Figure 1). Sites were surveyed in order to observe the effects of vegetation, resources, and rodent populations in the areas where mice behavioral preference was tested. Three sites of equal size (100x100 m) were used for this study. Around each site, ten coverboards were used to check rodent populations, via rodent presence, nest formation, and run usage. Coverboards were checked six times in the evening during the trapping period. At each site, visual obstruction readings (VOR) and percent cover were measured at six points using a Robel poll (VOR) and a Daubenmire frame (cover percentage). Six traps at each site were randomly selected, and vegetation sampling was performed one meter to the north of the selected traps. Grass and forb biomass were also sampled at the sites by clipping the 0.1 m^2 area surrounding the plot. Vegetation sampling was performed during the final week of trapping. Biomass and cover vegetation data were analyzed to observe potential effects of existing resources.

Trapping – Deer mice are generally nocturnal, and therefore trapping was performed overnight. Mice were trapped using collapsible Sherman traps. Twenty-four traps with varying food and risk treatments were placed in each of the three plots. Traps were placed along obvious rodent runs throughout the plot, and were placed so that traps were not within five meters of other traps. Treatments were also randomized throughout the traps in the plots, and six traps of each treatment group were in each plot. There were four treatments: scented/high food, scented/low food, unscented/high food, and

unscented/low food. One red nib candy was used as bait for low food plots, and three red

nib candies were used as bait for high food plots. In scented plots, a cotton ball saturated

with predator urine was attached inside the traps. In unscented plots, a cotton ball

without urine was attached inside. All 72 traps were set in the evening between 1800-

2100 h and checked in the morning between 600 and 800 h. Traps were set out for two

weeklong periods – one for coyote urine and one for mink urine. Caught rodents were

marked for identification by painting nails with nail polish. Upon capture, the species,

sex, weight and length of the animal were recorded, as well as the number and location of

any recaptures.

Statistical Analyses – I used two Pearson's chi-square tests to compare the combined

trapping success of all three sites with the factor of scent – one for coyote urine trapping

and one for mink urine trapping. A third Pearson's chi-square was used to compare the

trapping success of all sites with the factor of food amount. Regressions were used to

observe relationships between trapping success and vegetation biomass, VOR, and plant

cover. ANOVA tests were used to measure the relationship between vole length (cm)

and mass (g) and the factors of scent and food amount. Finally, in order to observe the

effects of the naturally available food in each plot, a regression was used to compare the

ratio of mice caught in high food traps and low food traps with the amount of forb

biomass at each site. All statistical data were normalized using Shapiro-Wilk tests.

Alpha value was set at $p = 0.05$.

RESULTS

Rodent Trapping Success

Over the course of the summer, 130 *Peromyscus maniculatus* were captured, 65 of which were marked recaptured individuals. One *Peromyscus maniculatus* was found dead in the trap, and two *Microtus pennsylvanicus* were trapped. Trap success for each site can be found in Table 1. Vegetation factors (biomass, VOR, and percent coverage) did not have a significant effect on the trapping success of each site. VOR did differ between the three sites ($F_{2,15} = 4.881$, $p = 0.0233$).

Effects of Scent and Food Amount

Among all sites, the number of mice caught in traps scented with coyote urine was not significantly less than the number of mice caught in unscented traps (Pearson's value = 0.5502, $p = 0.4582$; Figure 2). Likewise, the number of mice caught in traps scented with mink urine was not significantly less than the number of mice caught in unscented traps (Pearson's value = 0.0216, $p = 0.8831$; Figure 2). In both trapping periods, the number of mice caught in traps with high food treatments was significantly higher than the number of mice caught in traps with low food treatments (Pearson's value = 10.4396, $p = 0.001233$; Figure 3).

Mice Length and Body Mass

Body length of rodents caught in traps with high food treatments was not significantly different from body lengths of rodents caught in traps with low food treatments ($F_{1,128} = 1.057$, $p = 0.306$; Figure 4). Body mass of rodents caught in traps with high amounts of food was not significantly lower than weights of rodents caught in traps with low amounts of food ($F_{1,128} = 0.119$, $p = 0.731$; Figure 5). Mouse mass was normalized using a log transformation.

DISCUSSION

Although mice have been found to respond to predator scent in some cases (Jedrzejwski, et al. 2003), the foraging behavior of deer mice was not significantly affected by either the presence of coyote urine or the presence of mink urine. Some past studies have found similar results in the response of rodents to predator scent. Herman and Valone (2000) found that the foraging behavior of kangaroo rats was only affected by predator scent in the winter. Mazdzer, et al. (1976), found that mice responded to conspecifics of the opposite sex, but did not avoid the odor of a *Mustela* predator. It is possible that odor is more important to rodent species for the recognition of conspecifics than predators (Mazdzer, et al. 1976). Another possible explanation is that mice judge predator risk by factors other than scent. For example, oldfield mice were responsive to more consistent, indirect cues of predation risk (moon illumination, precipitation, and exposed habitat), but not to direct cues (urine of native and nonnative predators) (Orrock, et al. 2004). There is evidence that mice can discriminate among these predator scents, so it is possible that the payoff of discrimination is outweighed by opportunities missed during the act of discrimination (Orrock, et al. 2004).

Pusenius and Ostfeld (2002) also found that mammalian carnivore scent did not affect the amount or spatial distribution of predation by voles. They found their results to be consistent with several recent field experiments, yet these results often disagree with laboratory experiments that show clear behavioral responses to mammalian odors (Herman and Valone 2000). It is possible that this discrepancy in results comes from differences in the information provided to the rodents; scents imply the past presence of a predator, but do not necessarily suggest immediate danger. Pusenius and Ostfeld (2004) believe that the ability to distinguish between current and past presence of a predator

could be crucial for rodent foraging. In a natural setting, predators come and go frequently. Therefore, during longer periods of predation risk, mice may choose to ignore these risks in order to avoid starvation (Pusenius and Osfeld 2004). Herman and Valone (2000) believe that a single cue in a laboratory setting may induce a strong singular reaction, yet in the field individuals take in a variety of cues (vision, habitat, and olfaction) when assessing predation risk. This integration of cues to observe overall risk level may weaken the single cue of predator odor in the field.

Another consideration when working with predator scent is the composition of the urine used in experimental procedures. Nolte et al. (1994) found that changes in the diet of a coyote predator affected the repellency of the urine itself; sulfurous odors associated with meat digestion were essential to repel prey. The results suggest that the composition of the urine used may need to be considered in field experiments where the scent is intended to deter prey, as opposed to lure predators for hunting purposes.

It has also has been proposed that rodents primarily respond to factors other than terrestrial odor. The evidence of mouse preference for habitat with high plant coverage may show an adaptation for decreasing predation risk presented by birds of prey (Pusenius and Ostfeld 2004). Kotler's (1984) comparison of desert rodent communities and risk predation found *Peromyscus maniculatus* as the most vulnerable species to large birds of prey, due to its coloration, smaller auditory bullae, and less bipedalism. Deer mice restrict their foraging to the safety of high coverage, and respond to visibility conditions for avian predators, suggesting habitat selection is based on predation threat from birds (Kotler 1984). Optimally foraging mice may focus on safer areas of forest habitat to avoid birds, as opposed to avoiding mammals. White-footed mice have higher

fitness in areas of denser habitat and choose not to forage in edge habitat (Morris and Davidson 2000). Since birds of prey are abundant in western Montana, it is possible that the deer mice populations observed focus their concern on avian predators as opposed to terrestrial ones.

Besides terrestrial and avian predation, the risk of snake predation is strongest during the summer months (Herman and Valone 2000). Taking into account avian and snake predation may further push rodent focus on seasonality and habitat, as opposed to olfactory cues. Taitt (1981) observed the effects of extra food on predated communities of deer mice; granivorous rodents are known to expand their diet during the summer months to include arthropods, leaves, fruit, and seeds on growing plants. It is possible that the summer season had an effect on the foraging decisions of mice as well.

Although the presence of predator scent did not have an effect on the foraging behavior of deer mice, the varying amount of food did have a significant effect on trapping success. Among all sites, more mice were caught in traps with higher amounts of food. Therefore, food limitation in the area of the three sites was a factor in the decision-making of deer mice regarding foraging behavior. Based on the dry conditions of the area and the risk allocation hypothesis, it is possible that the pressure to forage for food simply outweighed the risk presented by the predator scent exposed in the traps, and that this pressure also encouraged the foraging in traps with higher amounts of food. Studies have shown that this preference for higher food amounts, along with the ability to distinguish between more profitable food sources, has been seen in rodent species (Taitt 1981). When provided with available food, deer mice increased their foraging to the point where typical winter weight loss became an overall weight gain, allowing mice to

reproduce and altering the normal breeding patterns (Taitt 1981). Taitt (1981) believes that seasonal availability of food limits deer mice, so that presented food will be seen as an advantage in the decision-making process to forage. In this experiment or in a laboratory setting, had no food been provided, it is possible that a different response to predation could have been observed.

Under laboratory conditions as well, mice have shown a clear preference for more profitable foraging decisions, such as foraging on foods with a higher value of energy/efficiency (Phelan and Baker 1992). Further laboratory studies have looked into the influence of provided food on animal behavior and the neural processing of reward (Schultz 2004). Neural response of reward should also be considered when providing trapping food, as animal learning theory and reward information can affect foraging behaviors in field experiments (Schultz 2004).

I hypothesized that mice of smaller lengths and weights would show a stronger preference for high food traps, yet length and weight were not significantly different between mice caught in traps with high amounts of food and mice caught in traps with low amounts of food. This result may suggest that all mice on the sites are pressured to forage due to low amounts of food available in the area, so there is no discrepancy between mice more or less in need of food.

With so much potential focus on environmental factors, such as plant coverage and food availability, a future experiment that performs more vegetation sampling on the plots may reveal more interesting foraging patterns in mice. For example, it could be hypothesized that on plots where natural food biomass is higher, mice are less preferential toward higher amounts of food. This potential study would observe mice

foraging in relation to the food availability existing naturally in the environment. With more study sites and vegetation sampling, field trapping could reveal a trapping success pattern that correlates with vegetation factors.

Another future experiment to consider would be trapping the mice in the area to observe in caged experimental foraging trials. With the differences seen in laboratory and field trials, past studies have shown mice to be more responsive to predator scent in a laboratory setting where other environmental factors are not integrated with the threat of the predator odor. Feeding times, giving up densities, and cache depths could all be potentially affected by the threat of a mammalian predator in the form of odor.

Overall, I believe that starvation pressure, avian predation, and prey focus on habitat variation may have influenced the response to predator smell and food amount in this experiment. Knowing how small mammals respond with behavior to predation is important to understand when studying community dynamics. To know how animals weigh foraging options in the tradeoff between food and society is crucial when observing animal behavior in a landscape of fear (Brown and Kotler 2004). This landscape of fear interacts with productivity and environmental physical features to influence ecosystems through the corresponding behavioral decisions of the residing animals.

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TABLES

Table 1. Summary of trapping success and vegetation of study sites. Trapping success was not significantly affected by the vegetation factors of biomass, plant cover, and VOR, or by the average number of rodent runs at each site.

Site	UTM Coordinates	Avg. Caught / Night	Avg. Forb Biomass (g)	Avg. Grass Biomass (g)	Avg. Plant Cover (%)	Avg. Robel Cover	Avg. Runs
C3	0703329 5241283	8.167	1.588	2.163	0.833	3.542	3.725
C4	0714361 5240695	10.667	0.543	0.283	0.103	2.083	1.694
C6	0714940 5240138	3.167	1.087	1.595	0.155	2.375	3.188

FIGURES
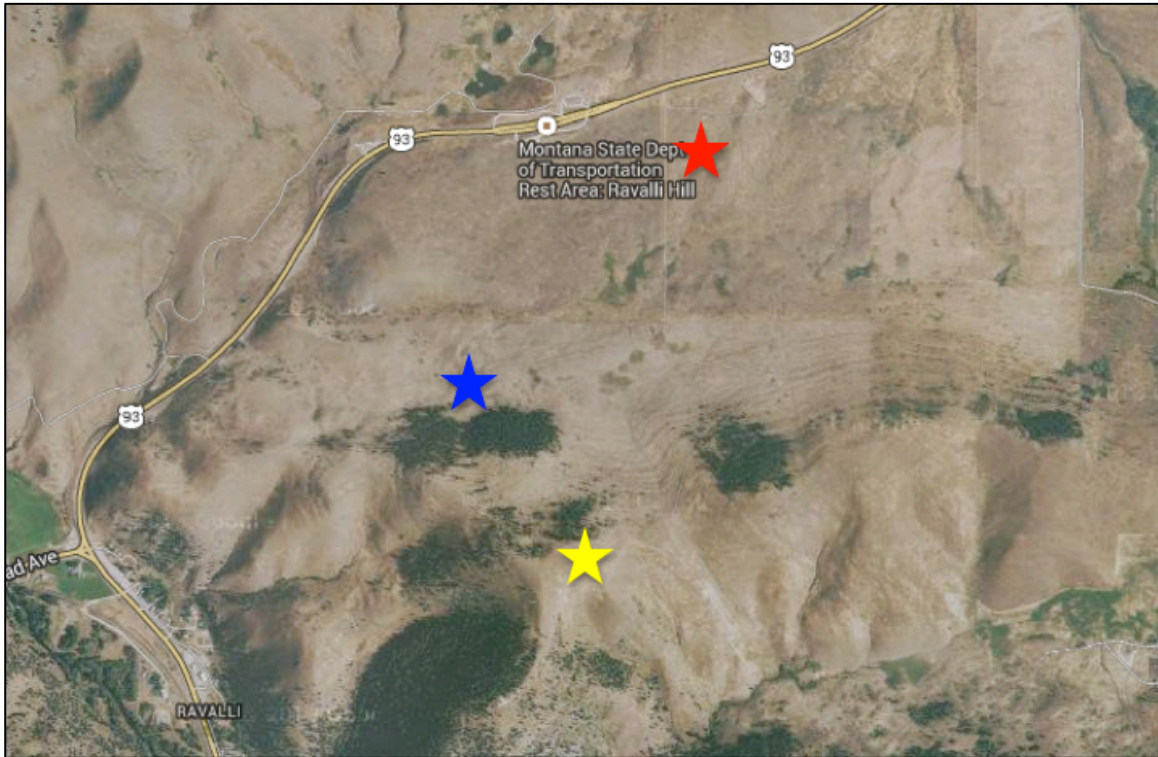
Figure 1. Map of study sites east of the National Bison Range in western Montana (©
Google 2013). The red star shows the area of site C3. The blue star shows the area of
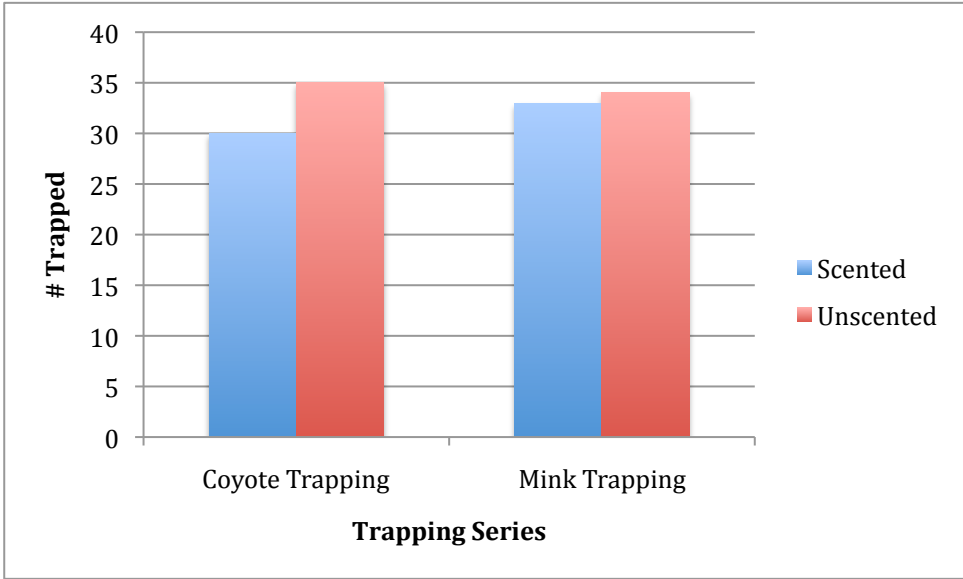site C4. The yellow star shows the area of site C6.

Figure 2. Trapping success with scent factor using both coyote and mink urine. The number of mice caught in traps scented with coyote urine was not significantly less than the number of mice caught in unscented traps. Likewise, the number of mice caught in traps scented with mink urine was not significantly less than the number of mice caught in unscented traps.
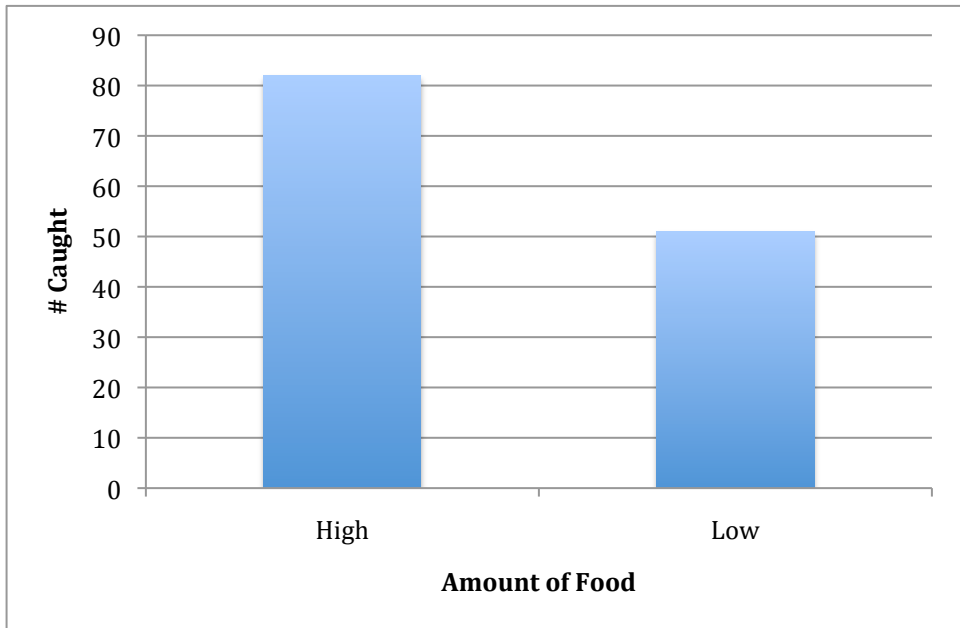

Figure 3. Trapping success with varying food factor. Combined between both trapping periods, the number of mice caught in traps with higher amounts of food was significantly more than the number of mice caught in traps with lower amounts of food.
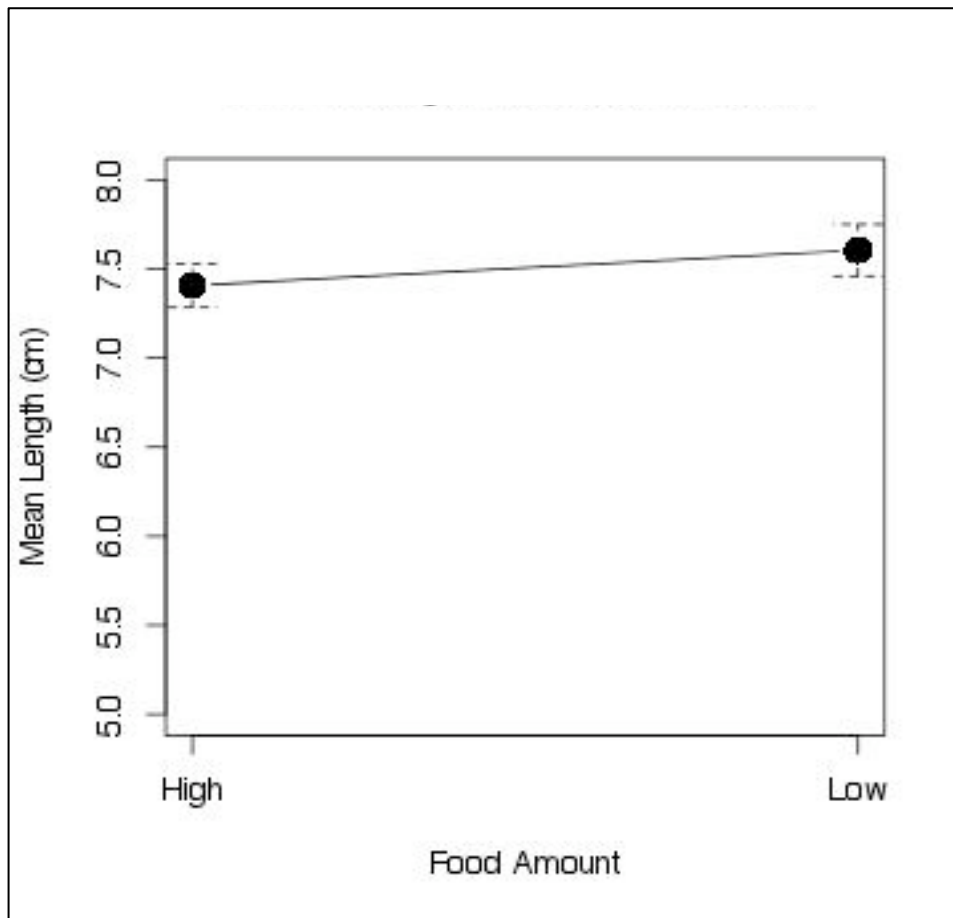
Figure 4. Mean length of mice foraging on varying food amounts. Length of rodents caught in traps with high amounts of food was not significantly lower than mouse lengths of rodents caught in traps with low amounts of food.
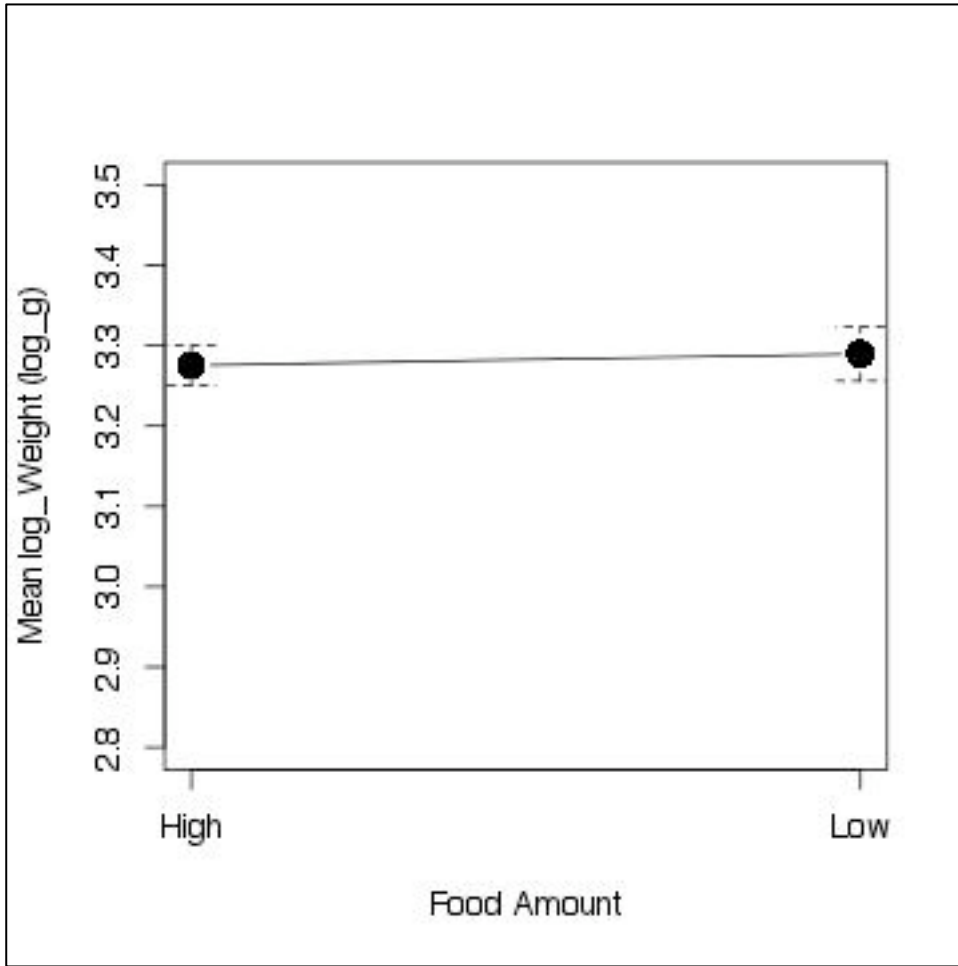
Figure 5. Mean weight of mice foraging on varying food amounts. Mouse weight of rodents caught in traps with high amounts of food was not significantly lower than weights of rodents caught in traps with low amounts of food. Mouse weight was normalized using a log transformation.