The Effects of Predator Cues on Vertical Foraging Habits in the White-footed Mouse (Peromyscus leucopus)

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The effects of predator cues on vertical foraging habits in the white-footed mouse

(*Peromyscus leucopus*)

By

**Caitlin Stark**

B.A., Saint Xavier University, 2009

THESIS

Submitted in partial fulfillment of the requirements

For the Degree of Master of Science,
With a Major in Environmental Biology

Governors State University
University Park, IL 60466

2014
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Literature Review

Introduction

Foraging behavior can be influenced by predation, population density, competition, and microhabitat selection. With the use of foraging trays, one can determine the GUD (Giving Up Density) of foraging species and learn their microhabitat preferences, perceived predation risks, and foraging efficiency (Brown 1988; Brown 1989; Yunger et al. 2002). The risk of predation during foraging results in reduced feeding activity and the forager will leave the food patch with little to no gain in energy (Brown 1992; Brown et al. 1992). A forager must determine if a food patch is worth the risk. It must assess the distance a foraging patch is from cover in the event that it encounters a predator while foraging. Also, it must evaluate the profitability of food items against predation risk. Vigilant individuals may choose the less profitable food item in order to better detect predators (Lima and Dill 1990).

Optimal Foraging Theory

Foraging is important for an animal's survival; it provides the individual the energy needed to grow, reproduce, and defend territory. The energy gained from foraging must outweigh the cost of the energy spent to get to the foraging patch and the risk of predation (Brown 1992; Lima 1998). When an animal comes to a foraging area the energy gain may be high at first, but as the individual forages the energy gain drops due to the depletion of food, predation risk, and other foraging restrictions (Brown et al.
1992). As a forager uses multiple patches, energy is used during travel between those patches. The forager must balance that energy loss due to travel by spending the optimum time at the next patch. If the forager leaves the patch too early it will have a low rate of energy return. Yet, if the individual stays too long at the same patch, the resources will become depleted while more energy will be spent searching for the remaining food, which will cause a net energy loss (Parker and Stuart 1976; Brown et al. 1992; Brown et al. 1994).

The ability to forage optimally should spread through natural selection. Animals that have developed skills to maximize the average rate of resource harvest at each patch could improve their fitness (Brown 1988). Lewis et al. (2001) found that *Peromyscus leucopus* primarily selects food to fulfill their energy requirements and avoid excess amounts of protein since it cost more metabolically. Optimum protein levels, along with other nutrients, are required for normal growth and reproduction. Foragers that have a lower net energy gain and increased time foraging or higher cost from predation risk have a reduction in fitness. Consequently, animals should have evolved to have better foraging tactics to maximize fitness (Brown et al. 1992; Lima 1998; Morris and Davidson 2000). Yunger (2002) found that *P. leucopus* went into reproductive activity two months earlier on food supplemented plots than on non-supplemented plots.

*Giving Up Density*

Giving up density (GUD) can be used to gain information on the energetic cost, predation cost, and missed opportunity cost of foraging. Comparing GUDs can allow one...
to draw observations on an animal's foraging abilities, such as food preference, ability to
determine the quality of the food patch, or the ability to detect potential risk of predation
at a food patch (Brown 1988). To measure GUD a plastic tray containing a food resource
mixed in with a substrate can be used. The substrate gives the animal an obstacle so that
it must spend time foraging (Brown 1989). A high GUD indicates decreased foraging
possibly due to perceived predation risk; while a lower GUD shows increased foraging
and a lower perceived predation risk (Brown et al. 1992; Thorson et al. 1998).

Shaner (2007) discovered that GUD increased for *P. leucopus* in experimental
foraging trays that had a lower overall amount of food but possessed an appropriate
variety of food types (e.g. millet seeds and mealworms). *Peromyscus leucopus* has been
found to forage resources to a lower GUD in forest habitats than in risky edge and
fencerow habitats (Morris and Davidson 2000; Wolf and Batzli 2004). It is also suggested
that when food availability is high, omnivore populations may occupy a narrower
omnivorous niche and when food availability is low they occupy a broader herbivory,
omnivory, or carnivory niche due to intra-population competition (Shaner et al. 2007).
Darwin's leaf-eared mouse (*Phyllotis darwini*) and the degu rat (*Octodon degus*) had
significantly lower GUD with the exclusion of predators. The two species also had lower
GUD during new moon phases than full moon phases (Yunger et al. 2002).

*Predatory Cues*

Pheromones are an integral form of communication in many species. The
Grüeneberg ganglion region of the olfactory system was found to act as an early warning
system that responds to stress hormones released by other members of the same species (Brechbühl et al. 2008). Fear response brought on by the scent of a predator is associated with the bed nucleus of the stria terminalis (BNST) (Takahashi et al. 2005). Red-backed salamanders (*Plethodon cinereus*) are able to assess predation risk by the chemical cues from predator urine. They can detect if a predator has recently consumed a member of the same species or has not eaten recently based on chemical cues (Murray and Jenkins 1999; Sullivan et al. 2005). The same ability to detect if a predator has been feeding on conspecifics was found in thrips (*Thysanoptera* sp.). Thrips larvae retreat to refuge in the presence of a predator that has been feeding on conspecifics (Venzon et al. 2000). Four different herbivorous rodents (mountain beavers (*Aplodontia rufa*), house mice (*Mus musculus*), deer mice (*Peromyscus maniculatus*) and guinea pigs (*Cavia porcellus*) showed more of an avoidance response to urine collected from coyotes fed a meat diet than urine from coyotes fed a fruit diet (Nolte et al. 1994). Predator odors used in large amounts are more likely to elevate the state of fear and reduce the likelihood of fear habituation (Takahashi et al. 2005). Despite the acute sense of smell of fox squirrels (*Sciurus niger*) and thirteen-lined ground squirrels (*Ictidomys tridecemlineatus*), olfactory predator cues had little to no effect on their foraging habits (Thorson et al. 1998). An experiment done with hedgehogs (*Erinaceus europaeus*) showed that they altered their foraging behavior more with predator scent in enclosure areas than in the wild (Ward et al. 1997).

When auditory cues are heard small-mammals will seek refuge (Wright and Barrett 2011). The nocturnal Darwin's leaf-eared mouse has large eyes and ears that allow
it to better detect predators via visual and auditory cues. That coupled with its longer back limbs that allow it to bound away and quickly escape predators may be why it is more willing to forage in open areas (Yunger et al. 2002).

A sparrowhawk model was used to study vigilance in chaffinches (*Fringilla coelebs*). Those who foraged faster and with their head up were able to respond to visual cues quickly (Cresswell et al. 2003). The Townsend's ground squirrel (*Urocitellus townsendii*) budgets more time to vigilance in dense shrub habitat than in open habitat because it relies on its visual detection of a predator (Schooley et al. 1996). *Peromyscus leucopus* have been found to use visual cues in navigation. During nights when a full moon is visible *P. leucopus* use the increased light levels to their advantage and rely on vision and use of landmarks to navigate. With increased illumination the risk of predation also increases and *P. leucopus* will tend to use objects with greater horizontal components such as logs and branches as a means to escape (Barry and Francq 1982).

Deer mice (*Peromyscus maniculatus*) prefer to walk across dry coniferous leaf litter to dry hardwood leaf litter. This is to reduce the chances of auditory detection by a predator. They will more readily traverse hardwood leaf litter when it is wet due to reduced sound. When in areas of hardwood leaf litter the mice are more likely to use logs as pathways than in coniferous leaf litter. Lowering the intensity of sound produced by freezing may cause the predator to lose interest if prey sound stops before being captured (Roche et al. 1999). This behavior was also observed in *P. leucopus* (Barnum et al. 1992).
Foraging Behavior and Predation Risk

Both direct and indirect predator cues have been seen to have an effect on an animal's decision making process (Orrock et al. 2004; Takahashi et al. 2005). For example, vervet monkeys (*Chlorocebus pygerythrus*) were observed climbing higher to forage when ground predators were present and climbing lower when aerial predators were present (Makin et al. 2012). However, *P. polionotus* responded more to indirect cues (distance to coverage, illumination and weather) than direct cues (predator urine) (Orrock et al. 2004). Similar behavior was also observed in *P. leucopus*; mice foraged more thoroughly during new moon phases and under more vegetation coverage, while the direct cue of predator scent had little effect on their foraging behavior (Fanson 2010).

Small mammals that have a variety of predators are influenced more by indirect cues of predation risk than direct predator cues when foraging (Morris and Davidson 2000; Orrock et al. 2004; Wolf and Batzli 2004; Fanson 2010). There is a higher risk of predation for *P. leucopus* at woodland edge than in forest interior (Morris and Davidson 2000; Wolf and Batzli 2004). Lab rats were observed preferring closed foraging patches to open foraging patches even if there was more food available in the open patches (Arcis and Desor 2003). If grazing animals such as cattle consume most of the ground cover it can decrease small mammal abundance because of decreased protection from the elements and predation (Moser and Witmer 2000).

Moon phase and microhabitat have a strong influence on small mammal foraging habits. *Peromyscus leucopus* forage more during new moon stages and in areas with more ground cover that are further away from the forest edge (Manson and Stiles 1998; Fanson
Phyllotis darwini also foraged more under new moon light conditions than full moon (Yunger et al. 2002). Kangaroo Rats (Dipodomys spp.) only showed illumination preference during the fall when the risk of encountering a snake was low (Kotler 1984; Bouskila 1995). Minimum nightly temperature also influences small mammals GUD; higher minimum nightly temperatures encourages more foraging behavior (Kotler et al 1993; Fanson 2010).

Distribution of prey species in relation to their predator species can be determined by their escape behavior and the landscape features (Wirsing et al. 2010). For example, if a bird species evades predator capture by aerial maneuvers it is more likely to choose open space than an area with significant ground cover by shrubs and trees (Lima 1990). Wywialowski (1987) found that red-backed voles (Myodes sp.) are more likely to use an area with more ground cover because they rely on quick maneuvers around obstructions to evade predators. Deer mice, however, rely on speed to escape capture and will use both open and covered areas.

Many heteromyids have been found to use different evasive maneuvers depending on the predator in pursuit. For example, if they were being attacked by an owl they would evade capture by lateral movements from the owl's strike trajectory where as they would jump up or back if lunged at by a snake. Also, heteromyids would have more frequent, but shorter activity periods in open areas and use dense shrubs for cover in the presence of an owl. Although snakes are ambush predators like owls, they are more likely to attack from bushes and shrubs. Therefore, prey species must assess and adjust use of microhabitat depending on the presence of certain predators (Longland and Price 1991).
In the presence of both owls and snakes gerbil species were more affected by the presence of owls. This could be because owls are perceived as a greater risk than snakes (Kotler et al. 1992). Different predators may be more abundant depending on the time of year, resulting in a seasonal rotation of foraging efficiency among different foraging species. Kangaroo rats (*Dipodomys spp.*) proportionally use more open area to bush microhabitat when snakes are present but do not avoid bush microhabitat during seasons when snakes are not active (Brown 1989; Bouskila 1995). Owls are more abundant during the summer and tend to hunt in more open areas, therefore smaller prey animals tend to prefer to stay in brush or shrub habitat for cover. During the summer, rattle snakes are mainly nocturnal sit-and-wait predators that usually stay in brush. When they are more numerous and owls are abundant ground squirrels are the most efficient foragers. Kangaroo rats (*Dipodomys merriami*) are more efficient when raptors are abundant and snakes are scarce. Pocket mice (*Perognathus amplus*) are most efficient when owls are scarce and snakes and other raptors are not uncommon (Brown 1989).

Allenby's gerbil (Gerbillus allenbyi) relies on both direct and indirect cues whereas the Greater Egyptian Gerbil (*Gerbillus pyramidum*) responded more strongly to the presence of owls than the level of illumination during foraging. The difference may be due to the size of their auditory bullae, which are larger in the greater Egyptian gerbil than in the Allenby's gerbil. Also, the greater Egyptian gerbil is able to adjust its response to different species of owl. It perceives the Barn Owl as the most dangerous and the Eagle Owl as the least dangerous. Areas with dense shrub cover are preferred more by the smaller Allenby's gerbil because it is more able to maneuver around the tangled branches.
and the shrubs provide protection from potential predators. Greater Egyptian gerbils, however, are better suited for open area habitats (Kotler et al. 1991).

Small mammal species such as *P. leucopus* and *Ochrotomys nuttali* spend more time foraging cacheable foods and feeding in their nesting sites than foraging away from refuge. This behavior could be due to perceived predation risk, especially during fall and winter when foliage coverage is low (Wright and Barrett 2011). Under the right coverage conditions a forager would be willing to consume food at a patch that is far from their nest site. Even after consuming seeds at the patch the forager still carries seed to cache. This foraging technique allows the forager to get benefits from higher energy intake and decrease risk from consuming food at the site right away (Shuai and Song 2011).

*Foraging Competition*

Niche overlap can cause interspecies competition, but differences in the use of space between species can allow them coexist and gain more opportunities to acquire resources when resources are scarce in the environment. The arboreal mammals, gray leaf-eared mouse (*Graomys griseoflavus*) and white-bellied fat-tailed mouse opossum (*Thylamys pallidior*), both use vertical space in the Monte Desert, Argentina. The gray leaf-eared mouse uses the ground more than arboreal levels; it uses vertical space more during the dry season and feeds primarily on foliage. The white-bellied fat-tailed mouse opossum uses the ground and arboreal levels equally and tends to be higher up in the trees due to its dietary preferences of *Prosopis flexuosa* leaves and bird eggs (Albanese et al. 2011). The golden mouse (*Ochrotomys nuttalli*) and the cotton mouse (*Peromyscus*
American red squirrels (*Tamiasciurus hudsonicus*) have been found to spend most of their time foraging on the ground even if there is more quantity or types food available in trees (Benhamou 1996). In a study done by Packer and Layne (1991), during which many small rodents were studied, the golden mouse (*Ochrotomys sp.*) and the cotton mouse (*Peromyscus gossypinus*) showed a much stronger tendency than the Florida mouse (*Podomys floridanus*) and the oldfield mouse (*Peromyscus polionotus*) to forage in elevated feeding stations and transport acorns to elevated nest boxes. The difference in arboreality may be due to their difference in size, with the smaller species being more arboreal than the larger species. Differences in arboreal activity have also been attributed
to differences in branch size and structure (Packer and Layne 1991). Yet, the suitable branch diameter for climbing could depend on the morphology of the small mammal. In Monte Desert, Argentina the white-bellied fat-tailed mouse opossum (*Thylamys pallidior*) selects the highest areas with the largest branch diameters to forage on the leaves of *Prosopis flexuosa*, bird eggs, and arthropods (Albanese et al. 2011).

Morphology and habitat structure can influence vertical stratification of bats (Hodgkison et al. 2004; Adams et al. 2009). Species with short, broad wings and low wing-loadings that have high maneuverability tend to fly in understory, species with medium wing-loadings fly below canopy, and species with long narrow wings and high wing-loadings fly above canopy (Hodgkison et al. 2004). In areas where logging has occurred, bat activity differed the most between young and old regrowth at sub-canopy and canopy heights, where the greatest changes in forest vegetation structure had taken place (Adams et al. 2009). Bumble bees prefer to pollinate flowers arranged on a level plane as opposed to flowers arranged on a sloping plane. This could be because foraging on a sloping plane is more costly for bees (Makino 2008). Vertical structures are more likely to be used as landmarks than as foraging targets (Arnon et al. 2009).

Predatory cues can influence vertical structure use and foraging. The wolf spider, *Pardosa milvina*, will avoid chemotactile cues of the larger wolf spider species, *Hogna helluo*. If the cue was located at the bottom of the container *P. milvina* would climb upward and if the cue was on the wall of the container *P. milvina* would climb downward. In the presence of a predator cue *P. milvina* would have to move slowly to avoid detection by *H. helluo*, which uses visual and vibratory cues to detect prey (Folz et al. 2006).
Larger brown trout (*Salmo trutta*) remain in the upper part of the water column between attacks on surface prey more often than smaller trout. This occurs because smaller trout typically experience high predation risk from aquatic predators that can be avoided if they stay closer to the bottom where coarse substrates can act as in-stream cover (Gustafsson et al. 2010). Juvenile sockeye salmon (*Oncorhynchus nerka*) use vertical migration in response to light levels. They move to remain at a constant light level that minimizes their detection by a predator (Scheuerell and Schindler 2003). Light levels are also important for Weddell seals (*Leptonychotes weddellii*), which are visual predators that use the under-ice surface as back-lighting when foraging (Heerah et al. 2013).

Many fish species use vertical movement through water columns to avoid hypoxic conditions. Depending on the tolerance to changes in ambient oxygen levels, some species (e.g. yellow perch (*Perca flavescens*)) can remain in the hypoxic region and continue to forage (Roberts et al. 2012). Sperm whales (*Physeter macrocephalus*) produce clicks and use echolocation during most of their descent in search of prey. If more time is spent foraging at more productive patches in the depths, sperm whales will make up for it with faster more efficient ascents (Watwood et al. 2006). During winter months Weddell seals reduce their foraging depths but increase dive duration with no effect on foraging effort. More time is spent at the bottom of their dives during the day and when a foraging patch is depleted they will make long shallow exploratory dives to find new holes or cracks in the ice associated with prey patches (Heerah et al. 2013). Body composition is thought to play a role in the ability of the elephant seal (*Mirounga leonina*) to dive in waters with high ice concentrations. Larger seals have been found to
forage in areas with higher ice concentrations (Muelbert et al. 2013). When prey is encountered, elephant seals increased decent rate and bottom duration but overall dive duration did not increase (Gallon et al. 2013).

*Natural History of* Peromyscus leucopus

*Peromyscus leucopus* is a semi-arboreal mammal that is distributed throughout North America (Fig.1; Smithsonian National Museum of Natural History). In an experiment done by M'Closkey (1975), he observed *P. leucopus* would climb trees and shrubs when released from traps more so than other small mammals in the area. Areas that have complex vertical structures such as shrubs and heavy herbaceous vegetation are preferred by *P. leucopus* (M'Closkey 1975; Kaufman et al. 1983). They have also been observed climbing simulated grass canopy set-ups to forage (Jenkanoski and Kaufman 1995). *Peromyscus leucopus* does most of its foraging and other activities at night (Duffy et al. 1997).

![Figure 1. Range map of White-footed mouse (*Peromyscus leucopus*).](image)
*Peromyscus leucopus* is a dietary generalist species that consumes a variety of foods such as acorns, millet, hickory nuts, dogwood fruits, insects including moth larvae, beetles, and spiders and they are even known to predate some songbird nests (Batzli 1977; Elkinton et al. 1996; Schmidt and Ostfeld 2003; Gibbes and Barrett 2011). Annual fluctuation in mast production has had an effect on *P. leucopus* population densities. Low seed production in the fall leads to lower population densities in the following spring (Kaufman et al. 1995; Elkinton et al. 1996; Yunger 2002; Scarlett 2004; Vessey and Vessey 2007). Precipitation also affects population densities from season to season. Higher precipitation rates during winter lead to lower population numbers in the spring. Yet, higher precipitation in the summer positively affected population density in the fall (Kaufman et al. 1995; Vessey and Vessey 2007).

*Peromyscus leucopus* has a behavioral plasticity that allows it to adjust quickly to changing environments, which is part of why it does so well in fragmented habitats across eastern North America (Vessey and Vessey 2007; Gibbes and Barrett 2011). Males have flexible home ranges (~0.2 ha) that vary with population density, while females have smaller more exclusive home ranges (~0.15 ha) that are presumably used to protect and defend the nest site and the young (Myton 1974; Vessey and Vessey 2007). They rarely travel more than 50 m once they are established in an optimal habitat (The Museum of Texas Tech University). Given its relatively "fast" life history, with early maturation and high reproductive effort, populations are able to respond quickly to favorable conditions (Elkinton et al. 1996; Vessey and Vessey 2007). While their population densities are low they will stay in their preferred habitat. It is not until their
population numbers become high that it is beneficial to move to a less-preferred habitat (Scott and Dueser 1992).

*Peromyscus leucopus* has an average litter size of 4.8. Litter size is not constant throughout a female's reproductive lifetime. It increases after the first litter at the onset of maturity, with the highest litter sizes occurring from the third through the ninth litters, after which it steadily decreases. The young nurse for around 21 days, any longer and the young have an increased chance of being located by a predator. It also increases the energetic cost on the mother and there is a greater chance that she will be predated during a feeding trip. Females are more likely to hoard food than males. This helps to reduce predation risk during lactation, and to maintain the energy needed to successfully raise the litter (Fleming and Rauscher 1978).

Nesting for *P. leucopus* can occur both in arboreal structures and in ground structures (Dooley and Dueser 1990). Females will move their young between nests after 20-25 days to allow the old nest to dry out before having another litter (Nicholson 1941). When the ambient temperature gets colder *P. leucopus* will huddle in groups and communally nest. This reduces the energetic costs of thermoregulation. These communal nests consist of related conspecifics (Nicholson 1941; Hayes 2000). By March and April *P. leucopus* will go back to singular nesting and remain mostly solitary during the breeding season; which occurs from March through October (Nicholson 1941).

During the breeding season there can be a lot of fighting occurring between members of the same sex. The invader is the most likely to be killed in these fights. Females are more likely to fight once they become pregnant. Once pregnant, the female
will not tolerate the presence of a male in her nest. She has the ability, however, to become pregnant within 24-hours after birth should she encounter a male when she leaves the nest. Males can be promiscuous if their territory overlaps multiple females' territories. After weaning her young the female will leave the young and create a new nest elsewhere for her next litter. In about three weeks the juveniles from the previous litter will disperse (Nicholson 1941).
Abstract

Predation risk can have a strong influence on foraging behavior. I hypothesized that 1) *Peromyscus leucopus* would climb trees and forage at greater heights if there is coyote urine present and 2) if there are owl pellets present, *P. leucopus* would avoid foraging at that tree. To explore these hypotheses, giving-up densities (GUDs) were measured by using foraging trays mounted on trees in an oak forest located in eastern Will County Illinois. Data was analyzed using repeated measures MANOVA. Scent was the only significant difference during owl pellet treatments (P=0.0471, df=1). A significant difference was found between scent (P=0.0183, df=1), scent and day (P=0.0447, df=5), day, season and scent (P=0.0801, df=9), and foraging heights (P=0.0420, df=2) during the coyote treatments. *Peromyscus leucopus* foraged more at trees with owl pellets. They also foraged more at trees with coyote scent and more at the base than up in the trees. Foraging at trees could be safer because of their ability to climb or hide to escape predation.

Introduction

Foraging provides the necessary energy for survival, growth, reproduction, and competition (Brown et al. 1992; Lima 1998). The ability to forage optimally is important for an individual's fitness. The energy gained from foraging must outweigh the energy spent to locate and arrive at the foraging patch and the risk of depredation (Brown 1992; Lima 1998). Initially, when a forager arrives to a patch the energy gain may be high, but as the individual continues to forage the energy gain drops due to food depletion, while
predation risk and other foraging restrictions hinder energy gain (Brown et al. 1992). As a forager uses multiple patches, energy is used during travel between those patches. The forager must balance that energy loss due to travel by spending the optimum time at the next patch. If the forager leaves the patch too early it will have a low rate of energy return. Yet, if the individual stays too long at the same patch, the resources will become depleted while more energy will be spent searching for the remaining food, which will cause a net energy loss (Parker and Stuart 1976; Brown et al. 1992; Brown et al. 1994).

Foragers that have developed the skills to maximize the average rate of resource harvest at each patch could improve their fitness (Brown 1988). Many factors can influence foraging behavior such as inter-species and intra-species competition, predation risk, and food patch depletion (Brown 1989; Lima and Dill 1990). An individual can use direct cues (olfactory, auditory, and visual) and indirect cues (ground cover and illumination) to influence its foraging decisions (Brown 1992; Ward et al. 1997).

Indirect predator cues have a greater impact than direct cues on rodents (Orrock et al. 2004; Fanson 2010). Some rodents have been found to forage more in covered areas than in open, illuminated areas, even if there were more food items in the open areas, because of perceived predation risk (Kotler et al. 1991; Arcis and Desor 2003). Midday gerbils (Meriones meridianus) were found to travel further to covered foraging areas and spend more time there eating before bringing left over cacheable seeds back to their nests (Shuai and Song 2011). In lab experiments, rodent species, including Peromyscus leucopus, show a fear response (freezing or avoidance) to predator odors (Kavaliers 1988; Hebb et al. 2003; Takahashi et al. 2005). Yet, P. leucopus shows limited response to
mammalian predator odors in a field experiment setting (Fanson 2010), but when a
predator is heard this species will seek refuge in covered areas or nest boxes (Wright and
Barrett 2011). As a result of decreased photo-period, *P. leucopus* has increased fear
response to predator cues. This may be attributed to the ecological changes that happen
with shorter day period, such as reduced ground cover, which leaves fewer places for *P.
leucopus* to hide (Walton et al. 2012). Predation risk has been found to decrease as *P.
leucopus* moves from the edge to the interior of the woodland because of increased forest
structure giving *P. leucopus* more hiding places (Wolf and Batzli 2004).

*Peromyscus leucopus* is semi-arboreal, climbing trees to explore a habitat, escape
from predators, and forage. Plant species used by *P. leucopus* for arboreal travel and
foraging differ with habitat location and season (M'Closkey 1975). Areas with large
shrubs were used equally, with or without trees, by *P. leucopus*. Yet, *P. leucopus* preferred
that areas with small shrubs also have trees over areas of small shrubs and no trees
(Kaufman et al. 1983). An alternative explanation to predator avoidance is the arboreal
use of a habitat could be used to reduce niche overlap (M'Closkey 1975; Kaufman et al.
1983).

Little research has been done to study the vertical use of habitat structure by *P.
leucopus*. A study done on other semi-arboreal rodents showed that the golden mouse
(*Ochrotomys sp.*) and the cotton mouse (*Peromyscus gossypinus*) displayed a much
stronger tendency than the Florida mouse (*Podomys floridanus*) and the oldfield mouse
(*Peromyscus polionotus*) to forage in elevated feeding stations and transport acorns to
elevated nest boxes. The difference in arboreality may be due to their difference in size,
with the smaller species being more arboreal than the larger species. Differences in arboreal activity have also been attributed to differences in branch size and structure (Packer and Layne 1991). Yet, the suitable branch diameter for climbing could depend on the morphology of the small mammal. In Monte Desert, Argentina the white-bellied fat-tailed mouse opossum (*Thylamys pallidior*) selects the highest areas with the largest branch diameters to forage on the leaves of *Prosopis flexuosa*, bird eggs, and arthropods (Albanese et al. 2011).

Giving-up densities (GUDs), a measure of what the forager leaves behind in a food patch, can provide a quantitative measure of the costs and benefits of the foraging animal (Brown et al. 1994). Giving-up density can be used to gain information on the energetic cost, and missed opportunity cost of foraging (Brown 1988). For *P. leucopus*, GUD increased in food trays that contained a mixture of millet seed and compared to trays with only millet seed. This difference could be attributed to the perceived quality of the foraging patch (Shaner et al. 2007). *Peromyscus leucopus* mainly selects food that will fulfill its energy requirements and will avoid food with excessive amounts of protein since it is more costly metabolically to process (Lewis et al. 2001). As GUD increased, and a large quantity and variety of food was available, the mice would occupy a narrower omnivory niche and as GUD decreased, quantity of food was available decreased, they would occupy a broader, herbivory - omnivory - carnivory niche (Shaner et al. 2007).

This experiment focuses on the foraging habits of *Peromyscus leucopus* and if they climb trees in response to mammalian and avian predator cues. I hypothesized that 1) *P. leucopus* would forage less in the presence of avian predator cues, and 2) that *P.
*leucopus* would climb trees and forage at greater heights in the presence of mammalian predator cues.

**Materials and Methods**

*Study area.*—The study site, a 13.36-ha oak-hickory forest, is located at the field station on the Governors State University campus, in eastern Will County Illinois, U.S.A. (41°26'35.07" N and 87°42'47.24" W: Fig. 1). The forest is primarily composed of black oak (*Quercus velutina*), white oak (*Quercus alba*), and shagbark hickory (*Carya ovata*) trees. The trees that were used for the foraging trays were *Q. alba* and *Q. velutina* due to their abundance, large size, and hard wood.

Figure 2. The polygon indicates the location of the field experiment.
**Experimental design.**—A total of 20 different sample locations were randomly selected (Fig. 3). The sample locations were at least 50-m apart from each other and located at least 25-m from the habitat edge. Fifty meters between sample locations was chosen because *Peromyscus leucopus* usually travel no more than 50-m once they are established in a suitable location (Lackey et al., 1985). There were 3 foraging trays per oak tree at three heights: ground level, 3-m above ground level, and 6-m above ground level (Fig. 4). The oak trees chosen for the foraging trays were >30-cm dbh. The sample locations were studied using simple segregation sampling (Krebs, 1999: 347).

Each foraging tray was filled with 2-L of sand and 10-g of millet seed. The millet seed was autoclaved to prevent germination while in the foraging trays. The trays were checked for foraging activity each day for 5 days, with millet being replaced as needed, then left devoid of seed between predator treatments.
Figure 3. The crosses represent the location of sample trees.
Data was collected seasonally from March 2013 to February 2014: spring (March - May), summer (June - August), fall (September - November), and winter (December - February). *Peromyscus leucopus* decrease their activity during the full moon phase (Jekanoski and Kaufman, 1995; Orrock et al., 2004). This behavior is attributed to the higher predation risk due to increased detection abilities of highly visual predators (Kotler et al., 1991; Fanson, 2010). Therefore, experimental procedures were only performed during new moon phases each month.
Each season of the experiment consisted of aerial predator treatments and controls during the first month, and ground predator treatments and controls during the third month. For controls, scent wicks were saturated in deionized water. For the aerial predator treatment, owl pellets were placed at half of the sample sites and the other half of the sites were used as controls for 5 days. Foraging trays were checked each day and millet was refilled as needed. Then the sites were left free of seed and predator scents for 3 weeks. For the ground predator treatment, 15-ml of coyote urine was placed on each scent sponge that was placed at half of the sample sites, while the other half had control set ups, for another 5 days while checking foraging trays each day and refilling millet as needed. Trays that showed signs of foraging activity were sifted and the remaining seed (if any) was weighed.

Trapping was performed following the American Society of Mammalogists guidelines (Sikes et al. 2011). Sherman traps were set for 6 nights during the second month of each season for estimates on population density. Density estimates are needed to compare against amount of seed foraged. The traps were baited with peanut butter and oats and checked early morning and late afternoon daily. The traps were set up in a 10 x 10 array with each trap spaced 10 m apart.

Statistical analysis.—Data was analyzed using a repeated measures MANOVA. Days and seasons were the repeated measures, heights were nested within each sample location, and the presence or absence of predator odor was the MANOVA analysis. Alpha was set at 0.10.
Results

*Owl Months.*—There was a significant difference in the effect of scent (Table 1; Fig. 5) on the foraging behavior of *P. leucopus*. The GUDs for owl pellet treatments were lower than for control sites. This indicated that *P. leucopus* foraged in trays located at trees with owl pellet treatments. There were no significant differences observed across heights, seasons, or days during the owl pellet treatments (Figs. 6-9).

*Coyote Months.*—There was a highly significant difference in the effect of scent during the coyote treatments (Table 2; Fig. 9). The GUDs for coyote urine treatments were lower than for the control treatments. This showed that *P. leucopus* favored foraging in trays located at trees with coyote treatments. A significant difference was observed between day × scent interactions during coyote treatments (Wilks Lambda, P=0.0447). At coyote treatments foraging increased as the days progressed (Fig. 10).

The day × season interaction was slightly different (P=0.1020) with a significant difference (Wilks Lambda, P=0.0801) occurring between day × season × scent. There was no foraging in the spring (Fig. 11a.). *Peromyscus leucopus* foraged to lower GUDs as the days progressed at the trees with coyote treatment during the summer (Fig. 11b.). The high foraging rate that occurred during the summer at coyote treatments is what brought the average GUDs down over the year. During the Fall there was no foraging occurring at trees with coyote treatment and control treatment trees had the most foraging on day 2 which decreased over days 3 and 4 and increased again on day 5 (Fig. 11c.).

A significant difference was found between heights (Table 2). A Tukey test was done to show which heights were significantly different from one another (Table 3).
There was only a significant difference between 0m and 6m. More foraging occurred at the base of the tree with GUD increasing as the trays were higher up on the trees. There was no significant difference found with height and scent (P=.1129). Foraging among heights at control treatments did not vary much, while foraging at coyote treatments had the lowest GUDs at 0 m and increased as tray height increased (Fig. 12).

*Population data.*—Trapping results showed low population numbers throughout the year. During the spring population estimates 6 individuals were captured, summer had 23 individuals and fall had 20 individuals. Population density estimates were not performed during the winter due to deep snow and temperatures reaching -26°C. Six of the individuals that were captured in the summer were also captured in the fall. A total of 43 unique individuals were captured over the year.

Table 1.—MANOVA table for giving-up densities of *P. leucopus* in response to owl pellet treatments.

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Type III SS</th>
<th>Mean Square</th>
<th>F Value</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>scent</td>
<td>1</td>
<td>7.7521688</td>
<td>7.7521688</td>
<td>4.13</td>
<td>0.0471</td>
</tr>
<tr>
<td>height</td>
<td>2</td>
<td>2.2734007</td>
<td>1.1367003</td>
<td>0.61</td>
<td>0.5497</td>
</tr>
<tr>
<td>height*scent</td>
<td>2</td>
<td>1.9393280</td>
<td>0.9696640</td>
<td>0.52</td>
<td>0.5997</td>
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<tr>
<td>Error</td>
<td>54</td>
<td>101.4439135</td>
<td>1.8785910</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 5. Mean giving-up density (GUD) of *P. leucopus* during Owl pellet months with standard error bars (n=200).

Figure 6. Mean giving-up density (GUD) of *P. leucopus* across height during owl treatments with standard error bars (n=200).
Figure 7. Mean giving-up density (GUD) of *P. leucopus* across seasons with standard error bars (n=50).

Figure 8. Mean giving-up density (GUD) of *P. leucopus* across days during owl treatments with standard error bars (n=40).
Figure 9. Mean giving-up density (GUD) of *P. leucopus* across days during a) spring, b) summer, c) fall, and d) winter owl treatments with standard error bars (n=10).
Table 2.—MANOVA table for giving-up densities of *P. leucopus* in response to coyote treatments.

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Type III SS</th>
<th>Mean Square</th>
<th>F Value</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>scent</td>
<td>1</td>
<td>10.10604100</td>
<td>10.10604100</td>
<td>5.92</td>
<td>0.0183</td>
</tr>
<tr>
<td>height</td>
<td>2</td>
<td>11.48244267</td>
<td>5.74122133</td>
<td>3.36</td>
<td>0.0420</td>
</tr>
<tr>
<td>height*scent</td>
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<td>7.75405067</td>
<td>3.87702533</td>
<td>2.27</td>
<td>0.1129</td>
</tr>
<tr>
<td>Error</td>
<td>54</td>
<td>92.15066333</td>
<td>1.71</td>
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<td></td>
</tr>
</tbody>
</table>

Table 3.—Tukey’s test table showing the significant difference between foraging heights.

<table>
<thead>
<tr>
<th>Tukey Grouping</th>
<th>Mean</th>
<th>N</th>
<th>Height</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>9.97997</td>
<td>300</td>
<td>6</td>
</tr>
<tr>
<td>A</td>
<td>9.8269</td>
<td>300</td>
<td>3</td>
</tr>
<tr>
<td>B</td>
<td>9.70383</td>
<td>300</td>
<td>0</td>
</tr>
</tbody>
</table>

Figure 10. Mean giving-up density (GUD) of *P. leucopus* during coyote treatment months with standard error bars (n=150).
Figure 11. Mean giving-up density (GUD) of *P. leucopus* across days during coyote treatments with standard error bars (n=30).
Figure 12. Mean giving-up density (GUD) of *P. leucopus* across days during a) spring, b) summer, and c) fall coyote treatments with standard error bars (n=10).
Figure 13. Mean giving-up density (GUD) of *P. leucopus* across height during coyote treatments with standard error bars (n=150).

**Discussion**

*Peromyscus leucopus* population densities were lower across all seasons than population sampling done in previous studies of this experimental site. It is unknown what caused the drop in population density. Seasonal weather conditions and mast production could have influenced these population numbers. Seasonal precipitation has a correlation with *P. leucopus* population density. Fall population numbers are positively correlated with summer rain. In contrast, spring population numbers are negatively correlated with winter precipitation (Kaufman et al. 1995; Vessey and Vessey 2007). Also, poor mast production can limit the amount of food available for foraging and caching which can affect the overwintering population numbers (Kaufman et al. 1995;
The low population numbers explain the overall lower foraging rates during this experiment.

Owl treatments only showed a significant difference due to scent with *P. leucopus* foraging more at trees with owl pellets than controls. This behavior, while unexpected, could be due to owl pellets not being perceived as a risk that an owl will be near. Another interesting outcome was that there was no difference in foraging among heights.

*Peromyscus leucopus* foraged similarly at all heights even though there was evidence of owls present. Owl pellets could possibly be perceived as a potential calcium source similar to shed deer antlers (Schmidt and Hood 2012). The mice were unable to get to the owl pellets used in this experiment because they were enclosed in a small wire cage that was staked to the ground at each owl treatment tree.

During the coyote scent trials *P. leucopus* foraged more at 0 m than 3 m and 6 m and foraged more at 3 m than 6 m. This was unexpected. I predicted that *P. leucopus* would climb and forage higher to avoid an encounter with a ground predator. They also foraged more overall at trees with coyote treatments than control trees. This may be because *P. leucopus* uses more indirect cues rather than direct cues to assess predation risk (Orrock et al. 2004; Fanson 2010). Additionally, foraging at trees could be safer for *P. leucopus* because of their ability to climb or hide in hollows to escape ground predators.

A day × scent interaction showed that GUD was lowest on day 4 at the coyote treatments and there was not a lot of foraging occurring at the control treatments. Generally, more foraging occurred as days progressed at coyote treatments. This could
possibly be due to dilution of the coyote urine as it was exposed to the elements over the 5 days. Another explanation could be the habituation of *P. leucopus* to the coyote scent.

There was also a day × season interaction that indicated that the most foraging occurred on day 4 during the summer. The least foraging occurred during the spring, where there was no foraging across all 5 days of the experiment. This data follows the population estimates for spring and summer. Foraging during the fall had the lowest GUDs on day 2 with a gradual increase to day 4 then decreased again on day 5.

Day × season × scent had a strong interaction. No foraging occurred at all during the spring. During the summer, coyote treatments had more foraging overall with GUDs decreasing daily. The lowest GUDs were recorded on days 4 and 5 at the coyote treatments during the summer which explains the day × season averages. Control treatment GUDs did not vary much during the summer trial. There was no foraging occurring at the coyote treatments during the fall. Control treatments had the lowest GUDs on day 2 with an increase on days 3 and 4 and a decrease on day 5. This seems to follow along with the population data collected. The lowest population numbers were recorded in the spring and the highest numbers were found during summer with a slight decline in numbers during the fall. *Peromyscus leucopus* switched from foraging at trees with coyote urine in the summer to foraging at trees with control treatments in the fall. This could be due to the change in foliage cover that would provide less coverage in the fall, making it less safe to forage at trees that may have ground predators nearby.

Not being able to keep predators out of the control areas could have been an issue in this experiment. Photos taken of the control sites by motion cameras did not show any
predators near the trays. Further research could be done by keeping ground and avian predators out of the experimental site by creating exclosures.

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