

The Effects of Varying Cache Depth and Mammalian Predator Scent on the Foraging  
Behavior of *Peromyscus maniculatus*

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**Abstract**

Previous work has shown that cache depth and perceived risks of predation can have an effect on the foraging behavior of many granivorous rodents. Olfaction plays a crucial role in both foraging behavior and assessment of predation risks in many of these species. The strength of olfactory signals depends on many factors, including cache depth, which can affect the search time of many granivorous species. Moreover, the threat of predation can also affect search time and thus can introduce a time-cost trade-off between foraging and being vigilant for predators. This study examined the effects of varying cache depth and mammalian predator scent on the foraging behavior of *Peromyscus maniculatus*. Mice did not alter their foraging behavior when assigned shallow (1 mm) or control (10 mm) seed caches in the absence or presence of urine. However, mice did reduce their foraging activity and search time when assigned deep caches (20 mm) in the presence of urine. These responses to deep caches and the presence of urine reflected a trade-off between foraging and vigilance for predators. *P. maniculatus* preferentially chose to utilize their time for vigilance rather than foraging and thus optimized their time by spending less time foraging (*i.e.*, searching) and more time remaining vigilant for predators. These responses provide implications for factors affecting foraging behaviors of many granivorous rodents.

**Introduction**

Granivorous rodents rely on their ability to successfully forage and cache seeds. By caching seeds when they are plentiful, rodents convert their intermittent food supply into a more reliable one, enabling them to have better control over food supplies. The

ability to control food supplies becomes increasingly important, especially in the fall and winter months, when food supplies become limited. Thus, selection for increased success in recovering caches and making accurate cache decisions during the seasonal harvest is essential for survival (Preston and Jacobs, 2009).

With granivorous rodents, olfaction plays an important role in seed procurement (Vander Wall *et al.*, 2003). They are attuned to olfactory signals (*i.e.*, volatilized organic molecules) emitted from seeds as they imbibe water. However, the strength of these signals is often affected by environmental factors such as cache size and depth. For example, Ord's kangaroo rats (*Dipodomys ordii*) harvested significantly more 10-seed caches at a depth of 12 mm than at a depth of 24 mm (Geluso, 2005). This indicates that odors emanating from one or more seeds behave like molecules diffusing from a point source; the signals perceived by rodents at a given surface should be stronger for shallower caches than for deeper ones of the same size (Geluso, 2005). Given these observations, it is hypothesized that buried seeds (>10 mm) will require a longer search time than those seeds buried in shallow depths or on the surface.

Coincidentally, other factors such as predation can also influence foraging behavior as well. For many systems, the threat of predation may be more important than the act of predation (Kotler *et al.*, 1991). When an increased risk of predation is perceived, a variety of responses can occur, including the avoidance of riskier habitats and reduced foraging activity (Herman and Valone, 2000). For example, in response to the presence of owls, gerbils (*Gerbillus allenbyi* and *pyramidum*) forage less, shift foraging activity to bush microhabitat and quit patches at a higher giving-up density (GUD) of resources (Kotler *et*

*al.*, 1991). These responses in behavior are often coupled with an energy trade-off between foraging efficiency and predation risk (Lima *et al.*, 1985).

There are many hidden costs associated with foraging: distance from foraging patch, travel time to foraging patch, weight of seeds, and handling time (time needed to handle or consume one food item) all add up to significant expenses. Lima *et al.* (1985) suggested that prey handling times in the great tit (*Parus major*) reflect a trade-off between the need to feed and the need to be vigilant for predators.

Many mammalian granivores rely on olfaction not only during foraging, but also to assess predation risk. They exhibit a variety of behavioral responses to predator odors found in urine, feces and anal gland secretions (Herman and Valone, 2000). For example, prey species such as hedgehogs (*Erinaceus europaeus*), snowshoe hares (*Lepus americanus*), mountain beaver (*Aplodontia rufa*), mice (*Mus musculus* and *Peromyscus maniculatus*), guinea pigs (*Cavia porcellus*) and voles (*Microtus spp.*) are repelled by mammalian predator odor or exhibit reduced foraging in its presence (Herman and Valone, 2000). In addition, Herman and Valone (2000) observed reduced foraging activity in kangaroo rats following exposure to mammalian predator scent. Therefore, it is hypothesized that rodents will exhibit reduced foraging activity following exposure to mammalian predator scent. Similarly, like cache depth, this investigation will contribute to the overall assessment of the role of olfaction in seed detection and foraging behavior of deer mice.

Our objective was to investigate the effects of both predation risk and cache depth on the foraging behavior of deer mice. We expected that both predation risk and cache depth (>10 mm) would influence seed detection and search time for each mouse, thereby

reducing foraging activity. These results provide a more accurate assessment of the role of olfaction as well as examine the ecological implications that may influence foraging success. Both predation risk and cache depth contribute to an important energy-trade off between the need to feed and the need to be vigilant for predators. The combination of these environmental pressures forces an individual to allocate their time and energy more efficiently and thus greatly influences their foraging abilities and success. Essentially, this experiment will provide a greater understanding of how this trade-off affects both the search time and role of olfaction in the foraging behavior of deer mice.

## **Materials and Methods**

This experiment was conducted on the property of the University of Notre Dame Environmental Research Center (UNDERC) in the Upper Peninsula of Michigan.

Vegetation in this area consists of second-growth forests dominated by sugar maple (*Acer saccharum*) and red maple (*A. rubrum*) trees.

### *Subjects*

Trapping was conducted from late May through July 2012. Grids (15 m x 15 m) were set up in five different sites on the UNDERC property. Twenty-five Sherman traps (0.17 m x 0.054 m x 0.065 m) were baited with rolled oats, sunflower seeds and peanut butter and were set at dusk in each 15 m x 15 m grid the night prior to experiments.

Individuals were housed at the UNDERC Aquatic Laboratory facility for approximately twenty-four hours in separate plastic cages (0.1905 m x 0.21 m x 0.1270 m) lined with sand. Mice were provided with sufficient food, water, shelter, and nesting materials prior to experimentation. Mice were starved approximately five hours before each trial.

### *Cache Depth*

Each trial was performed in a standard 15-gallon glass aquarium (0.62 m x 0.30 m x 0.30 m) filled with a set amount of sand that corresponded to each cache depth treatment –shallow (1 mm), control (10 mm), and deep (20 mm). Using latex gloves, seed caches were prepared, consisting of three sugar maple seeds per trial. Mice were randomly assigned one of six different treatments – shallow cache depth (1 mm), control cache depth (10 mm), or deep cache depth (20 mm) – and either the presence or absence of mammalian predator scent (mink urine).

### *Mammalian Predator Scent*

For trials with simulated predators, urine-saturated cotton balls were placed in a perforated film canister and placed at the side of the aquarium tank. If urine was not present, then water was used to saturate the cotton balls and were placed in the perforated film canisters and placed at the side of the aquarium in order to maintain a control treatment. Each trial was conducted in a separate aquarium (*e.g.*, control with predation vs. control without predation) and fresh sand was used for each trial. Trials were conducted at night and recorded using infrared lights and Sony Handycam DCR-DVD610 infrared sensing camera. The search time (*i.e.*, the amount of time it takes an individual to find a seed) was measured for each trial.

### *Data Analysis*

Data were analyzed with a two-way ANOVA performed using SYSTAT v. 13.0 to determine if there were significant effects of cache depth and/or the presence

mammalian predator scent on the search time of mice. The dependent variable was the search time (s) and the independent variables were seed depth [*i.e.*, shallow (1 mm), control (10 mm), or deep (20 mm)] and mammalian predator scent (*i.e.*, presence or absence).

## Results

### *Cache Depth*

There were no significant differences with respect to search time among the shallow, control, or deep seed caches (Fig. 1). The two-way ANOVA confirmed that there were no statistically significant differences between the cache depth treatments individually ( $F_{1,36} = 0.0312$ ,  $p = 0.969$ ).

### *Mammalian Predator Scent*

There were no statistically significant differences, with respect to search time, between trials with or without urine (Fig. 2). The two-way ANOVA confirmed that there were no statistically significant differences among the cache depth treatments in the absence or presence of urine ( $F_{1,36} = 0.858$ ,  $p = 0.360$ ).

### *Cache Depth\*Mammalian Predator Scent*

There was a statistically significant interaction between the main effects, cache depth and urine (Fig. 3). The two-way ANOVA confirmed the significance between cache depth and urine ( $F_{1,36} = 3.958$ ,  $p = 0.0279$ ). A post-hoc hypothesis test revealed a statistically nonsignificant trend for increased search time in shallow and control caches in the presence of urine ( $F_{1,36} = 3.041$ ,  $p = 0.0897$ ; Fig. 3). It is possible that the post-hoc test did not reveal significance for shallow and control caches because the difference between the treatments is reversed following deep caches in the absence or presence of

predator scent. However, a post-hoc hypothesis test comparing the effect of predator urine for deep caches revealed a significant decrease in search time in the presence of urine ( $F_{1,36} = 5.606, p = 0.0234$ ).

## Discussion

The results indicated that the two main effects, cache depth (Fig. 1) and urine (Fig. 2), independently did not have a significant effect on the foraging behavior of *Peromyscus maniculatus*. However, there was a significant interaction effect between cache depth and the presence of urine (Fig. 3). These results infer that seed caches (>10 mm) were uncovered faster (*i.e.*, reduced search time) in the presence of urine than those seed caches (<10 mm) in the absence of urine. Therefore, the hypothesis that both predation risk and deep cache depth will reduce foraging activity and consequently increase the search time of each mouse, was not supported.

The two main effects, cache depth and urine, independently were not statistically significant. Cache depth may not have been significant independently due to the laboratory setting and/or the amount of seeds per cache. While conditions were set to mirror nocturnal behavior during experimentation, it is possible that mice did not deem these conditions realistic and thus, marginalized the variability of seed cache depths. It is also possible that the amount of seeds influenced the foraging behavior of seed caches at different depths. Vander Wall (1993) found that yellow pine chipmunks bury larger caches deeper such that the top of the cache is approximately the same depth below the ground surface. In this experiment, seed caches were allotted 3 seeds per cache for all cache depths; however, it is possible that like the yellow pine chipmunks, mice prefer a

certain number seeds per cache depending on cache depth. Therefore, mice would have overlooked the variability of seed cache depths due to specificity of seeds per cache and cache depth.

In the same sense, the absence or presence of urine may have not been statistically significant due to laboratory settings or inability to detect the strength of the predator scent via olfaction. Although conditions were set to mimic mammalian predation via predator scent (*i.e.*, urine), the laboratory setting and absence of an actual predator may have influenced the foraging behavior (*i.e.*, search time). It is possible that mice did not consider the urine an immediate threat as they would ordinarily when faced with an actual predator. Thus, the laboratory setting may have negated the importance of the absence or presence of urine as an independent effect. It is also possible that the strength of the predator scent was not detectable via olfaction. In the field, individuals can assess predation risk level via a variety of cues, including vision, habitat structure, and olfaction (Herman and Valone *et al.*, 2000). Individuals in the field must integrate all of these cues to assess the overall predation risk level. Therefore, responses to experimental manipulation of any single cue, such as predator scent (*i.e.*, urine), may often be weaker than in the field. However, while there was no statistical significance between the two main effects independently, there was a significant interaction effect between the deep seed caches and the presence of urine (Fig. 3).

The interaction effect between deep seed caches in the presence of urine may be explained by a trade-off between vigilance (*i.e.*, the frequency of vigilant bouts) and feeding rate when predation risk is high. Routine vigilance is an important component for foraging and can occupy a large portion of this time (Baker *et al.*, 2011). Vigilance can

conflict with some aspects of foraging (*i.e.*, searching) and therefore can reflect an unforeseen time-cost between the frequency of vigilance and foraging behavior (*i.e.*, search time) among *P. maniculatus*. For example, Baker *et al.* (2011) measured the vigilance behavior of four species of granivorous bird, and found that there was frequently enough compatible handling time to accommodate routine vigilance; however, there was a high proportion of vigilance that occurred during non-compatible components of foraging, thus incurring a time-cost.

Similarly, in this experiment, it is possible that there was a time-cost or trade-off between the frequency of vigilance (*i.e.*, the frequency of vigilant bouts) and reduced search time in seed caches. For some species, including *P. maniculatus*, vigilance may conflict with search time, reducing the amount of time it takes to locate a seed. In other words, despite the depth of the seed cache, it may be more efficient to locate and uncover a seed cache as quickly as possible, leaving more time to detect and escape predators. This assumption is also based on behavioral observations during experimental trials, whereby the mice would sniff out the cache and then “hide out” until they deemed conditions “safe” for foraging or until they were hungry.

During the experiment, mice concentrated more on hiding from predators than foraging and searching for seed caches. When urine was present, mice would seek out seed caches via olfaction and commit its location to memory, but then chose to hide or seek refuge rather than continue foraging (*i.e.*, searching) for fear of predation. However, when mice did choose to forage, they optimized their time for vigilance by spending less time foraging (*i.e.*, reduced search time). In other words, mice preferentially chose to utilize their time for vigilance rather than foraging (*i.e.*, searching) when seed caches

were buried deep and when urine was present.

Congruently, it is suggested that the head position (*i.e.*, head-up position or scanning position) of many granivorous species is associated with anti-predatory vigilance (Coolen *et al.*, 2000). Baker *et al.* (2011) suggests that species that handle food in the head-up position can use the head-up component for vigilance without incurring significant time costs. During the experiment, mice would occasionally “survey” their surroundings by lifting their heads to scan for predators while uncovering seed caches. Mice would engage in this behavior more often during the predation trials, thereby insinuating bouts of vigilance while foraging. This behavior was also observed during the experiment, and echoes the postulation that mice preferentially chose to spend more time being vigilant and less time foraging (*i.e.*, searching) when seed caches were buried deep and urine was present.

On the other hand, when urine was absent, the mice preferentially chose to forage (*i.e.*, search) and uncover seed caches, rather than remain vigilant for predators. Without the immediate threat of predation, mice chose to forage, thereby optimizing their time under anti-predator conditions. The relatively short search times may be explained by the same time-cost trade-off between vigilance and foraging. When urine was absent, mice utilized time that might have been used for vigilance as prime foraging time. Overall, given these observations, it is assumed that the interaction effect between seed cache depth and urine was due to the time-cost or trade-off between vigilance and foraging behaviors (*i.e.*, search time).

While some of these factors may not be avoided, such as the laboratory setting, if the experiment were to be repeated, an increase in the amount of seeds per cache would

provide a more accurate assessment of the role of olfaction in seed detection. Geluso (2005) found that the ability of Ord's kangaroo rats to detect caches was significantly influenced by the size of caches. As size of caches increased, kangaroo rats removed greater percentages of caches. Additionally, the amount of seeds per cache should also vary depending on the depth of the cache. Vander Wall *et al.* (2003) found that as caches became smaller and deeper, they were more difficult for rodents to detect. Thus, varying the amount of seeds per cache would provide mice with a greater opportunity to find and uncover the caches at deeper depths.

Although there are many more possibilities for future experimentation, this experiment provided an opportunity to explore the effects of varying cache depth and mammalian predator scent on the foraging behavior of *P. maniculatus*. While this experiment did not reveal significance in the two main effects, cache depth and mammalian predator, independently, the interaction between cache depth and mammalian predator scent provided a valuable insight into the foraging behavior of granivorous rodents. Overall, these results reflect an important trade-off between foraging and vigilance, a fundamental component in understanding the role of olfaction and the complexity of foraging behavior of granivorous rodents.

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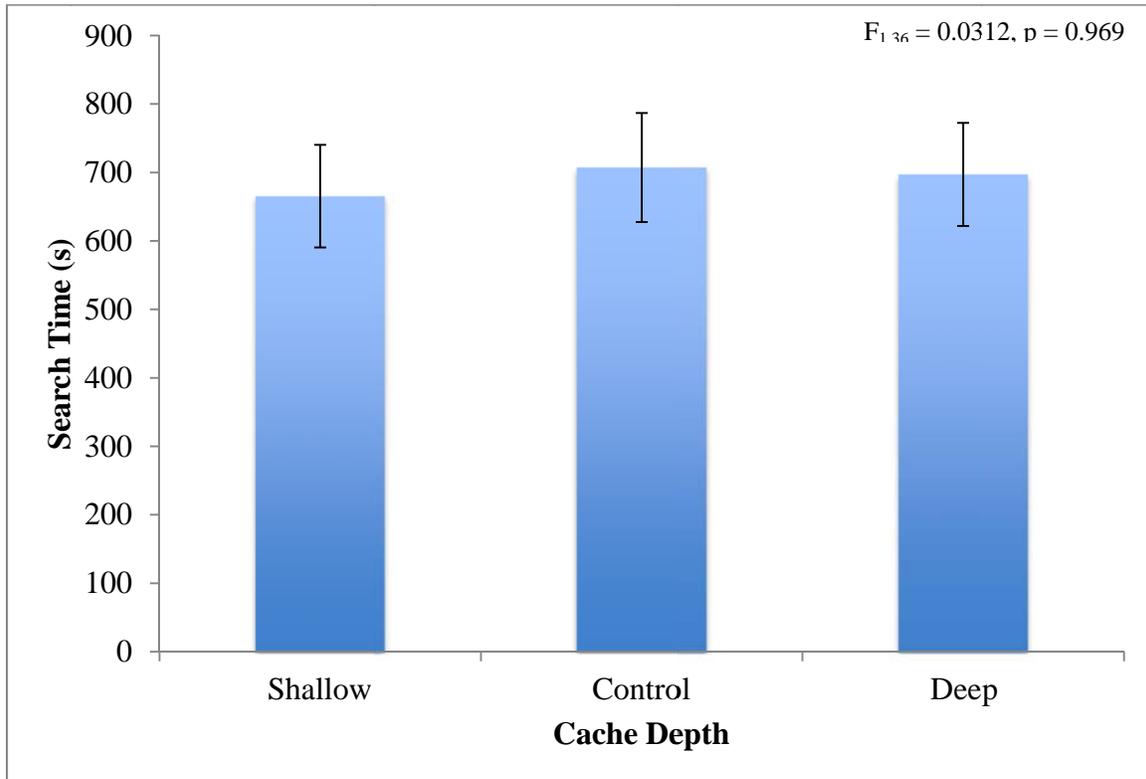
**Figures**

Figure 1. The effects of varying cache depth on the foraging behavior of *Peromyscus maniculatus*. Foraging behavior was measured by search time (s). There were no statistically significant differences among varying cache depths with respect to search time ( $F_{1,36} = 0.0312, p = 0.969$ ).

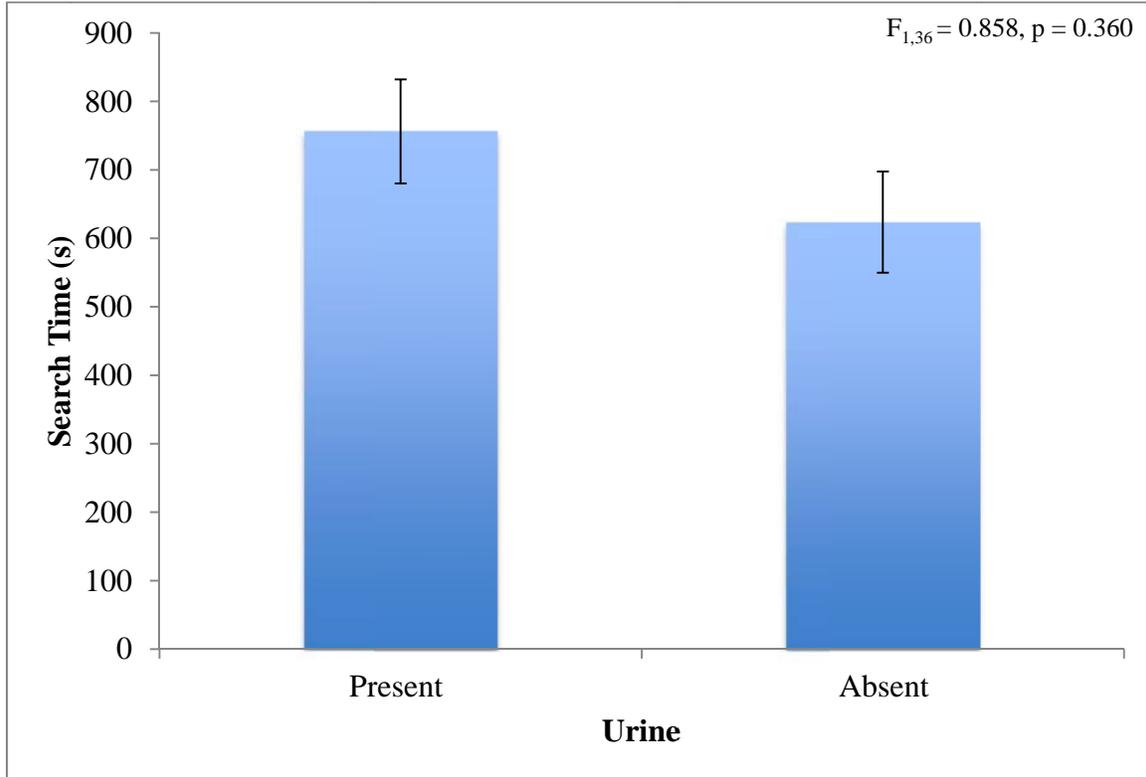


Figure 2. The effects of mammalian predator scent on the foraging behavior of *Peromyscus maniculatus*. Foraging behavior was measured by search time (s). There were no significant differences between the presence or absence of urine with respect to search time ( $F_{1,36} = 0.858, p = 0.360$ ).

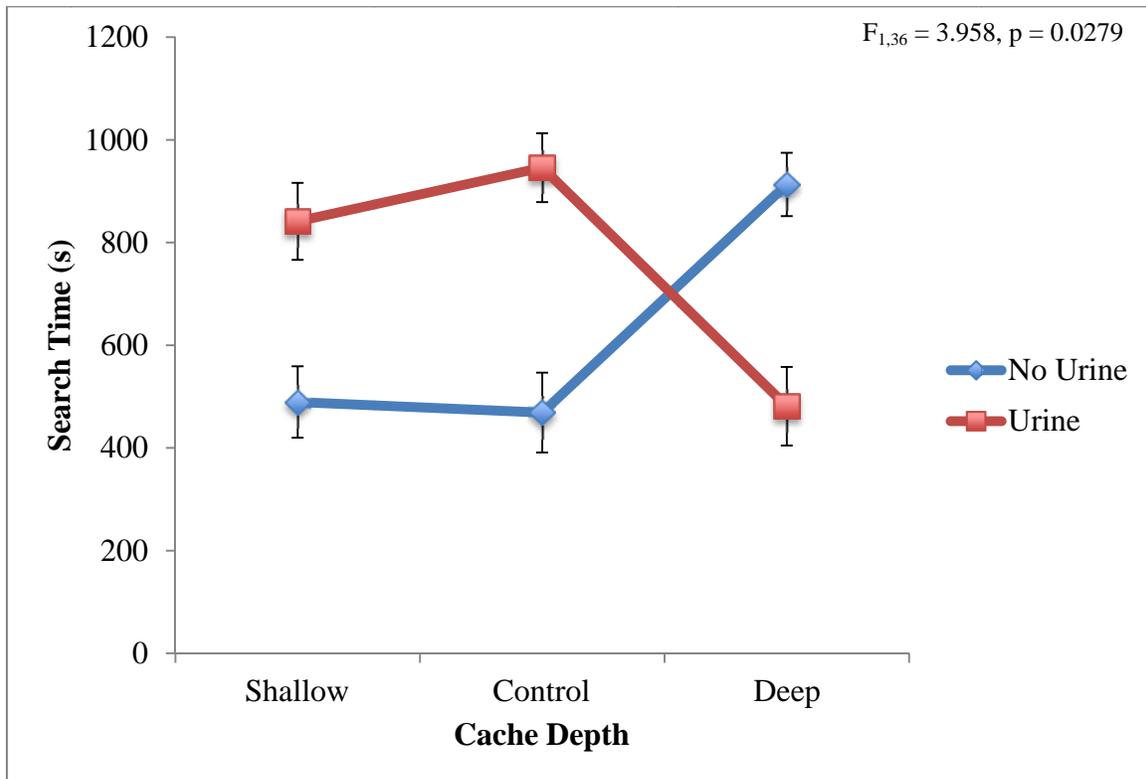


Figure 3. The effects of varying cache depth and mammalian predator scent on the foraging behavior of *Peromyscus maniculatus*. Foraging behavior was measured by search time, or the amount of time it took the mice to find the seed cache. There was a significant interaction effect between deep cache depth and the presence of urine ( $F_{1,36} = 3.958, p = 0.0279$ ).