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Anne E. Collier
Trinity College, anne.collier@trincoll.edu

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THE EFFECTS OF PREDATION RISK AND THERMOREGULATION COST ON THE FORAGING BEHAVIOR OF THE EASTERN GREY SQUIRREL (*SCIURUS CAROLINENSIS*)

BY

ANNE ELIZABETH COLLIER

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THE FACULTY OF THE DEPARTMENT OF BIOLOGY
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WITH HONORS IN BIOLOGY

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THE EFFECTS OF PREDATION RISK AND THERMOREGULATION COST ON THE FORAGING BEHAVIOR OF THE EASTERN GRAY SQUIRREL (*SCIURUS CAROLINENSIS*)

BY

ANNE ELIZABETH COLLIER

Honors Thesis Committee

Approved:

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Michael A. O'Donnell, Advisor

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Daniel G. Blackburn

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Scott R. Smedley

Date: ____________________________________

Abstract:

In this study, the effects of predation risk and thermoregulation cost on the foraging behavior of the urban eastern gray squirrel (*Sciurus carolinensis*) were examined. There were two objectives. The first was to determine if either thermoregulation cost or predation risk had a more significant effect on foraging behavior. The second was to find out if foliar cover or distance to refuge was a more important cue of predation risk. To accomplish these goals, giving-up density and temperature data were collected at feeding trays both under the canopy and outside of the canopy at two deciduous trees and two evergreen trees. It was found that there was no difference in temperature between areas under canopy cover and areas in the open, and therefore, thermoregulation costs did not affect foraging in terms of giving-up density. Also, giving-up density was always lower under the canopy than in the open no matter how much foliar cover was available. This finding indicated that distance to refuge is a more important cue of predation risk than canopy cover. Therefore, the effect of microhabitat on foraging behavior should be taken into account when considering urban wildlife management and conservation.

Introduction:

Urbanization is an on-going phenomenon, and human developments continue to expand and have a significant impact on wildlife. From 2000 to 2010, the urban population in the United States increased by 12.1%; currently almost 81% of its population lives in urban areas (United States Census Bureau 2012). There has been substantial habitat loss, and in areas with large human populations, high local extinction rates of native wildlife have been reported. Typically, the native species that become locally extinct are replaced by nonnative species (McKinney 2002). Habitat fragmentation, which limits the species that can use a habitat and therefore decreases species richness, also results from human development (Beissinger and Osborne 1982, Cooper et al*.* 2008). Species that remain in urbanized areas often exhibit behavioral and ecological changes (Ditchkoff et al*.* 2006). It is crucial to understand the effects that humans and urban development have on animals so that wildlife conservation and management can be carried out as effectively as possible (Ciuti et al*.* 2012). By doing so, it will also be possible to maximize positive interactions and minimize negative interactions between urban residents and urban wildlife so that experiences with wildlife will be more beneficial to the human population.

Urbanization and Wildlife

Many species are unable to survive in urbanized areas and either become locally extinct or are forced to find new habitats. However, species that show behavioral, ecological, and physiological plasticity are often able to adapt to urban life. Species that are able to survive in urban areas have been undergoing synurbization, the process of becoming urbanized. These animals exhibit certain characteristics, often referred to as "urban wildlife syndrome" (Parker and Nilon 2008). Urban populations typically have much higher population densities when compared to their rural counterparts. Urban animals exhibit more intraspecific aggression, which may be related to the increased population densities making it more competitive to attain food, mates, and shelter. Urban animals also become habituated to humans. Increased exposure to humans allows animals to learn that humans pose little threat, and may benefit the animals because humans often provide sources of food (Parker and Nilon 2008, Engenhardt and Weladji 2011).

Urbanization has caused ecological changes for many urban animals. These changes include shifts in reproduction strategies, different food and habitat selections, and increased population density. For example, gray squirrels' diets have changed in urban habitats. Approximately 35% of urban squirrels' diets consist of anthropogenic foods (Parker and Nilon 2008). Supplementing animals' nutrition with anthropogenic foods can alter reproductive life history strategies. Enhancing nutrition makes it possible for animals to have increased reproductive rates, larger litters, and greater survival rates for offspring. However, shifts in dietary selections can also cause disease among urban animals, particularly in scavengers that feed on trash because it is often contaminated with bacteria (Ditchkoff et al. 2006). In addition to alterations in diet among urban wildlife, studies have shown that urban animals change the timing of their activity to avoid daylight when humans are most active. This is particularly true for larger animals such as coyotes (McClennen et al.

2001). Similarly, high noise levels in urban areas have required that animals such as birds that rely on vocal communication for reproduction change their reproductive tactics to survive (Ditchkoff et al. 2006). The timing of reproduction can also be affected by urbanization. Urban scrub-jays begin breeding about 3 weeks earlier than their rural counterparts. This is most likely due to the abundance of food available to urban scrub-jays due to bird feeders and other anthropogenic food sources (Fleischer et al*.* 2003). Population density can increase drastically in urban areas where suitable habitat is fragmented and/or resources are more concentrated. Manski et al. (1980) reported that in an urban park in Washington, D.C., the density of gray squirrels ranged from 22.75 to 51.5 per hectare, which is much greater than the typical population density of 3-10 per hectare.

Aspects of animal behavior, including anti-predator behaviors, vigilance, and foraging behaviors, are also affected by urbanization. Mccleery (2009) found that fox squirrels (*Sciurus niger*) in urban habitats showed decreased anti-predator responses to hawks, coyotes, and humans. Flight initiation distances of squirrels are also shorter in areas of high human activity, which indicates a reduced perception of risk (Cooper et al*.* 2008). Altered anti-predator behaviors are most likely the result of fewer predators living and hunting in urbanized areas, which causes predation to be a less common occurrence (Ditchkoff et al. 2006).

Despite the decrease in some anti-predator behaviors in urban environments, vigilance increases in areas with larger human populations. Elk (*Cervus canadensis*) were more vigilant while foraging when there was a larger amount of vehicular traffic (Ciuti et al. 2012). Increased levels of vigilance are associated with less efficient foraging because more time is spent visually scanning the surrounding areas.

In addition to foraging becoming less efficient in urban areas due to increased vigilance, there is evidence that more foraging occurs (Bowers and Breland 1996). There is more foraging because there is usually less food available in urban habitats, which increases the marginal value of food. It has also become common for animals to supplement their diets with anthropogenic foods (Parker and Nilon 2008).

These behavioral changes are significant because behavior often contributes to an animal's fitness, which is measured by the number of viable offspring an individual produces during their lifetime. Maladaptive behaviors can decrease fitness by making an individual more prone to predation, less able to find shelter or a mate, or less adept at foraging. Appropriate behaviors, on the other hand, can help animals survive and successfully reproduce, thereby enhancing their fitness. It is believed that behavioral patterns that enhance fitness are favored by natural selection and detrimental behaviors are selected against due to a genetic component of behavior (Krebs and Davies 1993).

However, behavior is not strictly determined by genetics. The environment and specific ecological factors can modify behaviors. This is significant because changes within an environment can alter which behaviors are beneficial. As urbanization changes habitats, animals must adjust their behavior (Krebs and Davies 1993). Learning is also crucial for shaping animal behavior. Animals have become increasingly habituated to humans as they learn that humans do not pose a significant threat in most instances. Habituation can enhance animals' fitness because when they devote less time and energy to anti-predator behaviors in the presence of humans, they can devote more time and energy to other activities that are critical for fitness such as foraging or mating (Krebs and Davies 1993).

Foraging Behavior

Foraging behavior is important for an animal's fitness because it provides an energy source for the animal. The genetic basis of foraging behavior has allowed natural selection to act on it so that an optimal amount of time and energy are allocated to the activity (MacArthur and Pianka 1966). The first step in the process of foraging is searching. During this stage of foraging, no food source is detected, but the animal is using energy to actively look for food. The second stage is the encounter, when the forager detects food and ceases to search. The final stage is the decision, in which the forager must decide how long to stay foraging at the source of food it has discovered (Stephens and Krebs 1986).

The decision of how long to stay at a food patch is based on balancing the benefits of gaining energy from foraging with the costs of foraging. The ability to balance costs with efficient foraging greatly enhances an animal's fitness (Lima et al. 1985). Predation risk, energy spent searching for and handling food, and missed opportunity costs are common costs incurred by foragers. Predation risk is a significant cost of foraging because it can have a large impact on animal's fitness, and it has been shown to affect foraging behavior (Lima et al*.* 1985, Dill and Houtman 1987, Thorson et al. 1997). Energetic costs and missed opportunity costs are also important because they determine how long a forager should remain in a certain patch. Missed opportunity costs include missing a mating opportunity or being unable to defend territory due to being occupied by foraging (Orrock and Danielson 2009).

Most theories and models of foraging are based on a patchy distribution of resources in an environment. According to the optimal foraging theory, foraging within a resource-rich patch will continue as long as the benefits are greater than the costs. When the costs become greater than or equal to the benefits, foraging will stop because the rate of harvest will be so low that the forager will lose energy if it continues. However, many factors affect decision-making, and foragers can behave differently than predicted by the mathematical models of the optimal foraging theory (MacArthur and Pianka 1966). In addition to balancing costs and benefits of foraging, foragers must also take into account the travel time to the next resource patch. If an equivalent patch is a great distance away, it will be more favorable for the forager to remain in the current patch. However, the balance of costs and benefits also depend on the rate of energy gain (i.e., harvest rate) from the patch. Charnov (1976) developed the marginal value theorem, which predicts foraging behavior in patchy environments. The longer a forager remains in a given resource patch, the more total resources the animal has harvested. As the forager harvests more of the resources, the patch becomes depleted. This results in the rate of harvest decreasing as time spent in a patch increases. Therefore, the net energy gain also decreases as patch residence time increases. This results in a gain curve

(Fig. 1) with a diminishing slope indicating change in the rate of food consumption by the forager as time in patch progresses (Charnov 1976).

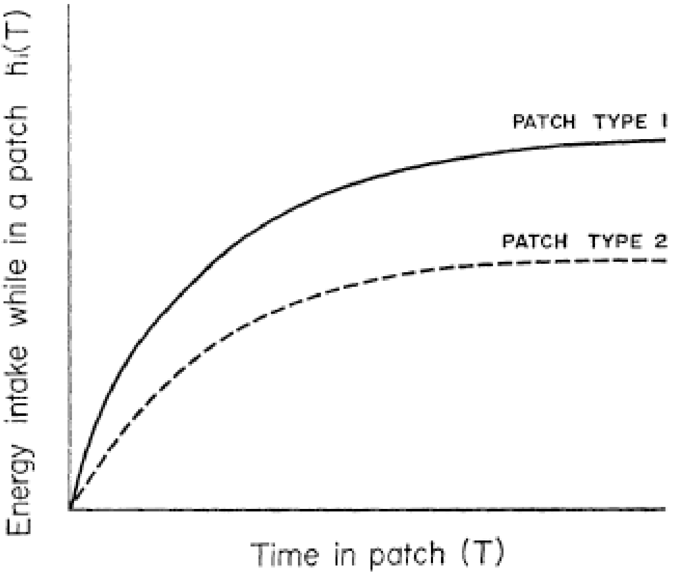

Figure 1. A gain curve showing the net energy gain by a forager as time passes for two patches of higher (patch 1) and lower (patch 2) resource density (Charnov 1976).

To attain optimal foraging, foragers must respond to a variety of stimuli to minimize the costs that they incur while foraging. Therefore, Brown (1988) developed an adaptation of Charnov's marginal value theorem in which the energy intake of a forager is dependent on energetic costs, predation risk, and missed opportunity costs.

It is possible to study how foragers perceive these risks and costs by measuring their giving-up densities, or GUD, which refers to the food left in a patch after foraging (Brown et al. 1992). At the time an animal leaves the patch, the food left in the patch (GUD) correlates with the quitting harvest rate, which refers to the rate of energy intake when an animal leaves a patch (Brown 1988). A high GUD indicates that the forager perceives a high level of risk or cost. In this situation, it is more favorable to quit foraging and leave more resources unused in the patch. A high GUD can also indicate that another patch was nearby, and it was favorable to spend time traveling to that patch rather than remaining in the original patch. A low GUD means that it is favorable to forage longer and use more of the resources the patch has to offer because the forager perceives little risk or cost. A low GUD can also mean that there are no patches close enough for it to be favorable for the forager to move on to a new patch. Changes in GUD in response to a stimulus indicate the forager's ability not only to detect the stimulus but also to respond to it based on the significance of the stimulus to the forager (Thorson et al*.* 1997).

The availability of shelter or cover that will shield a forager from the view of predators is a habitat variable that has been shown to affect GUD. Fox squirrels have a lower GUD when foraging under vegetative cover than in a more exposed area (Brown et al*.* 1992). Factors other than shelter can affect an animal's perception of predation risk. A study with oldfield mice (*Peromyscus polionotus*) found that cloud cover and low levels of moon illumination cause foragers to perceive that they are less visible to predators and therefore less susceptible to predation. This results in a lower GUD (Orrock et al. 2004).

When foragers are not shielded from the view of predators, the distance the forager will have to travel to shelter affects foraging behavior. Thorson et al. (1997) report that fox squirrels and thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*) forage more (and therefore GUD is lower) when there is shelter nearby that would allow the forager to escape predation more easily. These findings agree with Hughes and Ward's (1992) conclusions that Namib Desert gerbils (*Gerbillurus tytonis*) had lower GUDs when they were closer to shelter.

Along with shelter and protection from predation, extreme temperatures that lead to more significant thermoregulation costs also impact foraging behavior. Cold temperatures can limit the duration of foraging, particularly for small mammals that have a high surface area to volume ratio and lose heat more quickly, ultimately resulting in higher GUDs (Orrock and Danielson 2009). Kilpatrick (2003) found that when temperatures are cold, gray squirrels and American crows (*Corvus brachyrynchos*) forage more in the sun despite predation risk so that the animal has to exert less energy to maintain its body temperature. However, if temperatures are too hot or too cold, little to no foraging occurs and GUD is extremely high. Likewise, foraging was less frequent and of shorter duration when the degu (*Octodon degus*), a Chilean rodent, was under thermoregulatory stress. Degus also adjusted their behavior by carrying food from very hot areas to cooler ones (Bozinovic and Vasquez 1999, Bozinovic et al. 1999). According to Orrock and Danielson (2009), the relationship between temperature and foraging is only noticeable when other costs, such as predation risk, are reduced.

The quality and availability of food can determine how beneficial it is for an animal to forage. If food is abundant, it is not particularly valuable. Therefore, less time is devoted to foraging. It is also important for animals to balance the energy they obtain from food with the energy that they expend to obtain the food. Because of this, gray squirrels favor certain foods that are easily obtained or that provide them with a lot of energy (Lewis 1982).

The Eastern Gray Squirrel (Sciurus carolinensis)

The eastern gray squirrel, *Sciurus carolinensis*, is a useful study subject for foraging behavior experiments. There is a large body of research regarding its ecology. Like other members of the order Rodentia, it breeds quickly and can adapt rapidly (Gurnell 1987). Rapid adaptation is useful for observing behavioral changes due to phenomena such as urbanization. The eastern gray squirrel lives primarily in deciduous forests in the eastern United States, but it has also been introduced into England and South Africa. It nests in trees but primarily forages on the ground. It has also become prevalent in urban environments, making it an ideal subject for studying the effects of urbanization on wildlife. Its diurnal activity also makes the eastern gray squirrel an accessible study subject (Gurnell 1987).

The lower end of the thermal neutral zone of the eastern gray squirrel is approximately 25 °C. When they are winter-acclimatized, they have a peak metabolic rate that is roughly 13.5 times greater than their normal metabolic rate (Ducharme et al. 1989). Due to their small size, gray squirrels have a high surface area to volume ratio and lose body heat rapidly (Pereira et al. 2002). To maintain their body temperature, they use non-shivering and shivering thermogenesis (Ducharme et al. 1989).

Experimental Questions

In this experiment, the gray squirrel was studied in an attempt to answer two questions. First, which is a more significant cost of foraging: predation risk or thermoregulatory cost? To address this question, I compared GUD under vegetative cover, and thus in the shade, to GUD in a more exposed and sunny area. Predation risk is lower under cover, but the sun may aid in reducing thermoregulatory costs (Kilpatrick 2003). If GUD is lower in the sun than under cover, it is more profitable to reduce thermoregulatory costs while foraging than it is to lower predation risk. If GUD is lower under cover, it is more beneficial to the forager to reduce predation risk.

Second, is canopy cover more important than the distance to shelter in terms of a foraging squirrel's perception of predation risk? To answer this question, GUD patterns at deciduous and evergreen trees were compared. Other research has shown that when deciduous trees lose their leaves in the fall, there is no difference in GUD under the canopy compared to outside of the canopy (Khan 2010, Trinity College, unpublished data). GUD at evergreen trees should remain consistent throughout the course of the year, and were therefore used as a control. If GUD patterns at deciduous trees change when the trees lose their leaves, canopy cover is a significant cue for determining the predation risk that foragers perceive.

Methods:

Study site

This study was conducted in the southeastern corner of Rocky Ridge Park, adjacent to the campus of Trinity College in Hartford, Connecticut (Fig. 2). Despite its urban location, the 0.8-ha study site was isolated from the rest of the park and had relatively low levels of human traffic. Two roads, which have consistent daily vehicular traffic, bordered the southern and eastern edges, and the western edge was bordered by a steep wooded embankment that lead down to the main area of the park. Occasionally, domestic dogs were walked in the area, posing a potential predation threat to gray squirrels. However, the dogs were always leashed, and no direct attacks on squirrels were observed. The location was a mown grassy area with mature (diameter at breast height > 1.5 m) Norway spruce (*Picea abies*) and oak (*Quercus* sp.) trees. Aside from gray squirrels, only birds were observed in the area. The Red-tailed Hawk (*Buteo jamaicensis*), a predator of gray squirrels, was seen in the area, and direct attacks by Red-tailed Hawks on gray squirrels were observed on numerous occasions.

The study site contained two feeding areas, approximately 100 m apart, to ensure that the same individuals would not forage at both areas (Bowers et al. 1993). At each feeding area, two focal trees were selected: one deciduous tree (*Quercus* sp.) and one coniferous tree (*Picea abies*). The deciduous trees, which would lose their leaves in the fall, were used to determine if canopy cover affects giving-up density (GUD). The conifers, which would retain their canopy year round, served as a control for change in canopy cover. At each foraging site, one feeding tray (30 x 45 x 8 cm) was placed under the tree's canopy at the base of the tree, and another feeding tray was placed just beyond the tree's canopy in the open. By comparing giving-up densities under canopy cover and outside of canopy cover both when deciduous trees provide foliar cover and when they do not, it would be possible to determine whether foliar cover or distance to shelter is a more important cue to foraging gray squirrels. If GUD patterns at the deciduous trees changed as the trees lost their leaves and GUD patterns remained the same at coniferous trees, it would be possible to conclude that vegetative cover is an important cue for foragers.

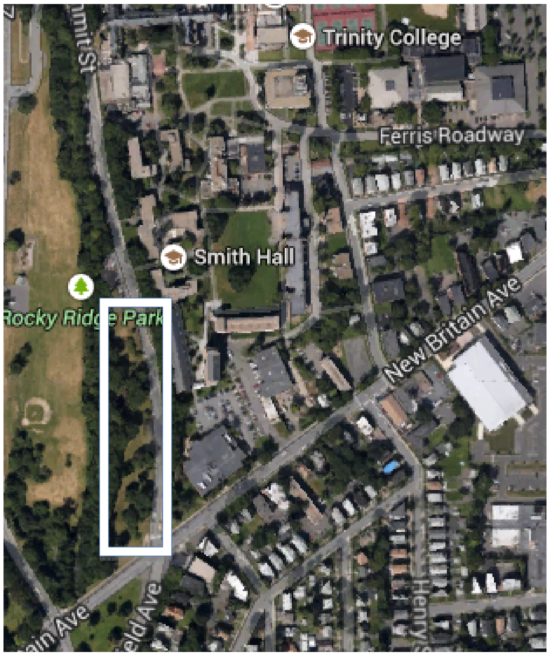

Figure 2: An aerial view of Trinity College and Rocky Ridge Park with the study site bordered in white.

Foraging trials

A total of eight feeding trays were used (a tray in the open and under the canopy for each of four trees, two deciduous and two coniferous). Following two weeks of pre-baiting with seeds on top, each feeding tray was filled with three liters of sand and 20 g of striped sunflower seeds. The sand served as a substrate to create a more realistic foraging experience that would produce a declining harvest rate. At each tree, a Day 6 Outdoors Plotwatcher camera was set up to enable direct observation of gray squirrel foraging and to ensure no other animals were feeding at the trays. The cameras also made it possible to determine when the squirrels were foraging throughout the day. The time-lapse cameras were set to take a picture every 10 seconds.

Temperature measurements

The feeding trays were also equipped with HOBO Pendant Temperature and Light Data Loggers programmed to record a reading every 30 minutes. The data loggers were used to determine if there was a temperature difference between areas under canopy cover, which would be more sheltered from the sun, and areas in the open, which would be exposed to more sunlight. Being able to determine if temperature varies between covered and open areas would make it possible to determine if temperature, and thus thermoregulatory costs, affected foraging behavior. It was presumed that due to increased sunlight in the open, temperatures would be higher in the open. However, this setup was not able to measure convective cooling due to wind, which would increase thermoregulatory costs experienced by foragers. If temperature varied between the open and covered microhabitats and thermoregulatory costs were an important cue for foragers, GUDs would be expected to be smaller in the warmer microhabitat, which was predicted to be the open microhabitat. Smaller GUDs in the warmer microhabitat would mean that it was more favorable for the forager to stay longer in the patch and leave fewer sunflower seeds behind because they would be incurring less of a thermoregulatory cost.

During the fall and winter (September 2013-March 2014), feeding trays were placed at the study site at 0830 h and collected at 1630 h. The sunflower seeds that remained in the trays were sifted out of the sand and weighed to measure GUD. Any debris, such as twigs, that got mixed in with the seeds during the day was removed before weighing GUDs. Higher GUDs were interpreted to mean that foraging was more costly, and less foraging occurred, resulting in a larger amount of sunflower seeds being left in the feeding tray. Lower GUDs were concluded to mean that foraging was less costly, more foraging occurred, and fewer seeds were left behind. The light and temperature data were retrieved from the loggers on a weekly basis, and then the loggers were reprogrammed.

Data analysis

After measuring skewness with Fisher's coefficient, we used logarithmic transformations of GUDs (i.e., weights of seeds left after foraging) as a means of normalization (Brown et al. 1992). Treating the two feeding trays (under canopy and in the open) at each tree as paired, repeated measures analysis of variance (ANOVA) was used to examine whether GUDs differed between feeding trays over time and between feeding areas. For the deciduous trees, GUDs were grouped into periods when the trees had 90% canopy and 0% canopy. Canopy percentages were visually estimated. The evergreen trees always had full canopies, so they were grouped according to the months that corresponded with either 90% canopy or 0% canopy. September and October corresponded to a full canopy, and March was the time when the deciduous trees had 0% canopy. Paired t-tests were used to compare GUDs in the open to GUDs under the canopies of the deciduous trees and the two evergreen trees during the 90% and 0% canopy periods. Temperatures recorded by the HOBO Pendant Temperature and Light Data Loggers were also compared using t-tests to determine if there was a significant difference between temperatures under cover and in the open. Analyses were performed with StatPlus, Microsoft Excel, and VassarStats (vassarstats.net).

Results:

GUD was compared in the open and under the canopy of two deciduous trees and two evergreen trees. Comparing GUD in the open and under the canopy of deciduous trees, which seasonally lose their leaves, and in the open and under the canopy of evergreen trees, which retain their canopy year-round, was done to determine if the canopy cover or the distance to shelter was a more significant cue of predation risk to foragers in urban areas. Data from the two sites were pooled for analysis because there was no effect of site on cover versus open GUDs at the deciduous trees ($F_{1,66} = 1$; $p = 0.32$) or the evergreen trees ($F_{1,66} = 1,5$; $p = 0.23$). When the deciduous trees had 90% canopy, GUD was lower under cover than in the open ($t_{31} = -8.6$; $p < 0.001$) (Fig. 3). When the deciduous trees had lost their leaves and had 0% canopy, GUD was also lower under cover than in the open ($t_{26} = -2.58$; $p = 0.016$) (Fig. 3).

The evergreen trees maintained their canopies throughout the study period. During the months of September and October the deciduous trees had full canopies and during the month March the deciduous trees had no canopy. In September and October, GUD was higher outside of the canopy of the evergreen trees than it was under the canopy ($t_{62} = -6.11$; $p < 0.001$) (Fig. 4). In March, GUD was also higher outside of the canopy than it was under the canopy of the evergreen trees ($t_{26} = -5.77$; $p < 0.001$) (Fig. 4).

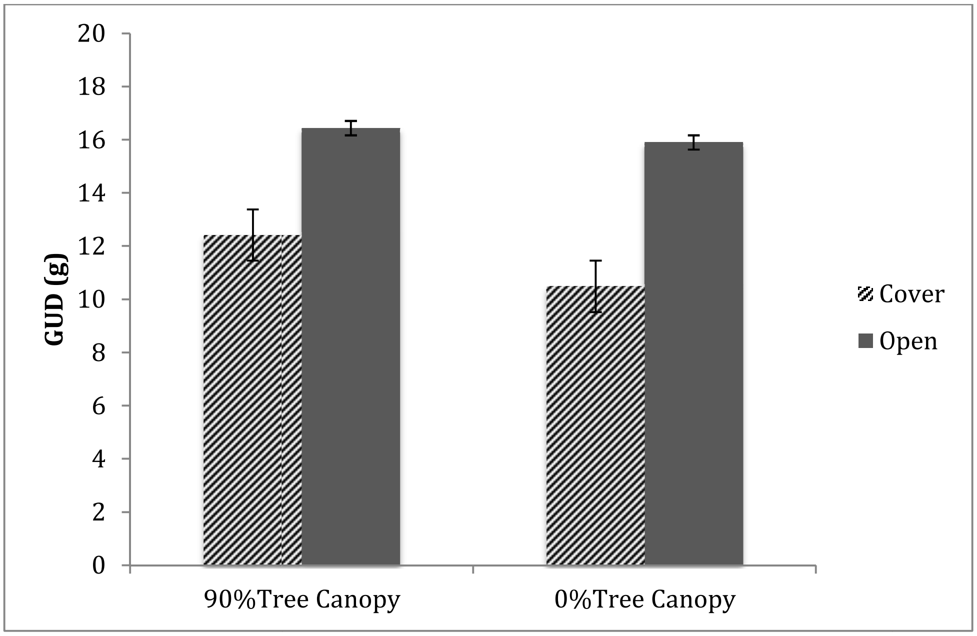

Figure 3: The effect of canopy cover and distance to shelter on GUD of gray squirrels at deciduous trees. GUD was lower under cover than in the open regardless of canopy foliage. Error bars represent one standard error (n = 46).

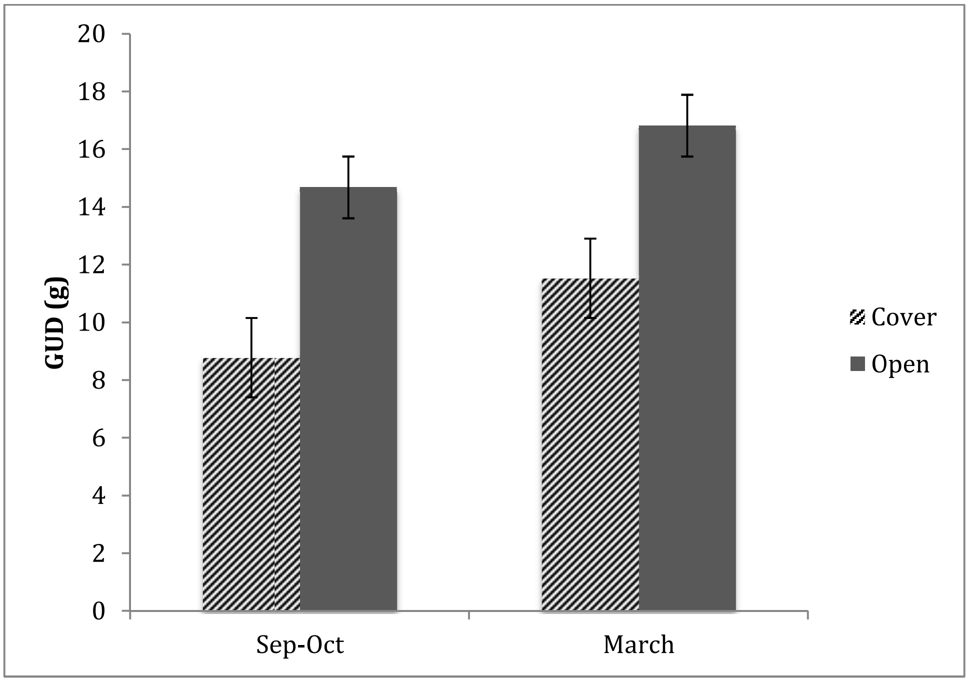

Figure 4: The effect of canopy cover and distance to shelter on GUD of gray squirrels at evergreen trees. GUD was smaller under canopy cover than in the open. Error bars represent one standard error (n = 46).

Temperature was recorded under the canopy and outside of the canopy for the two deciduous and two evergreen trees in order to determine if thermoregulatory costs are a significant cue to foragers. At all four trees, there was no difference in the temperature under the canopy cover and the temperature outside of the canopy cover (paired t-tests; $p > 0.1$) (Fig. 5). However, when the temperatures were compared under cover and in the open on a monthly basis, one difference was found. Temperatures in the open were lower than temperatures under cover during November only at the evergreens ($t_{19} = 2.99$; $p = 0.008$). In all other months, there was no difference between cover and open temperatures. There was no proportional relationship between temperature and GUD under cover at any of the four trees (Fig. 6). There was also no proportional relationship between temperature and GUD in the open (Fig. 7).

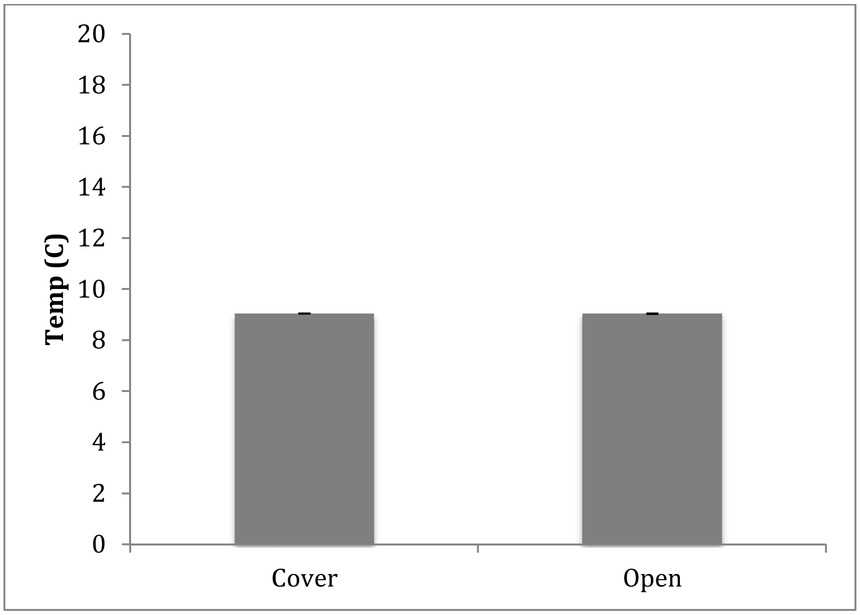

Figure 5: The temperature under canopy cover and in the open for the two deciduous trees and the two evergreen trees for the entire study period. There was no difference between the temperature under cover and the temperature in the open. The error bars represent one standard error (n = 136).

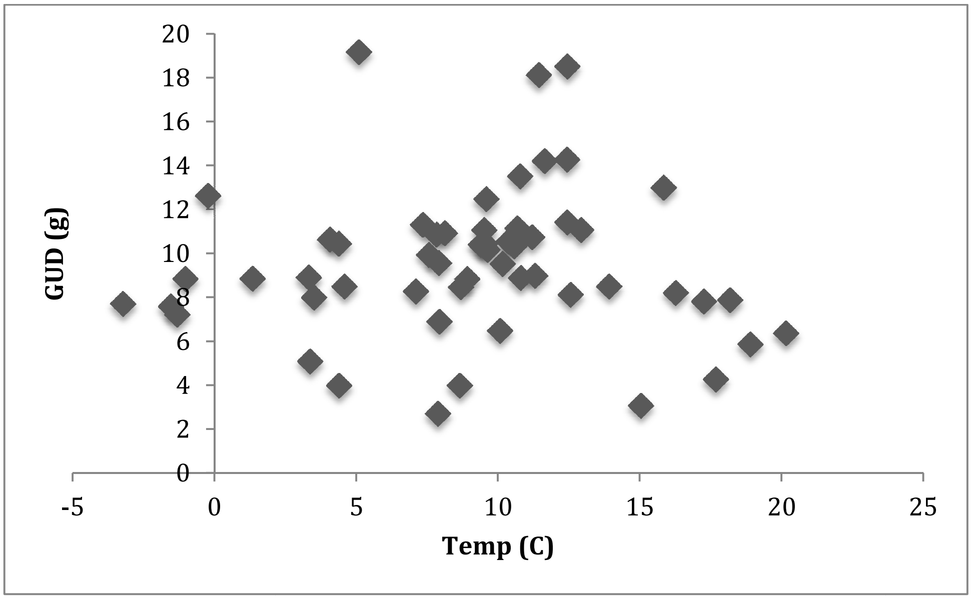

Figure 6: The relationship between GUD of gray squirrels under cover and temperature under cover at all four trees.

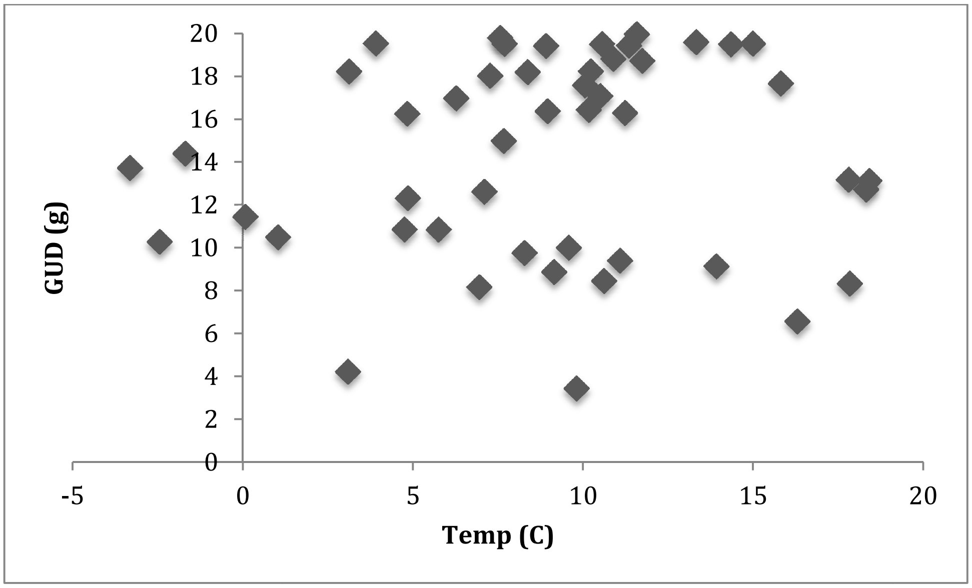

Figure 7: The relationship between GUD of gray squirrels in the open and temperature in the open for all four trees.

Seasonal effects were tested by comparing the relationship between GUD under cover and GUD in the open for each month of the study. For the deciduous trees (Fig. 8), month had a significant effect on overall GUD ($F_{3,62} = 6.25$; $p < 0.001$). GUD under cover and in the open were both lower in November than during other months. The microhabitat of the feeding tray (under cover or in the open) had a significant effect throughout the study ($F_{1,62} = 83$; $p < 0.0001$), with GUD under canopy always lower than GUD outside the canopy. However, there was no interaction between microhabitat and month on GUD ($F_{1,3} = 1$; $p = 0.40$). At the evergreen tree sites (Fig. 9), month had a marginally significant effect on overall GUD ($F_{3,62} = 2.5$; $p = 0.07$). Again, GUD was lower in November than in other months. Microhabitat of feeding trays at the evergreens had a significant effect throughout the study ($F_{1,62} = 96$; $p < 0.0001$), with GUD under canopy always lower than GUD outside the canopy. There was a significant interaction between microhabitat and month at the evergreen sites ($F_{1,3} = 4$; $p = 0.01$).

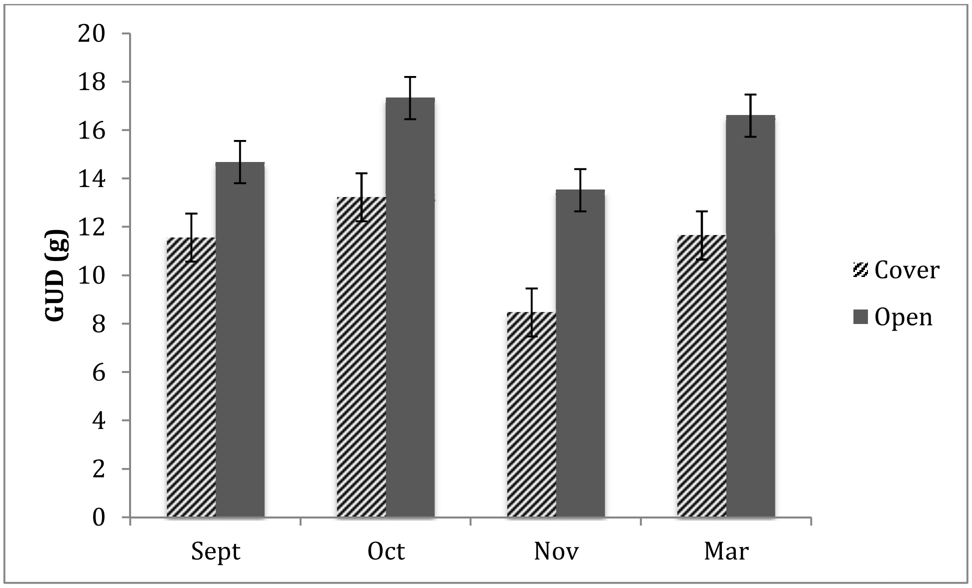

Figure 8: Cover GUD compared to open GUD at the deciduous trees for each month of the experiment. The month had a significant effect on GUD, but there was no interaction. The error bars represent one standard error (Sept: n = 8; Oct: n = 24; Nov: n = 20; Mar: n = 14).

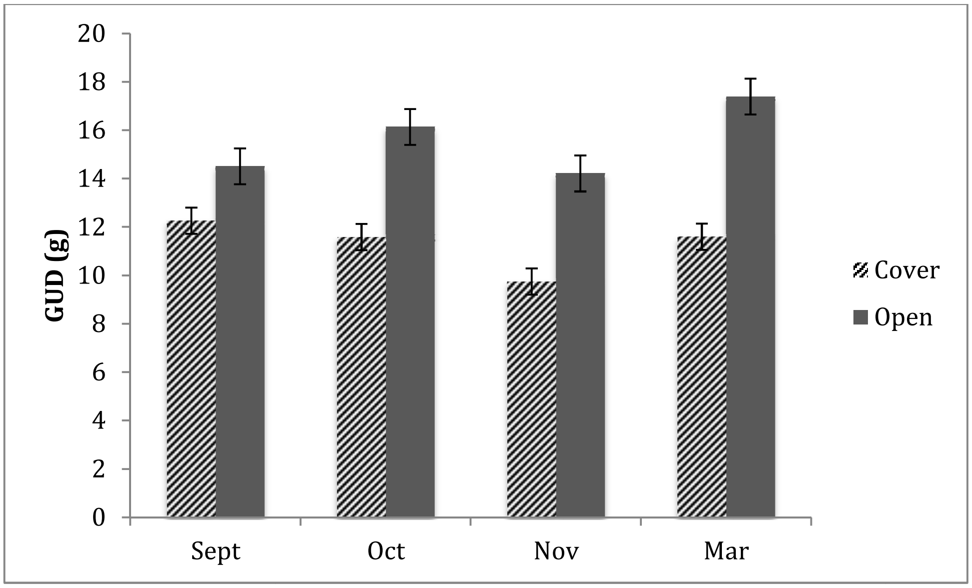

Figure 9: Cover GUD compared to open GUD at the evergreen trees for each month of the experiment. The month had a significant effect on GUD, but there was no interaction. The error bars represent one standard error (Sept: n = 8; Oct: n = 24; Nov: n = 20; Mar: n = 14).

Discussion:

Thermoregulation Costs Versus Predation Risk

Thermoregulatory expenditures and predation risk are both costs that are incurred by foragers and must be taken into account to achieve optimal foraging. Kilpatrick (2003) found that at cold temperatures more foraging by gray squirrels occurs in the open rather than under vegetative cover despite the increased predation risk because the forager expends less energy to maintain its body temperature relative to the increased risk of predation. The present study compared temperatures under canopy cover and in the open as well as GUD under canopy cover and in the open. The purpose was to determine whether Kilpatrick's findings could be duplicated and to determine whether thermoregulation cost or predation risk is more significant to foragers. If it was warmer in the open and GUD was lower in the open, it would be possible to conclude that thermoregulation costs have a greater impact on foraging behavior than predation risk. If it was warmer in the open and GUD was lower under cover, it would be determined that lessening predation risk was more beneficial to the forager than reducing thermoregulation costs.

There was no difference between temperatures at the open trays and temperatures at the under-canopy trays for any of the trees that were used in this experiment (Fig. 5). Additionally, GUDs were always greater in the open than under the canopy of the deciduous trees (Fig. 3, Fig. 8) and the evergreen trees (Fig. 4, Fig. 9). GUDs were independent of ambient temperatures in this study (Fig. 6, Fig. 7). These results do not support Kilpatrick's (2003) findings that GUD is temperature-dependent in the open at low temperatures because sunlight increases temperatures and reduces thermoregulation costs to foragers (Kilpatrick 2003). Instead, these findings demonstrate that temperature didn't change significantly between open areas and covered areas and that there was no relationship between temperature and GUDs in the open or under canopy cover.

In November, temperature was greater under the cover of the evergreen trees than it was in the open. This finding also disagrees with Kilpatrick's (2003) conclusion that temperatures are warmer in the open due to higher levels of sunlight. Instead, these results suggest that the ability trees to act as a windbreak might play a greater part in affecting the temperature of the covered microhabitat than sunlight does in affecting the temperature of the open microhabitat. However, because the HOBO data loggers did not measure wind speed, this study could not confirm that differences in convective cooling were responsible for the differences in temperature between the open areas and the areas under canopy cover. More research is needed to determine the cause of the disparity in temperature. Additionally, during November when there was a difference in temperature, there was no difference in the relationship between open and cover GUDs (Fig. 9). Because both predation risk and thermoregulatory costs were reduced under the cover of the evergreens in November, a greater disparity between GUD under cover and GUD in the open would be expected if thermoregulatory costs are significant to foragers. However, the relationship between GUD in the open and GUD under cover remained consistent despite a significant difference in temperatures between the two areas. This shows that temperature, and therefore thermoregulatory costs, are not as important to foragers as predation risk.

Because GUD was lower under cover where predation risk is lower, the results of this experiment agree with other studies that have found predation risk to be a significant cue to foragers and that foragers adjust their behavior to limit predation risk (Brown et al. 1992, Hughes and Ward 1992, Thorson et al. 1997). Whether in rural or urbanized habitats, foragers consistently engage in behaviors, such as foraging under cover, that reduce predation risk. Thus, despite predation levels generally being lower in urban areas than in rural areas, predation risk is still a significant cue to urban foragers (Mccleery 2009).

Based on the findings of this experiment, it can be concluded that predation risk has a significant effect on foraging behavior because there were lower GUDs under cover where predation risk was lower. Because there was no difference in temperature between areas in the open and areas under cover and no relationship between temperature and GUD (Fig. 6, Fig. 7), it was concluded that temperature, and therefore thermoregulatory cost, does not affect whether an animal forages in the open or under cover. The results showing that when temperature was greater under cover than in the open and the relationship between GUD under cover and GUD in the open did not change further supports the conclusion that thermoregulation costs are not significant to urban foragers. Orrock and Danielson (2009) found that at low temperatures, foraging is limited due to thermoregulation costs, but thermoregulation costs only affect foraging behavior when other costs, specifically predation risk, are limited. In this experiment, all of the observed temperatures were below the eastern gray squirrel's lower critical temperature, 25 °C (Ducharme et al. 1989), and other foraging costs were not controlled. Thus, it was not possible to determine if there is a difference in GUD at temperatures above and below a forager's lower critical temperature. Despite GUD being unaffected by temperature in this study, foraging behavior can be influenced by temperature in other ways. When a forager incurs significant thermoregulatory costs while foraging, it is beneficial for the forager to limit the time they spend exposed to extreme temperatures. Therefore, they use time-minimizing foraging behavior in which they forage more quickly and less often throughout the day. However, adjusting foraging behavior to limit exposure to extreme temperatures does not affect responses to predation risk (Bozinovic and Vasquez 1999).

Because this experiment was conducted at low temperatures, it was also not possible to draw conclusions about foraging behavior at extremely high temperatures. Other studies have shown that animals can adjust their foraging behavior to adapt to extremely high temperatures as well as extremely low temperatures. If high temperatures cause an animal to be under thermoregulatory stress, they may forage less or not at all. They may also collect food in the hot environment and then move to a cooler one to consume it to lessen their thermoregulatory costs (Bozinovic and Vasquez 1999, Bozinovic et al. 1999). In addition to reducing thermoregulation cost by moving to a less stressful environment, animals also adjust the timing of foraging to avoid extreme temperatures. For example, the gray squirrel changes its foraging times to early morning and evening to avoid the midday heat during the hottest summer months (Gurnell 1987).

Future research on thermoregulation costs and foraging behavior could be conducted over the course of a year so that a wider range of temperatures would be observed. By comparing GUD below an animal's lower critical temperature, within the animal's optimal temperature range, and above the animal's upper critical temperature, it would be possible to gain a better understanding of how temperature affects foraging behavior. Also, direct observation of foragers over a wide range of temperatures could confirm that animals adjust their behavior in ways such as gathering food at extreme temperatures and then moving to more moderate temperatures to consume it (Bozinovic and Vasquez 1999, Bozinovic et al. 1999).

Additionally, the HOBO Pendant Temperature and Light Data Loggers used for this study were unable to measure wind speeds. It would be interesting to measure wind speeds under cover and in the open to see if there is a difference in foraging behavior, and to compare GUDs on windy and calm days to see if convective cooling affects foraging behavior. The wind-chill factor may influence an animal's heat exchange with the environment more directly than sunlight. Also, humidity could be measured on hot days to see if a heat humidity index correlates more with foraging than simple temperature readings.

Vegetative Cover Versus Distance to Shelter

Vegetative cover and distance to shelter are both significant cues of predation risk for foragers. Brown et al. (1992) and Orrock et al. (2004) found that more foraging occurs under cover, and Lima et al. (1985) and Thorson et al. (1997)

found that more foraging occurs at sites that are closer to shelter. However, very little work has been done to determine if vegetative cover or distance to shelter has a greater impact on a forager's perception of predation risk. Khan (2010, Trinity College, unpublished data) found that when deciduous trees had a full canopy, GUD was higher in the open than under cover, and when the trees lost their leaves there was no difference between GUD in the open compared to GUD under the canopy. I compared GUDs within the canopy and outside of the canopy of two deciduous and two evergreen trees at the same study site as Khan. If GUD patterns changed at deciduous trees when they lost their leaves, it would be concluded that vegetative canopy cover was a more significant cue of predation risk than distance to shelter. If GUD patterns did not change at the deciduous trees when they lost their leaves, it would be determined that distance to shelter, rather than vegetative cover, had a greater affect on foraging behavior.

When the canopies of the deciduous trees were at 90%, GUD was higher in the open. When the deciduous trees lost their leaves and had 0% canopy, GUD remained higher in the open than under the cover of the canopy (Fig. 3, Fig. 8). September and October corresponded to the time when the deciduous trees had full canopy coverage. During this period, GUD was higher in the open than under the canopies of the evergreen trees. Similarly, March corresponded to the time when the deciduous trees had no canopy, and GUD was greater in the open than under the canopies of the evergreen trees during this time (Fig. 4, Fig. 9). The results of this experiment were consistent with the findings of others (Lima et al. 1985, Brown et al. 1992, Thorson et al. 1997, Orrock et al. 2004) that both vegetative cover and a shorter distance to shelter independently result in lower GUDs. However, the results were not consistent with Khan's findings that when deciduous trees lose their leaves there is no difference in GUDs in the open versus under the canopy of the tree. The results of this study also show that distance to cover has a greater affect on foraging behavior than canopy cover does.

The number of terrestrial predators is limited in urban areas, and the Red-tailed Hawk is the primary predator of the gray squirrel in urban areas (Ditchkoff et al. 2006). Therefore, it would be expected that squirrels would seek to be shielded from view and canopy cover would be significant. However, the results of this study showed that even when deciduous trees had no leaves, more foraging still occurred under the canopy. It is possible that the branches alone, with no leaves, provided the squirrels with a lessened perception of predation risk because the branches visually shield them to some degree. Future research could determine whether the density of branches is significant to foragers because a greater branch density would shield the foragers more from avian predators than a lower branch density. It could also be that the branches prevent avian predators from directly reaching their prey. This could provide the foraging squirrels with enough time to escape predation and could explain why it is more favorable to forage under the canopy even when foragers are not completely visually concealed from avian predators.

It may be more beneficial for foragers if a full canopy was not present. If a full canopy were present, the forager's view would also be obstructed and could prevent detection of an avian predator. Other research has shown that vigilance and visual obstructions that hinder vigilance affect foraging behavior. Gray squirrels that are foraging in areas that have either lateral or overheard visual obstruction change their positions to enhance their ability to scan the environment (Makowska and Kramer 2007). Future research could incorporate more direct observation of behavior to see how vigilance behavior is adjusted under trees with full canopies and no canopies.

Another possible explanation as to why GUD was lower under the canopy than it was in the open could be that it required less energy to get to the feeding tray at the foot of the tree. If a squirrel spent time in the tree where the feeding trays were located, the tray under the canopy would require less travel time and less energy expenditure to get to. Energy expenditure and travel time to a patch are both costs of foraging that should be reduced in order to optimize foraging behavior (MacArthur and Pianka 1966). Limiting travel time and reducing energy expenditure could also potentially reduce missed opportunity costs because time and energy not spent on travelling to a foraging patch can be devoted to other activities such as mating. Future research could examine how far the feeding trays are from trees with nests, and direct observation could make it possible to determine where the foragers are coming from to forage at feeding trays. Exploring this possible explanation would provide very useful insight into urban foraging behavior. Because there are fewer predators in urban areas than there are in rural areas it would make sense that energy expenditure and travel time could have a larger impact on urban foraging behavior where predation risk is not as significant (Ditchkoff et al. 2006).

Missed opportunity costs could also be influenced by the marginal value of food, not only travel time and energy expenditure. Brown et al. (1992) found that if the food supply was augmented, the marginal value of food was diminished and GUD increased. The results of the present study showed that there was a seasonal effect on GUDs. At the deciduous trees in November, GUDs under cover and in the open both dropped significantly. However, there was no interaction between the month and the placement of feeding trays (under canopy or in the open) (Fig. 8). In November, foragers prepare for winter by increasing their food intake. During this time, the marginal value of food is increased, and therefore, so are missed opportunity costs. However, despite the greater missed opportunity costs, the relationship between GUDs under cover and the open remained the same. More foraging occurred at both sites when the marginal value of food increased, but more foraging still occurred under cover than in the open. Increasing the marginal value of food resulted in more risk taking because more foraging occurred in the open when food was more valuable, but the perception of predation risk in the open relative to under cover remained constant as foraging under cover was still favored over foraging in the open. In urban areas, there is often less food available to foragers, and there is a lower risk of predation (Bowers and Breland 1996, Mccleery 2009). Therefore, it might be expected that the marginal value of food and missed opportunity costs would be more significant than predation risk in urban areas. Based on the results of this study, it appears that while an increased marginal value of food increases foraging overall and promotes risky behavior, it does not lessen the importance of predation risk.

These findings showed that GUD was consistently lower under canopy cover regardless of whether the canopy is full, which suggests that distance to refuge was a more important cue of predation risk to foragers than is vegetative cover. However, there are other possibilities that could explain these results, and further research would provide a more definitive conclusion.

Other Variables

There were seasonal effects on GUDs at both the deciduous trees and the evergreen trees. At the deciduous trees, there was no interaction between month and tray placement (under cover or in the open), and the relationship between GUD under cover and GUD in the open remained constant throughout all four months of the experiment (Fig. 8). For the evergreen trees, both month and the placement of trays (under canopy or in the open) had significant effects on GUDs, and there was a significant interaction between month and tray placement. The disparity between GUDs under cover and GUDs in the open increased as the months progressed, and there were lower GUDs in November both under cover and in the open (Fig. 9). It is possible that more foraging could have occurred under cover over time due to learning on the part of the squirrels, but this does not explain why there was only an interaction between month and microhabitat (cover or open) at the evergreen trees but not the deciduous trees. Another possibility could be that the threat of predation risk was greater in March than during the other months. Red-tailed Hawks were observed more frequently in March than during the other months. As many as three hawks were observed during one day, and the increased presence of

Red-tailed Hawks may explain why foraging under the cover of the canopy trees was favored more heavily. More research is needed to be able to explain the interaction between month and microhabitat.

Beginning in March, a Day 6 Outdoors Plotwatcher camera was set up at each tree to ensure that gray squirrels were the only animals foraging at the feeding trays. Birds also visited the trays, but most did not stay longer than ten to twenty seconds. There were also no photographs of the birds holding or eating the sunflower seeds. Therefore, the resulting GUDs are from gray squirrel foraging.

It was also hoped that the cameras could provide information about feeding times of the gray squirrel. The cameras captured images of the squirrels foraging at various times throughout the entire eight-hour period, 0830 to 1630 h. A larger sample size would be needed to determine if there are certain times at which gray squirrels feed. In this study, a large sample size was not possible because the cameras were ordered and received late in the study. After the cameras were received, their use was limited due to inclement weather. However, the trays were most commonly visited between one and two times per day. At most, the tray under the canopy of an evergreen tree was visited four times in one day. Some trays were not visited at all during certain days.

Weather did not only limit camera use, it also limited the days that feeding trays could be put out, and therefore reduced the sample sizes of GUD and temperature measurements, particularly during the month of March when the deciduous trees had 0% canopy. Due to the deep snow it was not possible to put trays out at all in February because they would sink into the snow.

The months of winter during 2014 were some of the coldest recorded in Hartford, Connecticut, and also had unusually high levels of precipitation, namely snow (Murphy 2014). The weather hindered this experiment to some degree, but in terms of GUD and temperature, enough data were collected to determine that there were no significant temperature differences between areas under cover and in the open. Therefore, in this study GUD was independent of temperature.

This study provides evidence that predation risk is more significant to foragers than thermoregulation cost. However, even though GUDs were independent of temperature, foraging efficiency may be affected by thermoregulation costs (Bozinovic and Vaquez 1999). Future research could examine foraging behavior using a measurement other than GUD, such as patch residence time, which could be monitored by Plotwatcher cameras. The data collected also made it possible to determine that distance to shelter is a more significant cue of predation risk than vegetative cover because GUDs were lower under the canopy covers of all trees, including the deciduous trees that had lost their leaves. Despite urban animals becoming habituated to humans and having reduced anti-predatory responses, perception of predation risk has an impact on foraging behavior (Parker and Nilon 2008, Engenhardt and Weladji 2011). Therefore, the affects of microhabitat on foragers' perception of predation risk and foraging behavior must be taken into account when considering the conservation and management of urban wildlife.

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