

**Effects of terrestrial and aerial predators on rodent  
foraging: Do GUDs differ between protective cover types?**

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## **Abstract**

A predator's influence on a forager extends beyond killing and eating it as prey. The perceived threat of a predator can influence where and how the forager obtains energy necessary for survival and reproduction, thereby affecting the fitness of the prey. Prey will feed most intensively in patches that they perceive to be safest; however, the level of safety in a patch will depend on the type of predator. For example, the risk of predation by aerial predators may be greater in open patches, while shrub cover may conceal terrestrial predators. In this study, the relative risk perception of these two categories of predators by nocturnal and diurnal rodents was evaluated using giving-up densities of food resources (GUDs). GUDs were measured in feeding trays providing vertical cover, horizontal cover, or no cover. Rodents foraged most heavily, thereby leaving the lowest GUDs, in the patches they perceived as safest. Diurnal rodents had highest GUDs in trays with horizontal cover possibly because the cover acted as a visual obstruction, hindering vigilance. Nocturnal rodents had lowest GUDs in trays with vertical cover, indicating they perceive owls as a greater threat than terrestrial predators.

## **Introduction**

One of the most important decisions a forager must make is how to forage while avoiding predators. Many prey species trade-off energy intake for increased safety from predators (MacArthur and Pianka 1966). A predator's influence on prey can extend beyond killing and consuming prey. For example, the foraging behavior of prey can be altered by a predator's recent presence in an area or by a higher perceived risk of an attack. The perceived level of risk depends on factors such as the level of illumination or

the amount of concealment due to vegetative cover (e.g., Brown 1988, Kotler et al 1991, Kotler 1992, Kotler et al 1993).

The degree of risk perceived by a forager can influence the choice of foraging patch. Different foraging patches present the forager with different threats. The type of threat may be determined by surrounding physical structures that alter the visibility of prey to the predator or hinder an attack. For example, a patch with less protective vegetative cover above the patch (hereafter, vertical cover) may make it easier for owls to catch cursorial rodents. Patches with less protective cover around the patch (hereafter, horizontal cover) may increase rodent susceptibility to snake predation. Consequently, a forager is frequently faced with deciding which patch will provide the best food with the lowest chance of being eaten (Brown 1988). Assuming roughly equal energetic benefits, patches perceived as riskier will be used less than patches that are seen as safer from predation.

According to optimal foraging theory, a forager should continue feeding in a patch until the losses or risks outweigh the energy gained from the patch (MacArthur and Pianka 1966). Charnov (1976) defined Giving Up Time (GUT) as the time an individual remained in a patch after the last capture of a food item. A forager is more likely to spend time in patches that are safer and patches that have more available food relative to the surrounding environment. Brown (1988) introduced the use of Giving Up Densities of resources left in a feeding patch (GUDs) to determine the influence a predator has on prey foraging decisions. GUDs rely heavily on optimal foraging theory and predictions of energetic compromises (Brown 1988). Determining GUDs usually involves placing feeding trays in locations or microhabitats that provide differing levels or types of protection and then measuring the variations in feeding preference among the trays (e.g., Kotler et al 1993, Leaver and Daly 2003). GUDs will increase as the risk of being killed in a patch also increases; GUDs should be smaller in patches that the forager perceives as

safer (Brown 1988). Although the quantitative use of GUDs is somewhat controversial, it is generally accepted that GUDs qualitatively reflect foraging differences in presence and absence of predators (Price and Correll 2001, Brown and Kotler 2004).

Previous rodent foraging studies have primarily focused on single predator systems. For example, Kotler et al (1991) found that in the presence of owls, both *Gerbillus allenbyi* and *G. pyramidum* foraged from fewer seed trays and also foraged proportionally more from seed trays in microhabitat that provided protective cover from predators, called bush habitat, rather than in the open. In addition, the rodents showed similarly altered foraging behavior under increased illumination, simulating brighter moonlight, with no predators present. Kotler et al (1991) proposed that this behavior was due to a perception of increased risk; owls are more effective hunters in brighter moonlight and, thus, would exert a greater predation pressure. In a similar study, Kotler et al (1993) found that *G. allenbyi* and *G. pyramidum* responded to the presence of snakes by increasing GUDs in bush habitat. Therefore, these foraging rodents perceive snakes as a greater threat in the bush habitat than in the open. However, the responses differed between the species. *G. allenbyi*, an inhabitant of mainly stabilized sand fields and dunes, showed preference throughout the study for bush habitat. By comparison, *G. pyramidum*, which inhabits shifting dunes more often, showed a bias toward the open habitat. Kotler et al (1993) concluded that this habitat separation might arise from different predatory pressures.

However, few studies have evaluated the effects of multiple predators. Different predators often pose conflicting threats to foragers. For example, terrestrial predators such as snakes and weasels generally cause a relative increase in GUDs in the bush habitat, while avian predators induce higher rodent GUDs in open habitats (Kotler et al 1993, Korpimäki et al 1995, Kotler et al 1991). Therefore, terrestrial predators present a greater risk in the bush habitat while avian predators may be seen as a greater risk in the

open habitat. Korpimäki et al (1995) also found that when both a kestrel and a weasel were present, field voles spent more time in bush microhabitat than in open, suggesting that the voles perceived the kestrel to be the greater risk. Arenz and Leger (1997) found that thirteen lined ground squirrels (*Spermophilus tridecemlineatus*) in city parks responded to complete as well as lateral visual obstruction in feeding boxes by increasing vigilance during foraging, but showed little or no response to vertical obstruction. They proposed that the squirrels withdrew more frequently from boxes with horizontal obstruction to reassess their surroundings because of a loss of environmental information. A greater perceived risk from terrestrial rather than aerial predators may be the cause of the squirrels' response to horizontal obstruction and lack of response to vertical obstruction (Arenz and Leger 1997). Therefore, the importance of different predators may depend on a combination of species and habitat (Kotler et al 1993, Korpimäki et al 1995, Arenz and Leger 1997). However, studies evaluating the relative importance of multiple predators to rodent foragers in both natural and controlled settings are generally lacking.

In this study, GUDs were used to qualitatively determine the relative pressures of predators on rodent foragers in the mixed deciduous forests of the University of Notre Dame Environmental Research Center (UNDERC). This experiment tested for responses by rodents to terrestrial and aerial predators. Common diurnal rodent foragers include red squirrels (*Tamiascurius hudsonicus*) and least chipmunks (*Tamias minimus*). Common nocturnal foraging rodents include meadow vole (*Microtus pennsylvannicus*), southern red backed vole (*Myodes gapperi*), and *Peromyscus* species. Aerial predators include the diurnal *Accipiter* species, especially the northern goshawk, as well as multiple *Buteo* species of which the red-shouldered hawk and the broad-winged hawk are the most common. Nocturnal aerial predators are owls. Terrestrial predators include coyote (*Canis latrans*), gray fox (*Urocyon cinereoargenteus*), and several Mustelid species including

weasels and fisher (UNDERC, unpublished records, and Choate, personal communication). Shade cloth screens above feeding trays offered rodent foragers vertical protection from aerial predators while screens around different feeding trays provided rodents horizontal protection from land predators. Control feeding trays offered no protection. The differences in GUDs among the three types of trays should reflect the relative importance of terrestrial predators and aerial predators to both nocturnal and diurnal foragers. The trays that the rodents perceive to be safer should have correspondingly lower GUDs than those perceived as riskier.

### **Materials and Methods**

This study was conducted in a patch of mixed deciduous forest dominated by sugar maple on UNDERC-East property, located at 46° 13' N, 89° 32' W. The site contained 30 stations in a 5 x 6 grid with 50 m in between stations (Fig. 1). Each station consisted of three feeding trays placed approximately 1 m apart.

The feeding trays were 36 cm x 46 cm x 2 cm plastic cafeteria trays (Atlas Restaurant Supply, South Bend, IN) and were each filled with a mixture of 1.5 L sand and 2.5 g  $\pm$  0.02 g unshelled sunflower seeds. Each station of three feeding trays was placed in the open away from ground cover. The first tray provided no cover and served as the control. The second tray provided cover with a shade cloth sheet (56 cm x 46 cm) suspended 20 cm above the seed tray (vertical cover). The third tray had shade cloth (50 cm x 20 cm) attached vertically on two opposing sides of the seed tray (horizontal cover). Wooden stakes supported the shade cloth at each corner of the feeding trays, with stakes also placed at the corners of the control trays (Fig. 2).

To determine GUDs of nocturnal rodents, the sand and seed mixture was placed in each seed tray within one hour of sunset (Seillie, unpublished). Uneaten seeds left in the feeding trays were collected and weighed each morning at sunrise. The same process

was carried out for diurnal rodents, except the trays were filled at sunrise and the seeds collected at sunset. The experiment was conducted over 12 days. For the first three days, 2 tbs unshelled sunflower seeds were added to the trays with 1.5 L sand as a pre-baiting period to allow the rodents to acclimate to the trays. GUDs were not measured during pre-baiting, and remaining seeds were removed prior to the first day of measurements (Kotler et al 1991). Data were collected for the remaining 9 days and nights. Because of complete consumption of seeds in many of the feeding trays, one cup of unshelled seeds was scattered around each station as an augmentation for days 7 – 9 and nights 6 – 9. The augmentation reduced the marginal value of the seeds in the trays, thereby increasing GUDs to an amount that could be measured. These seeds were heated in a microwave oven for 4 minutes prior to use to prevent germination (Leaver and Daly 2003, Bouskila 1995).

Repeated Measures ANOVA (RM ANOVA) was used to analyze the GUD data. Each day or night was treated as a repeated measure. GUDs were the dependent variable and the cover placed around or on top of the feeding trays was the treatment: open (control), vertical cover, and horizontal cover. Nocturnal and diurnal rodent GUDs were analyzed separately. Specific differences in group means were evaluated with planned contrasts and univariate tests. Analyses were conducted in SYSTAT 10.0 (SYSTAT Software, Inc.; Point Richmond, CA). For all analyses,  $p$ -values  $\leq 0.05$  were considered significant.

## **Results**

Overall GUDs did not fit a normal distribution and transformations did not improve the fit to normality. This occurred primarily because of the complete consumption of seeds during the unaugmented days and nights. However, the more lenient assumption of sphericity for a repeated measures was not bad based on the

Hyunh-Feldt Epsilon and the Greenhouse-Geisser Epsilon tests, suggesting that the repeated measures analysis, for at least the augmented data, was reasonable. Sphericity calculations for all nine days were low; the Hyunh-Feldt Epsilon was 0.6365 and the Greenhouse-Geisser Epsilon, a more conservative test, was 0.5850. Sphericity for all nine nights was also low (Greenhouse-Geisser Epsilon = 0.3934, Huynh-Feldt Epsilon = 0.4192). The repeated measures ANOVA of all nine days showed significant differences in GUDs for the different treatments ( $F_{2, 87} = 4.052, P = 0.021$ ). There were also significant differences in GUDs across days ( $F_{8, 696} = 103.21, P < 0.001$ ). There was no interaction between the day and the treatment ( $F_{4, 174} = 1.105, P = 0.356$ ). GUDs tended to decline across all days, causing the significant day effect (Figs. 3). In addition, a significant transect effect was observed ( $F_{5, 82} = 5.100, P < 0.001$ ).

Similar results were seen for the RM ANOVA of all nine nights. There were significant differences both for treatment ( $F_{2, 87} = 12.779, P < 0.001$ ) and for nights ( $F_{8, 696} = 110.657, P < 0.001$ ). As with the days, the significant night effect was caused by declining GUDs across all nights (Fig. 4). There was no significant interaction between night and treatment ( $F_{6, 261} = 0.703, P = 0.648$ ) and no significant transect effect ( $F_{5, 82} = 2.104, P = 0.073$ ).

The analyses of only the augmented days and nights showed similar trends and effects while more closely fitting the model assumptions. The RM ANOVA of days 7 - 9 showed significant differences across treatments ( $F_{2, 87} = 6.7196, P = 0.002$ ) and across days ( $F_{2, 174} = 22.011, P < 0.001$ , Fig. 5). The Huynh-Feldt Epsilon (1.0000) and Greenhouse-Geisser Epsilon (0.9823) were much higher, indicating a better fit to sphericity. GUDs of diurnal rodents were significantly higher in horizontal cover trays than in vertical cover trays on day 7 ( $F_{1, 87} = 6.211, P = 0.015$ ) and day 8 ( $F_{1, 87} = 10.005, P = 0.002$ ). A nearly significant difference between open and vertical cover trays was



seen for day 7 ( $F_{1,87} = 3.421, P = 0.068$ ) and marginally for day 8 ( $F_{1,87} = 2.687, P = 0.105$ ). Horizontal cover trays had the highest GUDs for days 7, 8, and 9 (Fig. 5).

GUDs also declined across nights 6 – 9 ( $F_{3,261} = 23.438, P < 0.001$ ) and differed among treatments ( $F_{2,87} = 12.828, P < 0.001$ ). Sphericity was also better for only the augmented nights (Huynh-Feldt Epsilon = 0.8325, Greenhouse-Geisser Epsilon = 0.7903). GUDs of nocturnal rodents were higher in open trays than in vertical cover trays on all four nights (Planned contrasts:  $F_{1,87} = 7.763, P = 0.007, F_{1,87} = 15.674, P < 0.001, F_{1,87} = 11.097, P = 0.001, F_{1,87} = 9.172, P = 0.003$ , for nights 6 – 9, respectively). GUDs were higher in horizontal cover trays than vertical cover trays on night 7 ( $F_{1,87} = 7.726, P = 0.007$ ), night 8 ( $F_{1,87} = 6.031, P = 0.016$ ), and marginally for night 9 ( $F_{1,87} = 3.234, P = 0.076$ ). No significant differences were observed between open and horizontal cover trays. However, GUDs were highest on all four nights in open trays (Fig. 6).

## Discussion

GUDs of both diurnal and nocturnal rodents tended to decrease over the course of the experiment (Fig. 3,4). As the rodents become acclimated to the trays, they spend more time foraging in them, resulting in declining GUDs over a period of days. Three days and nights of pre-baiting were used to enhance the effects of the treatments by providing rodents with time to become accustomed to the trays. In previous experiments, differences in GUDs were difficult to detect for the first few days without a pre-baiting period (Seillie, unpublished data). Neither day nor night GUDs stabilized by the end of the experiment. However, Shaner et al (2007) found that *P. leucopus* GUDs usually stopped decreasing after the third day. Therefore, since the trays were augmented for three days and four nights, the decrease in GUDs across days seen with augmentation in this experiment may be due to acclimation to the augmentation, not the trays. Increasing the number of nights with augmentation may help resolve this issue.

The significant transect effect, with lower GUDs in transect A of the grid, may have been caused by changes in rodent density. A small change in density, which is conceivable since transect A was on the border of the grid, could have led to a greater number of foragers from outside the grid and, therefore, lower GUDs across all or part of the transect. Rodents on the interior of the grid would have more options of stations to visit, resulting in lower GUDs. However, there was no trapping as part of this experiment, so actual densities are unknown.

The beginning of the augmentation can be clearly seen by a sharp rise in the GUDs of both nocturnal and diurnal rodents (Fig. 3, 4). The difference in GUDs between augmented and non-augmented days and nights increased the variability and skew of the data, resulting in a poor fit of sphericity, one of the assumptions of RM ANOVAs. However, analyzing the augmented GUDs separately eliminated much variability, allowing the RM ANOVA to more closely meet this assumption. In addition, because GUDs were very low for most of the days and nights without augmentation, differences among treatments were difficult to detect. Augmenting the trays with scattered seeds around them increased GUDs by decreasing the marginal value of the seeds in the trays, thereby making the differences among the trays more pronounced (Fig. 7, 8).

The only significant differences among trays for the augmented diurnal rodent trials were between horizontal and vertical cover trays on days 7 and 8. However, GUDs were highest on all augmented days in the horizontal cover trays and lowest in the vertical cover trays (Fig. 5). This would suggest that the diurnal rodents perceived the horizontal cover trays as the riskiest patches. These results are similar to those found by Arenz and Leger (1997) in their study of *Spermophilus tridecemlineatus*. They concluded that squirrels increased vigilance when their lateral sight was obstructed to the same extent as when sight in all directions was obstructed. The squirrels in their study showed no significant change in vigilance when sight above was obstructed. Although the trend

in this experiment was that GUDs were higher in open trays than in vertical cover trays, there were no significant differences. Thus, as in the study by Arenz and Leger (1997), the diurnal rodents showed no significant preference for the vertical cover over the open trays. The rodents most likely viewed the horizontal cover trays as riskiest because the cover acted as a visual obstruction, hindering vigilance or concealing predators, rather than as protection by hiding from predation.

During the four augmented nights, nocturnal rodents had the lowest GUDs in vertical cover trays. There were significant differences between open and vertical cover trays on all four augmented nights as well as significant differences between horizontal and vertical cover trays on nights 7 and 8. Many studies have shown that nocturnal rodents prefer covered patches over open patches (e.g., Korpimäki et al 1996, Kotler 1992, Kotler et al 1993). However, no significant differences were seen in this experiment between open trays and horizontal cover trays. Seillie (unpublished data) found that in sugar maple forests on UNDERC property, nocturnal rodent GUDs were higher in open patches than in patches under brush cover. However, most of the natural vegetative cover in her study consisted of vertical cover, and no distinction was made between vertical and horizontal cover. In this study, although GUDs were highest in open trays, nocturnal rodents showed no significant distinction in risk between open trays and those with horizontal cover. Thus, the nocturnal rodents viewed the trays with vertical cover as the safest of the three patches. This is most likely due to a higher perceived risk of predation by owls and a lesser perceived threat from terrestrial predators. Korpimäki et al (1996) found similar results in a controlled study of *Microtus agrestis* under predation pressures of least weasels and kestrels. When both predators were present, the voles behaved as if only the kestrel were present. Kotler et al (1993) found that the effects of illumination, simulating increased owl predation, and of the presence of snakes may depend on the species of rodent. Had the trays been acting as visual obstructions as with

the diurnal rodents, the safest patches would have offered the least hindered vigilance, i.e., the open trays that would allow better detection of both terrestrial and aerial predators. Because open trays were seen as the riskiest rather than the safest patches, the cloth was acting as protective cover from nocturnal predators. In addition, deer mice such as *P. leucopus* have poor vision (King and Vestal 1974). For example, Zollner and Lima (1997) found that *P. leucopus* had a visual range of 20 m. This limited visual range may imply that *P. leucopus* does not rely heavily on vision to detect predators. Nocturnal rodents that might rely on hearing to readily detect terrestrial predators would hide from owls under cover because they cannot readily detect them. Consequently, nocturnal rodents in this study may perceive a greater threat from owls than terrestrial predators.

Therefore, the effects of vertical and horizontal cover are different for nocturnal and diurnal rodents. Diurnal rodents perceive the horizontal cover as a visual obstruction that hinders vigilance and do not have a significant preference of vertical cover over a lack of cover. Nocturnal rodents perceive owls as the greatest threat and, thus, have the lowest GUDs in trays with vertical cover. Future studies could extend the number of days and nights with augmentation to determine with more certainty the perception of risk from terrestrial predators. The impact of acclimation on rodent perception of risk could also be studied; the declining GUDs across days and nights suggests that reaping the benefits of a reliable source of food may be worth risking predation. Also, species of rodents could be identified and giving-up times could be measured to determine if certain species or genera of rodents perceive predation risks differently.

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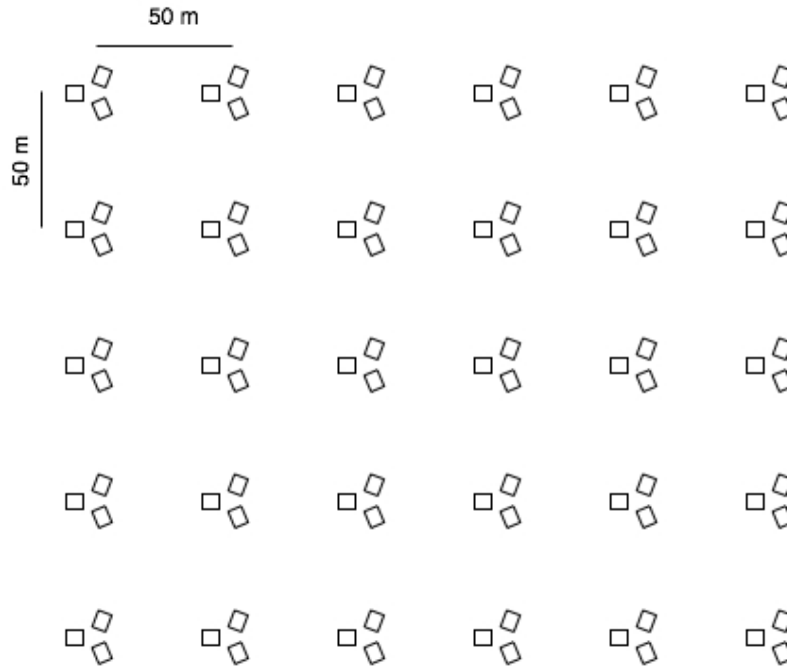


Figure 1. Foraging station grid design with 50 m between stations. The 5 x 6 grid consisted of 30 stations with 3 trays placed approximately 1 m apart from each other.

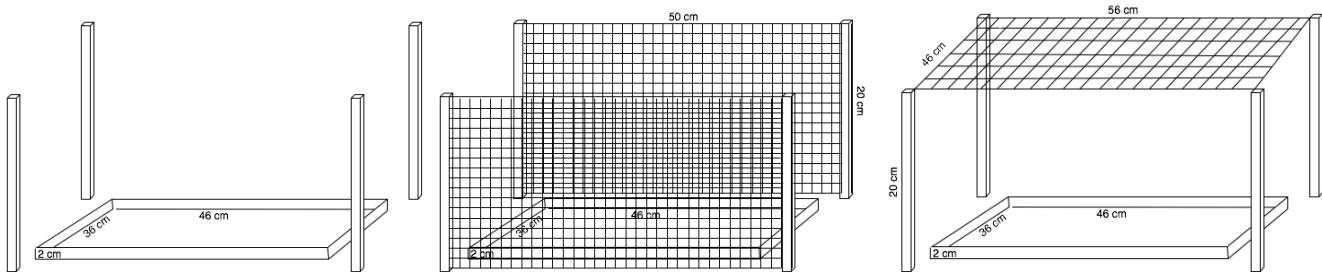


Figure 2. Design for the three feeding trays at each station. The control tray (left) offered no cover. One tray offered horizontal cover (middle). The third tray provided vertical cover (right). Shade cloth was used to provide the horizontal and vertical cover.



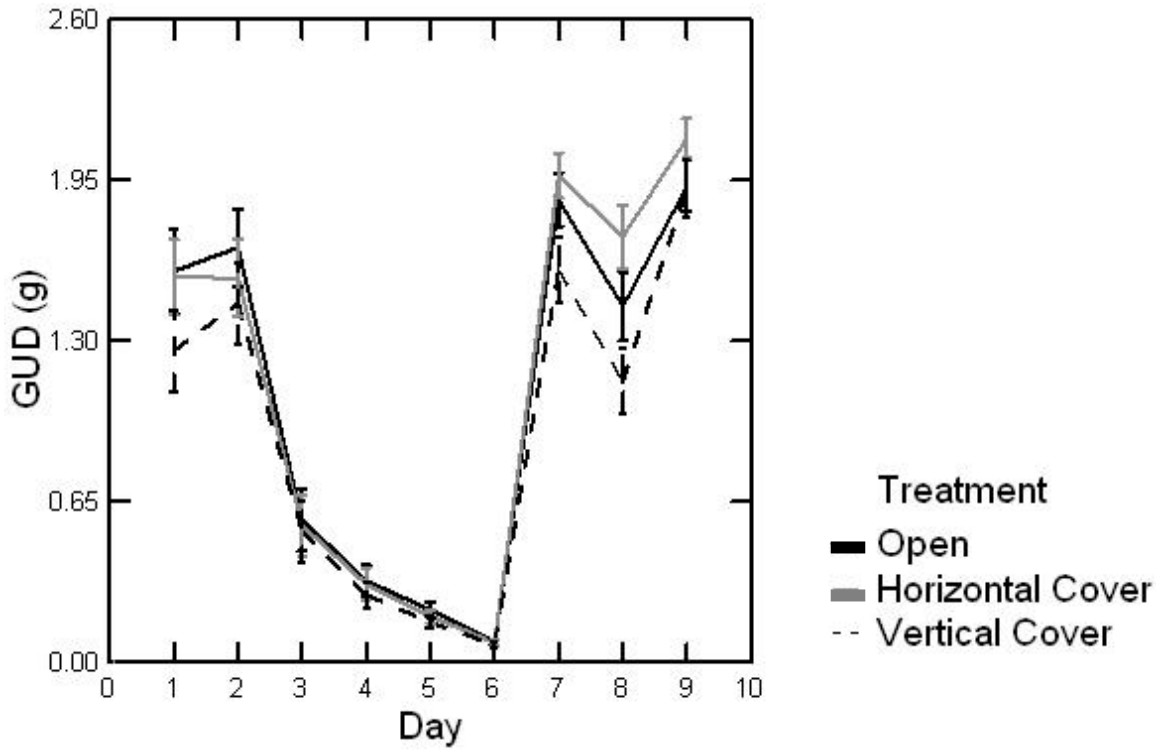


Figure 3. Mean giving up densities by treatment across all days. Error bars indicate standard error. GUDs significantly declined across all days ( $F_{2, 174} = 22.011, P < 0.001$ ) and differed among treatments for days 7 and 8. The differences in GUDs by day did not interact with differences by treatment.

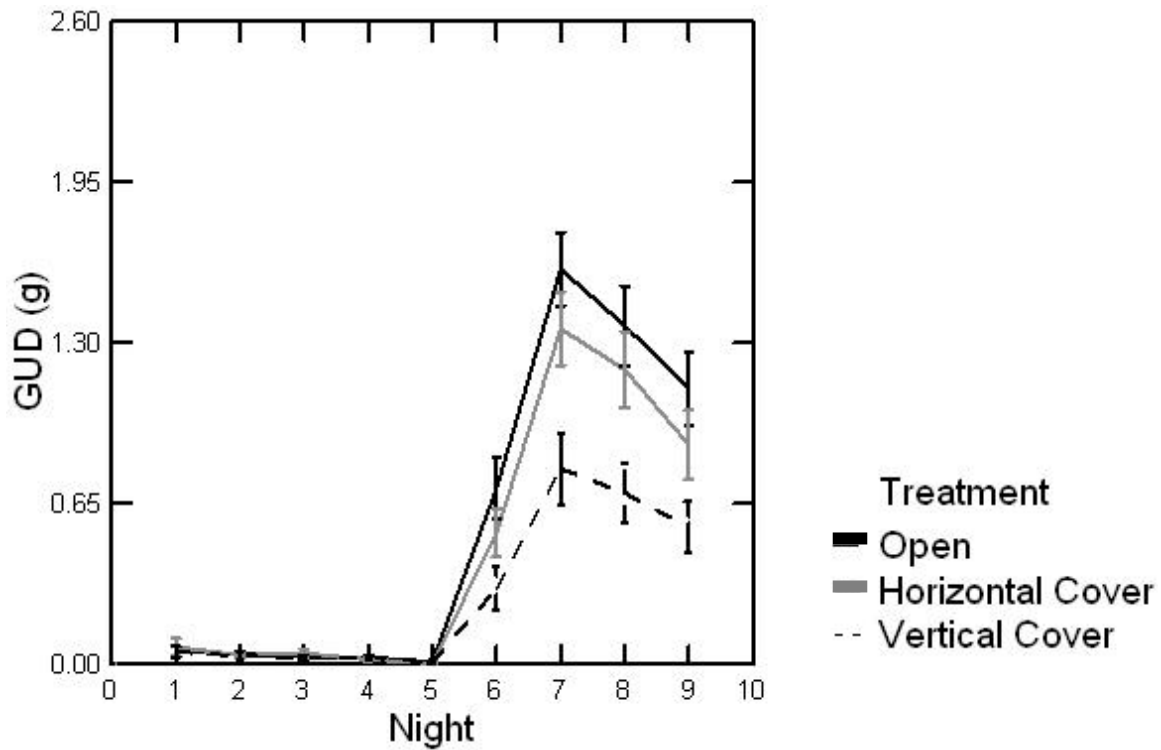


Figure 4. Mean giving up densities by treatment over all nights. Error bars indicate standard error. GUDs significantly declined across all days ( $F_{2, 174} = 22.011, P < 0.001$ ) and differed among treatments for days 6 – 9. The differences in GUDs by day did not interact with differences by treatment. Augmentation began on night 6, marked by a rise in GUDs across all treatments.

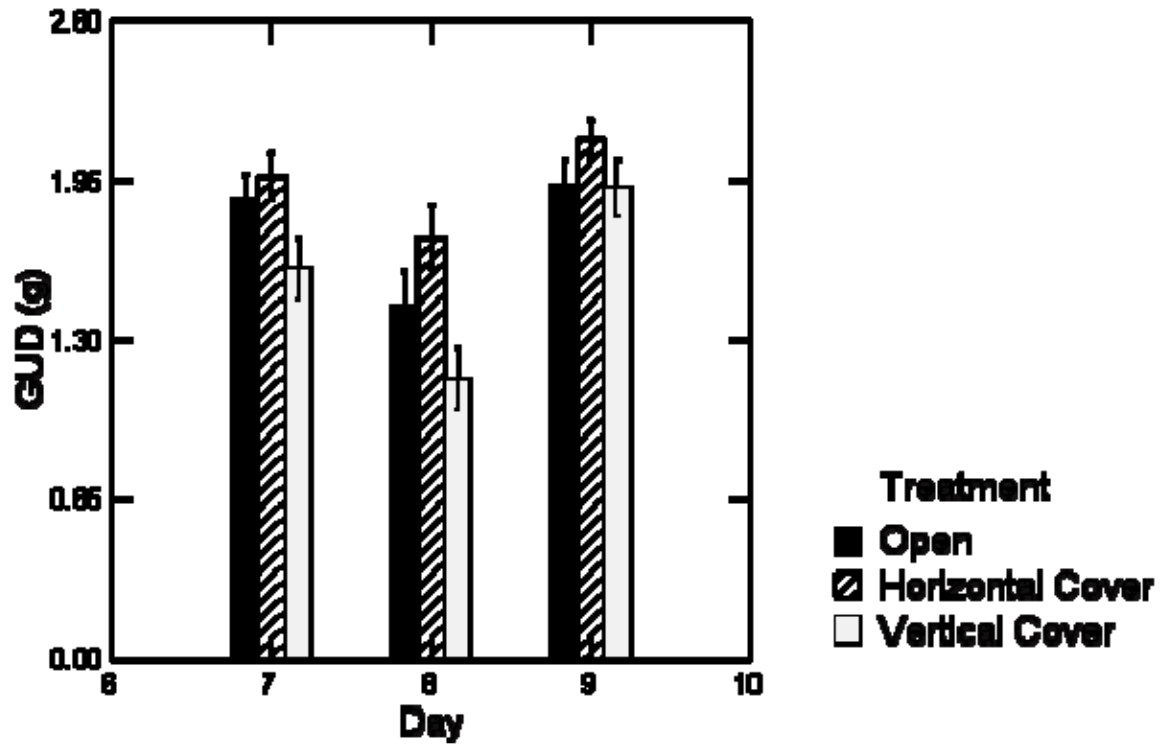


Figure 5. Mean giving up densities of diurnal rodents during augmented days. Error bars indicate standard error. Significant differences are seen only between horizontal cover and vertical cover trays on day 7 ( $F_{1, 87} = 6.211, P = 0.015$ ) and day 8 ( $F_{1, 87} = 10.005, P = 0.002$ ) and day 8. No significant differences were seen for day 9.

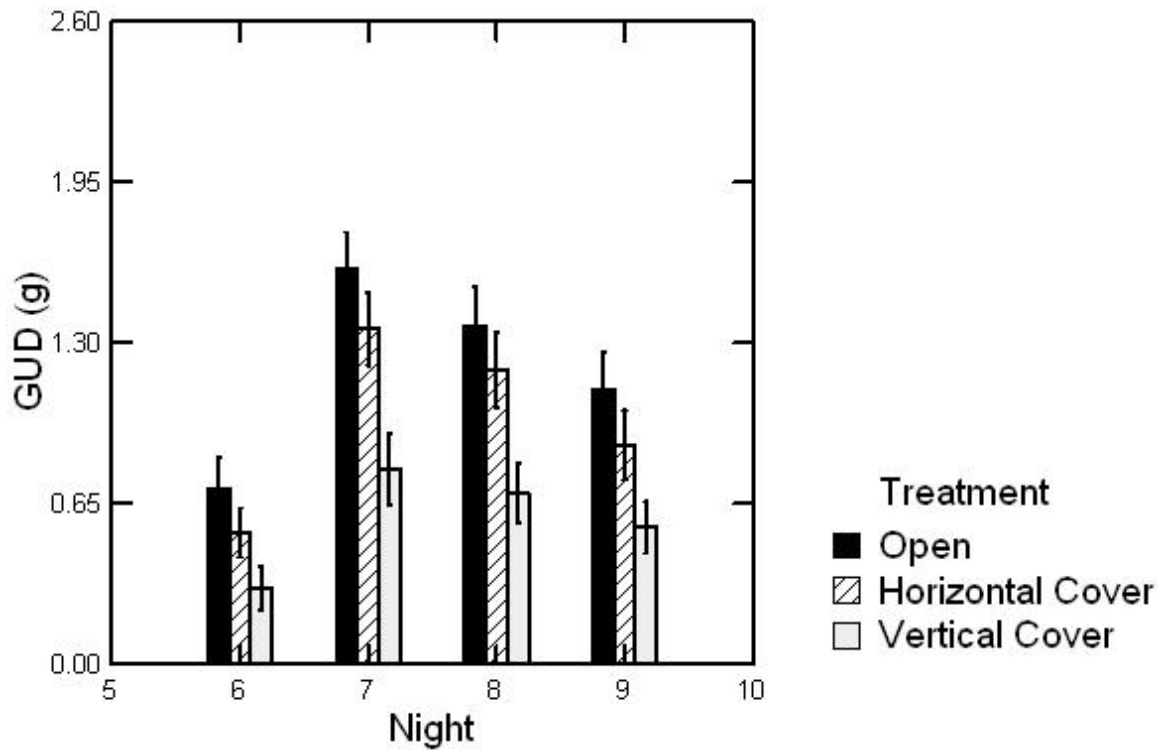


Figure 6. Mean giving up densities of nocturnal rodents during augmented nights. Error bars indicate standard error. Significant differences were observed between open and vertical cover trays on all four nights (Planned contrasts:  $F_{1, 87} = 7.763, P = 0.007, F_{1, 87} = 15.674, P < 0.001, F_{1, 87} = 11.097, P = 0.001, F_{1, 87} = 9.172, P = 0.003$ , for nights 6 – 9, respectively). Significant differences were seen between vertical cover and horizontal cover trays on night 7 ( $F_{1, 87} = 7.726, P = 0.007$ ), night 8 ( $F_{1, 87} = 6.031, P = 0.016$ ), and night 9 ( $F_{1, 87} = 3.234, P = 0.076$ ).

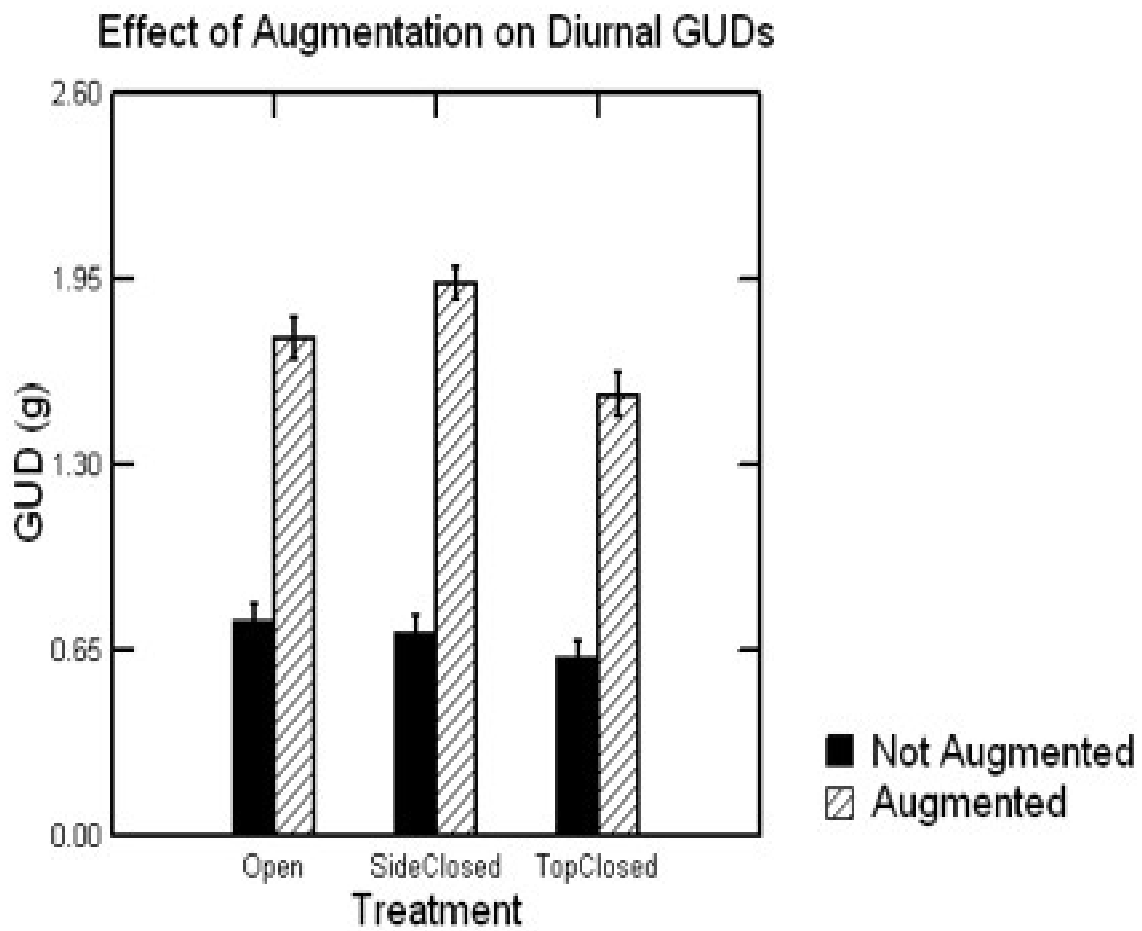


Figure 7. Mean effects of augmentation by tray type on diurnal GUDs. Error bars indicate standard error. Augmenting the trays with seeds spread around them increased GUDs, allowing significant differences to be seen among the three tray types.

### Effect of Augmentation on Nocturnal GUDs

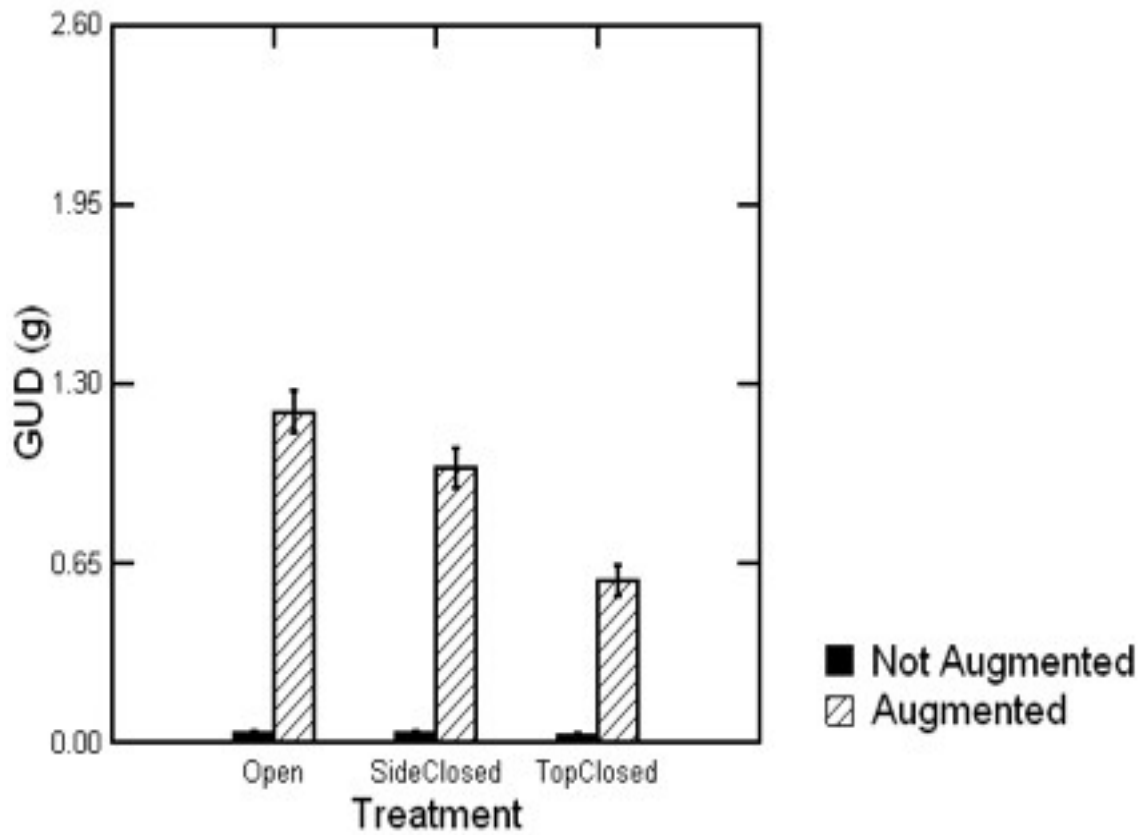


Figure 8. Mean effects of augmentation by tray type across all nights. Error bars indicate standard error. Augmentation increased GUDs of all tray types and significant differences among cover types were seen in the augmented trays.