

Foraging decisions under the risk of predation: does habitat type influence rodent foraging?

BIOS 355022: Practicum in Environmental Field Biology

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Abstract

Prey animals must balance foraging with anti-predator behaviors to increase fitness in areas where predation risk is present. This perception of risk is determined by habitat features such as canopy cover and ground cover which can hinder predators' ability to hunt. In this study, I measured predation risk perceived by nocturnal rodents in a forest setting by comparing giving-up densities (GUDs), or the amount of seeds left in an artificial patch, in open versus covered patches, as well between three forest types (*Acer saccharum* forests, mixed deciduous forests, and coniferous forests). Additionally, I attempted to correlate GUDs to habitat structure measurements of canopy cover, ground cover, ground cover height, and total vegetation volume. Despite the complexity of forest structures, closed patches had significantly less GUDs across all habitat types; however, no other correlations were found between GUDs and vegetation measures. This suggests that rodents utilize microhabitat cover structures as a measure of predation risk as opposed to overall habitat type or structure

Introduction

While foraging is critical for animals, it is also necessary for them to engage in other behaviors that contribute to fitness such as anti-predator behaviors, mate selection, reproduction, territorial defense, and nest preparation (Brown 1988). Predators influence such behaviors as prey animals alter their

activities to avoid getting killed (Lima and Dill 1990). Examples of anti-predator behavior include vigilance to cues of predator presence, group formation, reduction of foraging time to increase vigilance, and choosing habitat patches that minimize discovery by predators (Altendorf 2001). Optimal foraging theory predicts that when foraging in a patch under predation pressure, animals balance the energetic rewards of foraging with risks associated with predation in order to maximize energy intake and fitness (Pyke 1984, Brown 1988). Essentially, animals may trade the rewards of foraging for safety in order to increase survival, for instance, by choosing patches that may not be as energetically rewarding, but are safer from threat (Altendorf 2001).

A prey animal's perception of predation risk has been shown to be dependent on microhabitat features, namely canopy cover and ground cover (Kotler et al. 1991, Korpimaki et al. 1996, Orrock et al. 2004). Rodents are particularly good study subjects due to the wide array of organisms that prey upon them, including birds, mammals, and reptiles (Orrock et. al 2004). In a controlled experiment, Kotler and others (1996) found that in the presence of owls, rodents were more likely to be found foraging under brush cover. While brush cover provides refuge from avian predators, it also provides stalking cover for terrestrial predators including reptiles and mammals, thus may encourage rodents to avoid such cover where terrestrial predators are more prevalent (Kotler et al. 1991, Orrock et. al 2004). Interestingly, while these indirect cues (as in factors not

directly inferring to predator behavior) have been shown to have a strong effect on foraging behavior, direct cues of predator presence has been found to have a less significant effect (Orrock et al. 2004).

Rodent foraging behavior has been measured with several methods, including direct observation, measurement of giving-up times (GUT), and trapping. One method of measuring predation risk, called the giving-up density (GUD), is based on the marginal value theorem which states that foragers should leave a patch when its resource density is depleted to the average resource density of the surrounding areas (Charnov 1976). If the forager is under predation risk, however, the forager may choose to leave the patch before reaching the average resource density, thereby “giving up” food in order to avoid getting killed (Brown 1988, Brown 1997). As a result, the amount of food remaining in foraging patches can be used to assess a forager’s perceived level of risk from predators.

This study will use GUDs to measure the impact of microhabitat features on the foraging behavior of small, nocturnal mammals in the forested areas of the University of Notre Dame Environmental Research Center (UNDERC) property. I will test the hypothesis that rodents will preferentially forage in covered patches compared to open patches, as previous studies have suggested. I expect GUDs to be higher in open patches compared to closed ones; however, the abundance of cover at multiple levels within the forest, including the canopy cover and ground cover may confound the effects of cover over a particular patch (e.g. open or

closed patches under heavy canopy cover). Similar studies have been conducted in open field and in patchily wooded habitats, but conducting this in a heavily forested area is a novel aspect to the study (see Brown 1988, Jacob and Brown 2000, Ovadia et al. 2001).

Additionally, I hypothesize that GUDs will be correlated to measurements of habitat structure complexity such as canopy cover, ground cover, and total vegetation volume (here, an index of foliage height diversity). Specifically, I expect that increasing cover or foliage height diversity will hinder the predators' ability to find or capture prey, and thus provide a safer foraging environment, as a result, lowering GUDs in these environments.

Methods and Materials:

Study Site

The University of Notre Dame Environmental Research Center (Gogebic Co., WI) is a 7500 acre tract of land bounded on three sides by the Ottawa National Forest (UNDERC, unpublished). The property represents a wide array of habitat types including sugar maple (*Acer saccharum*) forests, aspen-birch (*Populus* spp. and *Betula* spp.) forests, and conifer forests, in which I will be conducting my study.

Common nocturnal woodland rodents found on property include southern red-backed voles (*Clethrionomys gapperi*) and deer mice (*Peromyscus maniculatus*), and the predators that specialize in the night time hunting of rodents

include American marten (*Martes americana*), fisher (*Martes pennanti*), long-tailed weasel (*Mustela frenata*), and various species of owls (Kurta 1995, Udvardy 1994, Whitaker 1997). While the presence of these predator species has been recorded, their ranges across the property are yet to be determined.

Foraging behavior of rodents

This study was conducted in three vegetation communities, sugar maple forests, mixed deciduous forests, and conifer forests, previously selected for mesocarnivore surveys on UNDERC property (Lemmon, unpublished data). I selected three stands of each forest type using ArcView GIS 3.3 (HCL Technologies, Ltd.; New Delhi, India) and within each stand, I randomly placed a 4000 m² square grid with care to avoid wetlands (*Figure 1*). Nine foraging stations, each consisting of two foraging patches, were placed in each grid, with stations positioned every 100 m ($n=18$ patches per grid site, see *Figure 2*). Each foraging patch consisted of a brown plastic tray (36 cm x 46 cm x 2 cm) filled with 2.5 g of unshelled sunflower seeds (mean, 51.1 seeds, $n=10$, SE=0.61) mixed with 1.5 L of fine sand. I placed one patch under brush cover (branches about 20 cm above the ground) and the other in the open (i.e. no ground cover) about 2-4 m away.

I conducted this study in three, five night sessions during the summer of 2006 (June 5, 7-11; June 26- July 1; July 16-21). One site from every habitat

subtype was studied during each session. I placed new seeds in the feeding trays every evening between 1700 h and 2100 h, then retrieved the remaining seeds using sieves (gaps=2.5mm) the following morning (500 h ~ 730 h). Collected unshelled seeds were dried and weighed to determine the GUD (Brown 1988, Brown 1997; Choate, personal communication).

Habitat features

Six randomly selected stations within each grid were used to assess habitat features that influence predation risk. I measured percent canopy cover using a concave spherical densitometer at the station site (centered between 2 foraging trays) as well as 10 m away in the bearings of 0°, 120°, and 240°, facing each of the cardinal directions at every point ($n=16$). These percentage cover measurements were averaged (mean) to give the estimated canopy cover over the entire station (Francl, personal communication).

At these same points, I measured vegetation volume (here, an index of vertical stratification) with protocols used in Mills et al. (1991) with some adjustments: I raised a 4.5-m range pole with markings at 50 cm increments and counted the number of the increments that touch vegetation (touched increments, or “hits” range from 0-1 for every half meter; Mills et. al 1991, Francl, personal communication; $n=4$). Range poles were lifted 0.5 m off the ground to extend measurements to 5 m above the ground. I calculated the total vegetation volume

(TVV) as:

$$TVV = h/10v$$

where “h” is the total number of hits over the entire sampling area and “v” is the number of replicates in the sampling area ($n=4$, Mills 1991). Additionally, at each of these four points, I measured the height of ground cover provided by low lying plants not including coniferous trees.

Percent ground cover was measured by placing a 1 m² quadrat on the ground at three random points along three 10 m transects that extended 0°, 120°, and 240° away from the station center. A quadrat frame was marked in 20 cm increments on each side to allow the visualization of 25 cell grids and was used to estimate the percent coverage of the ground by small plants, grasses, small shrubs, and detritus. Values were averaged over the entire station to give an estimated percent ground cover ($n=9$).

Finally, to test our assumptions of habitat subtypes (e.g. maple, deciduous, conifer), we measured tree species composition and density along the three 10-m transects drawn as mentioned for ground cover. Each tree with a dbh >10 cm found within 0.5 m on either side of the transect was counted and dbh measured.

Statistical Analysis

SYSTAT 11.0 (SYSTAT Software, Inc.; Point Richmond, CA) was used to analyze all data collected in this study. I ran separate ANOVA and Kruskal-

Wallis tests for comparing grids of the same habitat type to determine the degree of similarity within the habitat types followed by similar tests to compare differences between habitat types. p -values ≤ 0.05 were considered significant.

I compared GUDs between open and closed patches, among the three different vegetation communities, as well as between study sessions using a nested, repeated measures multi-way ANOVA (general linear model procedure, GLM), using sampling nights as the repeated measure, and grid sites nested within habitat types. Finally, I assessed potential correlations between vegetation measurements and average GUDs of a given grid via a correlation analyses that provided Bonferroni probabilities.

Results

Vegetation measurements

Conifer forests had a significantly higher conifer tree density compared with the other two forests ($p=0.037$, $U=9.0$, $df=2$ against both maple and deciduous forests; *Fig. 2*). Sugar maple and non-maple deciduous tree densities were analyzed using one-way ANOVA. Sugar maple densities were not significantly different between the habitats, even though the sugar maple forest had the highest density of the three habitat types (2.5 ± 0.452 trees per 30 m^2 ; *Fig. 2*). Similarly, differences in non-maple deciduous tree density between the habitats were not statistically significant, even though the deciduous habitats had

the highest density (2.167 ± 0.579 trees per 30 m^2 ; *Fig. 2*). In order to determine if the habitat measurements were more variable between habitat classifications than among grids within a classification, I conducted Kruskal-Wallis one-way analyses of variance tests between grids of the same habitat type. Across all grids, only sugar maple densities varied significantly within coniferous forest classification ($p=0.019$, $U=7.937$, $df=6$)

Habitat structure measurements were compared between the three habitat types using Kruskal-Wallis analyses for percent canopy cover (since the data were not normally distributed and transformations failed to normalize them) and ANOVA for TVV, ground cover height, and percent ground cover (*Table 2*). No significant differences were found at the habitat level; however, conifer forests had a biological trend towards having less canopy cover ($p=0.066$).

GUD analyses

Overall, 803 GUDs were measured over three 5-night study periods ($n=401$ for open, $n=402$ for closed patches, ~ 270 for each habitat). Mean GUD for all open patches was 1.800 ± 0.057 g (mean \pm SE) and 1.594 ± 0.056 g for all closed patches.

To determine the effect of tray cover (or microhabitat) and habitat on foraging behavior, I used data from all habitats and compared GUDs (transformed to the power of 8) in open and covered patches as well as between habitats using

an ANOVA repeated measures analysis where nights were the repeated variables (*Table 1*). Values for Greenhouse-Geisser Epsilon and Huyhn-Feldt Epsilon were 0.947 and 1.000; thus the model error was acceptable for this analysis. Between subject analyses revealed that GUDs were significantly lower (see *Table 1*) in covered patches, with a mean of 1.595 ± 0.053 g compared to 1.800 ± 0.052 g in open patches. Additionally, deciduous forests had significantly higher GUDs compared to conifer and maple forests with a mean of 2.084 ± 0.052 g (averaged over the 3 deciduous sites for both microhabitat types ($F=$, $p<0.000$). The interaction between habitat and microhabitat was not significant ($p=0.675$). Additionally, the within factor analyses of GUDs revealed that night had a significant effect, where GUDs on the fifth study night were almost always lower than GUDs of the first night ($p<0.000$, *Fig. 4*). There was an interaction between nights and the grids that were nested within the habitat types ($p<0.001$), which can be observed as a general lack of variance in GUDs over the five nights during the first research session compared to the other two research sessions (see *Figure 4*). Furthermore, GUDS declined across sampling sessions, particularly between the first and last sessions ($p<0.000$, *Figure 5*).

Finally, correlation analyses were conducted to test if vegetation measurements averaged over grids were related to the average open and closed GUD values of the same grid. No significant correlations were uncovered

between GUDs and TVV, ground cover height, percent ground cover, or percent canopy cover (*Table 3*).

Discussion

At the finest spatial scale, rodents indeed preferentially forage in covered patches as opposed to open ones even in forested habitats. This is in agreement with previous studies conducted in open woodland and desert habitats that provided little, if any, canopy cover besides the brush cover under which the covered patch was placed (Brown 1988, Kotler et al. 1991, Orrock et al. 2004). Since this finding was consistent over all three forest habitat subtypes (sugar maple, mixed deciduous, and coniferous), this suggests that rodent anti-predator behavior is likely not related to species composition. Rather, rodents may choose habitats according to structural characteristics that offer protection such as canopy cover, ground cover, and foliage height diversity rather than species composition alone.

GUDs were significantly higher in mixed deciduous forests compared to maple and coniferous forests, suggesting that this environment presents more risk to foraging rodents. To determine whether this difference is based on the physical structure of the vegetation, I tested for correlations between GUDS and percent canopy cover, TVV (as an indicator of vertical stratification of vegetation), percent ground cover, and the height of the ground cover of each habitat type.

Mixed deciduous forests did not differ significantly from the other habitat types in any feature except for canopy cover, which was greater than canopy cover in conifer forests but less than that of sugar maple forests. Based on my hypothesis, I expected habitats with more canopy cover to be less risky for rodents, and thus have lower GUDs. The opposite effect is seen here, where a habitat with less canopy cover (conifer forests) has lower GUDs than an area with more canopy cover. In fact, vegetation surveys suggest that mixed deciduous forests may potentially provide better cover for rodents at all forest strata compared to conifer and maple forests. On the other hand, maple forests and conifer forests had similar GUDs despite a significant difference in canopy cover, as well as minor differences in ground cover and TVV measurements. Habitat structure, then, may not provide a good indicator of predation risk in forested areas. The lack of correlations between GUDs and habitat structure measurements at the grid level confirm this idea. Although this is seemingly contradictory to the significant effect that patch cover has on decreasing GUDs, it is possible that microhabitat features are more important than overall habitat characteristics. In other words, no matter how the general habitat is structured, rodents may rely more heavily on the finer spatial scale of microhabitat features to avoid predation. Future studies on this subject should focus on forest habitats that vary greatly in terms of structure as opposed to stratifying habitats according to species composition as I did (e.g. no ground cover vs. all ground covered).

Additional factors that were not measured in this study might have also lowered the marginal value of the artificial food patches in mixed deciduous forests, thus making them less desirable or necessary to visit than observed in during other studies. For example, the mixed deciduous forests have higher densities of red maple (*Acer rubrum*) trees compared to all other sites, which were observed to produce seeds earlier in the summer (i.e. during study session 1). During this period, I observed that a large amount of red maple seeds had fallen in to the feeding trays, alluding to the high density of seeds dispersed throughout the forest. This increase, or augmentation, in food availability has been studied previously by Brown et al. (1992) with fox squirrels (*Sciurus niger*) in a forest edge environment. They demonstrated that if a 2 m radius area around the foraging patch is augmented with a cup of sunflower seeds, GUDs become lower in both the open and covered patches, even if the density of seeds around the patches were lower than in the seed trays (Brown et al. 1992). If red maple seed rain augments the food density of the habitat, then the marginal value (or the difference in energetic rewards of feeding in trays compared to feeding in natural habitat) of the seeds in the feeding trays are decreased, thus increasing GUDs. The importance of cover over artificial patches in my experiment is maintained even in augmented habitats in accordance to Brown's findings (1992).

The significant differences seen in GUDs between the research sessions, particularly between the first and the latter two, may in part be explained by these

red maple seed rains. Graphs comparing study sessions across all grids (*Figure 4*) show that the mean GUDs at all sites for both open and closed were higher during the first study sessions than during the second or the third. This may reflect the pattern of seed dispersal by the red maple trees, where the majority of the seeds are dispersed towards the beginning of the season, then slowly diminishing for the following few weeks. Factors other than natural food availability that could drive seasonal changes in foraging behavior include the breeding status of the community and changes in foliage density and/or cover (Whelan and Maina 2005). It is necessary to conduct more detailed studies on temporal and spatial patterns of red maple seed dispersal and foliage growth, as well as community structure to better understand this interaction.

Another time related variable that significantly impacted GUDs was the length of time that the feeding trays had been in the habitat. In almost all grids and across all study sessions, GUDs decreased towards the end of the five day period. This suggests that rodents either do not find, or are reluctant to visit the newly placed foraging trays, and that rodents do not visit trays randomly. Lack of visitation undoubtedly increases the average GUDs across all spatial scales (no visit=2.5 g of seeds remain in tray), and thus gives an overestimate of predation risk at that level. The decreasing GUDs seen as the session progresses is indicative of the habituation of rodents to the trays.

This suggests that visitation of trays is not random, as assumed by Brown (1988) and by Charnov in his marginal value theorem (1976). During the study session, rodents will find specific foraging trays, remember their locations, and revisit these sites repeatedly through out the week. In essence, this means that predation risk may be a major influence in patch choice by rodents, but it is certainly not the only factor affecting GUD measurements. Price and Correll (2001) tested these assumptions during their study and found that Merriam's kangaroo rats (*Dipodomys merriam*) violated the assumptions by learning the locations of feeding trays and visiting multiple trays within one night, even if resources at any single patch is not depleted. This is counter to Charnov's hypothesis that organisms will forage at one site until the marginal value of the patch is depleted (1976). Even with the rodents' ability to learn, the marginal value theorem may still be applicable: even after the locations of multiple patches are known, rodents still must choose sites at which to forage for longer periods of time. Previous studies have facilitated the learning of feeding tray positions by placing feeding trays out at their respective stations days prior to the commencement of the experiment (see Price and Correll 2001 and Orrock et al. 2004). Another way to decrease the impact of this learning curve is to extend the study sessions beyond five days, perhaps to 14 or more days (Price and Correll 2001).

Two crucial factors were not measured in my analyses on predation risk perceived by rodents. First, I began this study not knowing the rodent density/abundance within the particular grid. This step is necessary since lower densities of rodents would necessarily produce lower visitation patch visitation rates compared to areas with high rodent densities given a similar habitat and food availability. Additionally, I do not know the predator density, distribution, or relative habitat use on UNDERC property. While Orrock et al. (2001) claim that indirect cues of predator presence such as time of day, weather, and vegetation type are more influential in prey foraging decisions, it is still possible that rodents were less willing to visit foraging trays due to high predator densities in the area. Replicates of this study should not be conducted without knowing these densities due to their ability to skew GUD data.

In conclusion, my study demonstrated that microhabitat features (open or closed patches) have a significant impact on rodent foraging behavior; whereas habitat wide vegetation structures such as ground and canopy cover did not. Confounding effects such as season, tree seed dispersal, and the necessity for rodents to get used to the foraging trays potentially affected my results; thus, in order to fully determine the effect of habitat structure on foraging behavior, it is necessary to repeat this study with care to habituate rodents to the patches and avoid seasonal seed dispersal times in addition to measuring rodent and predator abundance within the study sites. This study will not only be useful in delineating

predator-prey interactions, but also determine where and how rodents may affect seed dispersal within forests.

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Tables and Figures

Table 1. Table of multivariate results for repeated measures of ANOVA comparing GUDs (transformed to the power of 8) between microhabitats and habitats and within subjects across nights (5 nights for total $n=162$). Note that grids are nested within its specific habitat type. Additionally, for all factors testing effect of night, p -values were consistent with Greenhouse-Geisser Epsilon and Huyhn-Feldt Epsilon values. Overall, $G-G= 0.9471$ and $H-F= 1.000$; thus the model error was acceptable for the data.

| Factor | <i>df</i> | Mean squared | F-ratio | <i>p</i>-value |
|--------------------------------|------------------|---------------------|----------------|-----------------------|
| Habitat (H) | 2 | 1.08186E+07 | 10.635 | 0.000 |
| Microhabitat (M) | 1 | 4551047.757 | 4.474 | 0.036 |
| HxM | 2 | 400333.541 | 0.394 | 0.675 |
| Site nested in H (Site (H)) | 6 | 1.18966E+07 | 11.694 | 0.000 |
| Error | 144 | 1017291.778 | | |
| Night (N) | 4 | 4341707.158 | 12.554 | 0.000 |
| NxH | 8 | 386223.225 | 1.117 | 0.350 |
| NxM | 4 | 504037.100 | 1.457 | 0.214 |
| NxHxM | 8 | 110150.257 | 0.318 | 0.959 |
| Nx Site(H) | 24 | 1508891.884 | 4.363 | 0.000 |
| Error | 576 | 345848.913 | | |

Table 2. ANOVA outputs comparing total vegetation volume (TVV), ground cover height (GC height), and proportion of ground cover (GC), as well as Kruskal-Wallis analysis outputs for canopy cover differences across three habitat types ($n=3$ per habitat). Canopy cover was not statistically significant, but may show a biological trend where coniferous forests have the least canopy cover.

| Vegetation measure | Mean Maple (SE) | Mean Deciduous (SE) | Mean Coniferous (SE) | df | Mean squared | U | F | <i>p</i> |
|-----------------------|-----------------|---------------------|----------------------|----|--------------|-------|-------|----------|
| TVV (m ³) | 0.29 (0.005) | 0.479 (0.051) | 0.45 (0.073) | 2 | 0.031 | - | 3.411 | 0.102 |
| GC height (cm) | 19.93 (3.13) | 20.278 (7.687) | 16.458 (2.844) | 2 | 13.383 | - | 0.174 | 0.845 |
| GC (out of 1.0) | 0.378 (0.067) | 0.469 (0.116) | 0.572 (0.064) | 2 | 0.028 | - | 1.284 | 0.343 |
| Canopy cover | 0.972 (0.005) | 0.975 (0.006) | 0.884 (0.051) | 2 | - | 5.422 | - | 0.066 |

Table 3. Results of correlation analyses between GUDs of open or closed patches against various vegetation structure measurements. GUD and vegetation values were averaged over entire grids prior to analyses. Note that none of the correlations were significant ($n=9$)

| Vegetation measurement | Open Trays | | | Closed Trays | | |
|------------------------|--------------------------|----|----------|--------------------------|----|----------|
| | Bartlett Chi-square stat | df | <i>p</i> | Bartlett Chi-square stat | df | <i>p</i> |
| TVV | 1.175 | 1 | 0.278 | 2.620 | 1 | 0.106 |
| GC height | 0.678 | 1 | 0.410 | 0.479 | 1 | 0.489 |
| % ground cover | 1.618 | 1 | 0.203 | 2.259 | 1 | 0.133 |
| % canopy | 0.074 | 1 | 0.785 | 0.074 | 1 | 0.785 |

| | | | | | | |
|--------------|--|--|--|--|--|--|
| cover | | | | | | |
|--------------|--|--|--|--|--|--|

Mesocarnivore Survey & Predation Risk Foraging
Experiment
Study Sites 2006

UNDERC
2005 Vegetation Community
Classifications

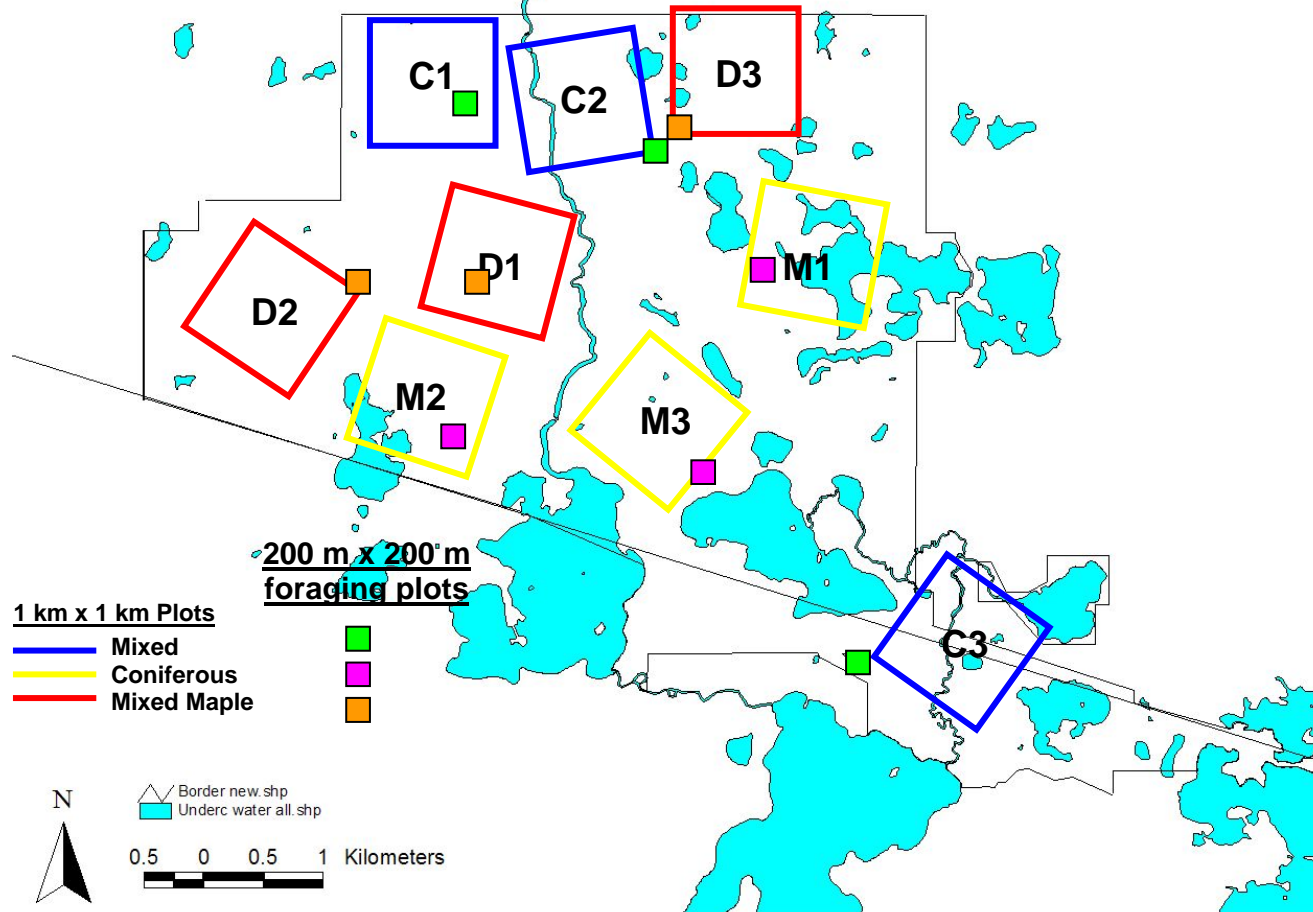


Figure 1. (Former page) Map of study sites scattered across UNDERC property. Three 200 m x 200 m grid was placed in each of three forest types (sugar maple, mixed deciduous, and coniferous). Larger squares indicate locations of a concurrent mesocarnivore survey conducted by Zak Lemmon. Note that the two studies used similar locations but study sessions did not overlap. (Map created by Dave Choate with minor modifications)

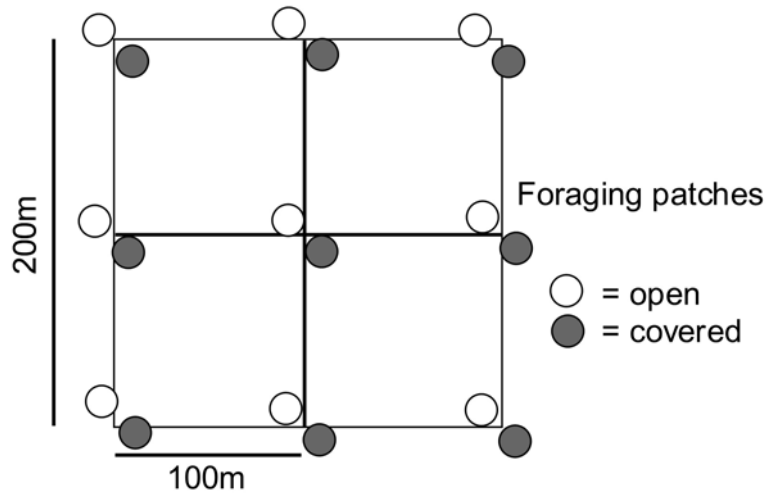


Figure 2. Illustration of grid set up for foraging experiment. Each grid will consist of nine evenly distributed stations with two foraging patches each. One patch will be placed under brush cover of about 20 cm in height and the other patch will be placed 2-4m away in the open ($n=18$).

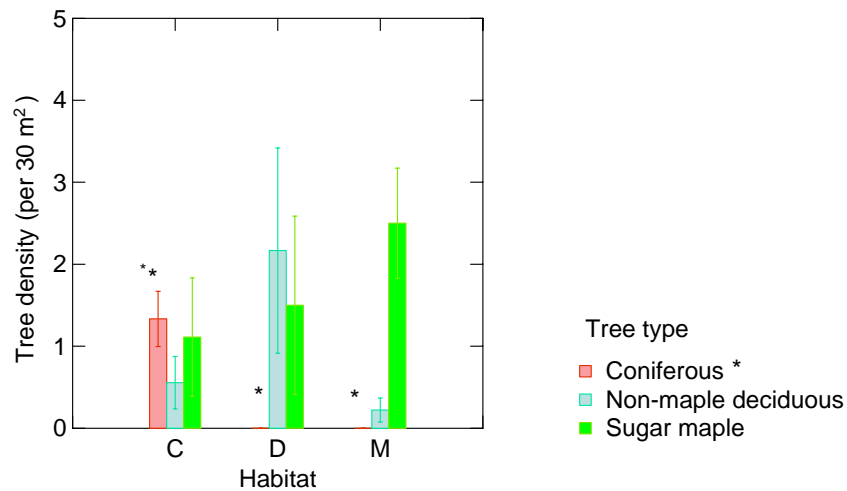


Figure 2. Comparison of densities of tree species in three habitats, (from left to right) conifer forests, mixed deciduous forests, and conifer forests ($n=3$ for each bar). * indicates significant differences in conifer tree densities ($p=0.022$). While differences in deciduous tree densities were not statistically significant, mixed deciduous forests appear to have the highest density in that category. Differences in sugar maple tree densities were not statistically significant.

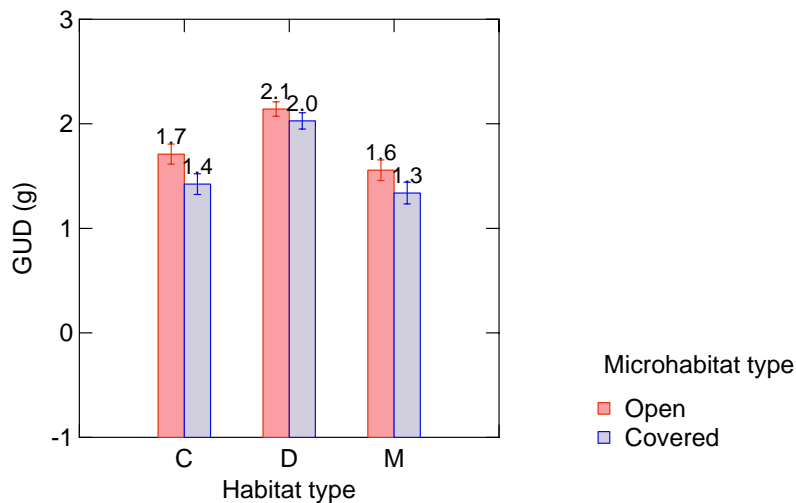
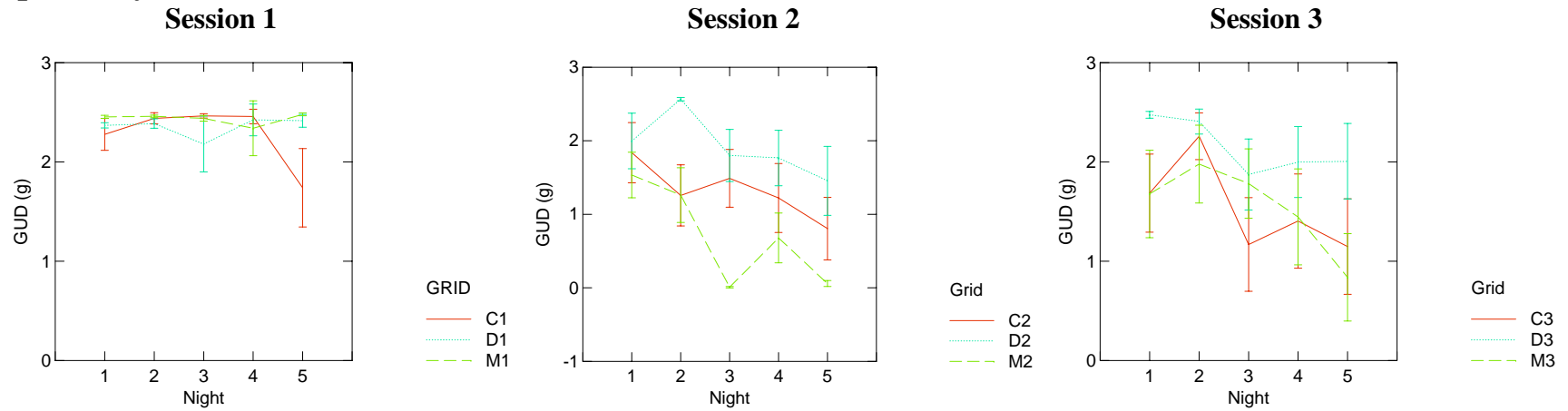


Figure 3. Comparison of GUDs between open and covered microhabitats for each habitat type, where (right to left) C= coniferous forests, D= deciduous forests, and M= sugar maple forests. Numbers shown above are means and error bars indicate standard error ($n=27$ per bar). Note that while this graph shows raw GUD (g) data, all statistical analyses were conducted using transformations to the power of 8.

Open Trays



Covered Trays

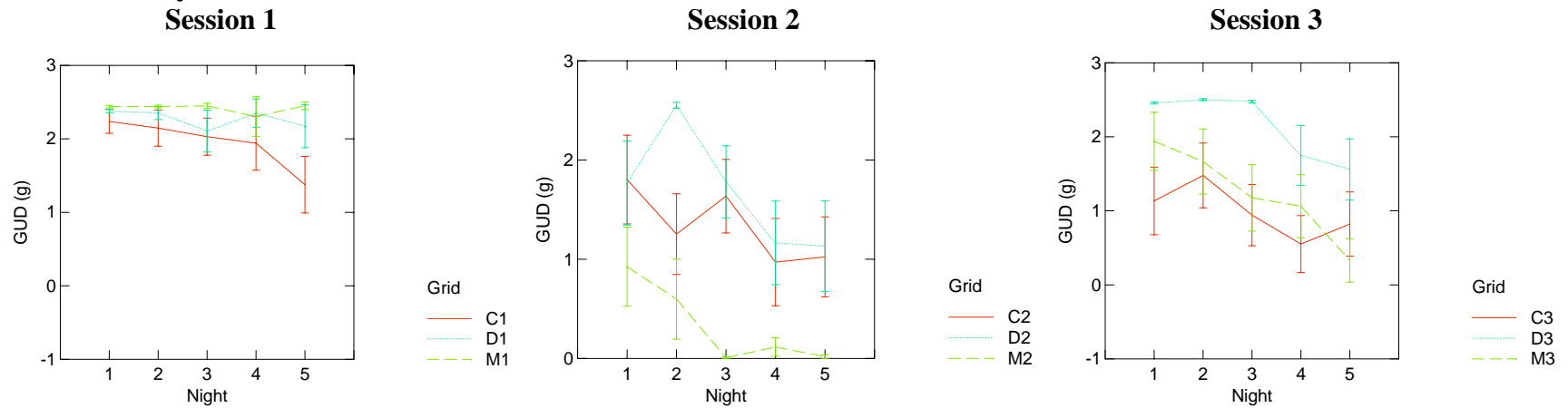


Figure 4. Comparison of GUDs in each habitat across 5 nights, separated in to open trays (top row) and covered trays (bottom) as well as by session numbers. $n=9$ for each night per line and error bars indicate standard error. Note that graphs are based on raw data, but tests were run on transformed data (power of 8).

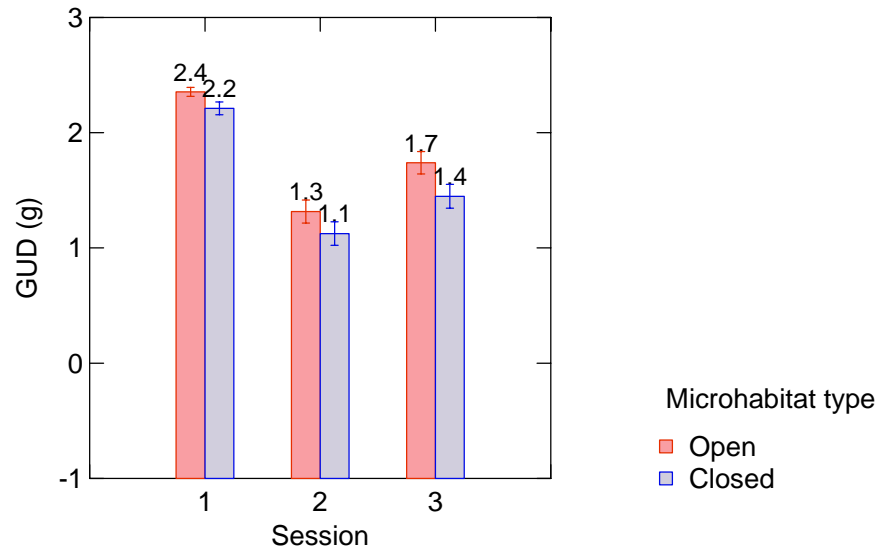


Fig.5. Comparison of GUDs for both microhabitat types across the three study sessions. Numbers shown above bars indicate means and error bars indicate standard error (n=27 per bar). On the X-axis, 1= June 5, 7-11; 2= June 26- July 1; 3= July 16-21, 2006. The first session has significantly higher GUDs than the later two sessions (n=156, p<0.000, df=2, F-ratio= 14.783)