Optimal foraging and predation pressures: the importance of woody debris to the foraging behavior of *Peromyscus maniculatus gracilis*.

BIOS 35502: Practicum in Field Biology
Collin McCabe
Advisor: Dr. Michael J. Cramer
2008

Abstract: Foragers under predation pressure must constantly weigh the risk of being preyed upon against the need to maximize energy intake. In such circumstances, foragers are presented with many choices and ought to choose the one which allows for the greatest energetic benefit relative to predation risk. This study focused on determining how the sylvan subspecies of deer mouse, *Peromyscus maniculatus gracilis*, which forages both on the ground and in trees, would alter its foraging patterns in response to increased predation pressure on the ground via removal of woody debris. Giving-up densities (GUD) were recorded for paired arboreal and terrestrial feeders at six sites, three control sites and three randomly selected experimental sites, from which all woody debris greater than 3cm in diameter was removed. No feeding was observed in any experimental site, with both arboreal and terrestrial GUDs significantly greater in experimental sites than in control sites. Among control sites, terrestrial GUDs were significantly less than arboreal GUDs, suggesting that mice preferred feeding on the ground. The predation pressures of mustelids, which are also both arboreal and terrestrial predators, is a likely driving factor behind terrestrial foraging, with more escape routes than arboreal foraging for *P. m. gracilis*. The complete absence of feeding within experimental sites suggests that combined predation pressure of terrestrial predators (mustelids) and aerial predators (owls) in such a patch outweighs any energetic benefit to an individual for feeding in that patch. Thus it was concluded that woody debris is a vital component of *P. m. gracilis* habitats, necessary for alleviation of high predation pressures in its environment.

INTRODUCTION

The theory of optimal foraging is one which plays a fundamental role in much of behavioral ecology. This theory depends upon the assumption that given all available prey, a predator seeks to maximize energy intake relative to energy expended in obtaining prey. Originally proposed by Robert MacArthur and Eric Pianka (1966), an individual should engage in an activity as long as the resulting gain in time spent per unit food exceeds the loss, until engaging in that activity would entail a greater loss than gain. Variables which decrease net energy are the cost of searching for food items and the handling cost of food items (Molles 2008). A revolutionary concept which made estimating the optimal foraging model possible was that of a giving-up density, or GUD (Brown 1988). GUDs are defined as the food density at which a forager will cease to forage on a food source; in terms of the optimal foraging model, a GUD should

correspond to a harvest rate that just balances the metabolic costs of foraging, the handling time, and the missed opportunity cost of not engaging in alternative activities (Brown 1988).

This theory, however, does not take into account the effect of predation on the forager. Predation pressure could potentially and greatly increase the search cost value because of the high amount of energy and time expended scanning for predators while feeding, so as to ensure individual fitness. The foraging decisions made in response to predation pressures, however, are much more complicated than simply increasing search cost through increased scanning, and predation pressure must be considered independently from all other original optimal foraging cost variables. Sih (1980) suggests this very fact, having found that young backswimmers would actually alter feeding patterns to feed in safer, but less energetically rewarding patches in the presence of cannibalistic adult backswimmers. This choice, based on the variable of predation risk, was developed into a foraging cost variable, μ, or the instantaneous rate of being preyed upon while engaged in a risky activity (Brown 1992). Predation risk of an activity (μ) is balanced with the reward of that foraging activity in energy acquired (f) and of the many combinations of activities, the one chosen will be the one which minimizes μ/f (Gilliam and Fraser 1987; Brown 1992). In fact, the predation cost of a foraging decision, μ, can be very large and often comprises the largest foraging cost to a forager (Brown and Kotler 2004). The most interesting aspect of μ is that predator-inflicted mortality is not necessary, only the threat and possibility of such mortality.

As previously discussed, predation pressures can also indirectly augment the time spent searching and or handling a food source due to predator scanning. This activity,

also referred to as apprehension, in conjunction with time allocation, μ/f, are used by foragers to manage predation risk (Kotler et al. 2004). Foragers can either decrease feeding on food or can increase apprehension, or both in response to predation pressures (Brown 1999).

One distinct choice for foragers is the choice to either forage on the ground or in a tree. Each of the two choices provides differing predation costs, assuming that an arboreal forager has more cover from aerial predators through tree branches and leaves, and protection from all terrestrial predators unable to climb. Also, however, the energetic reward of foraging in a tree, at least in northern hardwood forests, would be less than on the ground due to the absence or large temporal spacing of major masting fruit and nut trees. One particularly useful system for analyzing time allocation between arboreal and terrestrial feeding is the northern hardwood sylvan deer mouse subspecies, *Peromyscus maniculatus gracilis*, which can spend as much time foraging in trees as it does on the ground (Kurta 1995). Furthermore, as a nocturnal small mammal, *P. m. gracilis* is exposed to both nocturnal terrestrial (snakes, mustelids, foxes, and wolves) and nocturnal aerial predators (owls) (Kurta 1995).

Many studies have positively linked fallen woody debris to abundances of *Peromyscus* species in forests throughout North America. Downed logs and stumps are often utilized by two concurrent species of *Peromyscus*, *P. maniculatus* and *P. leucopus*, for traveling, foraging, and nesting (Bowman et al. 2000). Another study found that large amounts of course woody debris improve habitat quality of pine forests and increase abundances of another *Peromyscus* species, *P. gossypinus* (Loeb 1999). One proposed reason for the increase of species abundance as course woody debris increases is that

downed logs provide cover during foraging to *Peromyscus* spp., decreasing predation risk (Loeb 1999). Another hypothesis is that *Peromyscus* spp. utilize logs as travel routes to reduce predation risk because traveling on logs is quieter than traveling on leaf litter (Barnum et al. 1992). Regardless of how it is approached, though, course woody debris plays a significant role in decreasing predator risks to *Peromyscus* species.

The purpose of this study was to determine whether deer mice alter foraging behavior as woody debris is removed from a foraging patch, and thus, theoretically, terrestrial predation risk increases. It was hypothesized that in the absence of woody debris, *Peromyscus maniculatus gracilis* would alter its foraging habits in response to increased predation pressure from both terrestrial and aerial predators by foraging less on the ground and more in trees than in areas with woody debris present. If the hypothesis is supported, then it is predicted that GUDs will be lower for arboreal feeding in areas with woody debris removed than in control areas with woody debris remaining, and GUDs will be greater for terrestrial feeding in areas of woody debris removal than in controls.

MATERIALS AND METHODS

Six sites were selected for study in this experiment (UTM: Site 1 – 16T 0305963, 5121209; Site 2 – 16T 0304090, 5122420; Site 3 – 16T 0306638, 5123772; Site 4 – 16T 0303355, 5125459; Site 5 – 16T 0307069, 5120758; Site 6 – 16T 0308900, 5120792) (Fig. 1). Sites were selected because of similarities in composition: all were northern hardwood, sugar maple (*Acer saccharum*) dominated forests with woody debris, leaf cover, and understory growth present.   Feeding grids within each site consisted of nine pairs of feeders, arboreal and terrestrial, in a 3 x 3 square arrangement with 15m spacing

(Fig. 2). Each grid was studied for two consecutive nights; the first night, however, was

conducted as a pre-baiting period, in order to allow acclimation to the novel food source,

and thus was not considered in analysis. On each night, within 1 hour of sunset, each of

the eighteen feeders was filled with a mixture of 20.00 ± 0.01g of black oil sunflower

seeds (pre-dried as a control for 1 hour at 60˚C) and 150ml of sand. Then, each morning,

within 1 hour of sunrise, all feeders were emptied, and contents were transported back to

the lab for sorting. Seeds were sorted from sand through sifting and then dried for 1 hour

at 60˚C with a 5.00g, pre-dried control, in order to verify that no seed mass was lost in

drying. Then, all split, opened, or otherwise manipulated shells without seeds were

removed and the remaining, whole seeds were weighed.

Each set of feeders were paired: one arboreal feeder, which was secured to the

trunk of a tree with two black, nylon, ratcheting straps 3m above the ground; and one

terrestrial feeder, which was set on even ground, directly underneath the arboreal feeder

(Fig. 3). The arboreal feeder resembled an off-center T-shape, constructed of two pieces

of two-by-fours: the base, which was 35cm long, and the platform, 20cm long and affixed

to the base 22.5cm from the top. The arboreal feeder was secured to the tree with one

strap around the base above the platform and one below, for stability. The terrestrial

feeder consisted of only one piece of two-by-four: a base board, 35cm long. Two drywall

screws protruded from the underside of the feeder for the purpose of anchoring it to the

ground.

Despite the differences in the construction of the two types of feeders, both

utilized the same uniform feeding cups, 400ml plastic sample cups with securable lids.

One hole, 2.5 cm in diameter was cut into the side of the cup, with the center of the hole

3.25cm from the lip of the cup, and another hole, small enough for only a drywall screw

to fit into, was made in the center of the bottom of the cup, and the hole was covered with

rubber caulk outside and inside to seal the hole. The specific diameter of 2.5cm was

chosen in order to exclude larger nocturnal mammals, such as flying squirrels, from

feeders (Moore et al. 2007). The securable lids of the feeders allowed for an accurate

GUD to be obtained even in rainy conditions, and the rubber caulk allowed for the cups

to be screwed and unscrewed from the feeders every morning without losing any sand or

seeds.

Three of the six sites were randomly selected for experimental treatment (Site 3,

Site 4, and Site 5) (Fig. 1). Experimental treatment in this study consisted of the removal

of all course woody debris, CWD (>10cm in diameter) (Harmon et al. 1986) and any

woody debris large enough for a mouse to walk along (3cm-10cm in diameter), for the

purposes of this paper, referred to as medial woody debris, MWD. All CWD and MWD

was cleared within a 60m x 60m square plot of forest with no edge of the plot less than

15m from any road (Fig. 2). For control among removal, each of the three sites received

20 man-hours of removal labor without mechanized equipment. Only fallen, woody

debris was removed in this treatment; all leaf cover and understory growth remained

intact in each of the grids. Some woody debris, however, was too large to move without

mechanized equipment, and this was factored into the planning of the plots so that none

of these logs intersected the 30m x 30m feeding grid. All clearing at each site was

completed 24 hours before set-up of the feeding grid, allowing a one night

acclimatization period for the *Peromyscus* population to adjust to any habitat disturbance

caused by the removal of woody debris.

RESULTS

A repeated measures analysis of variance (RM-ANOVA) was utilized to analyze the differences between treatments of the giving-up densities of arboreal and terrestrial feeders, which were taken as paired instances, or repeated measures (Fig. 4). GUDs differed significantly between control and removal treatments, with control showing lower giving-up densities and greater difference between arboreal and terrestrial feeders than removal ($F_{1, 48} = 232.219$, $p < 0.000001$). Within GUDs over both treatments, terrestrial GUDs were significantly lower than arboreal GUDs ($F_{1, 48} = 35.479$, $p < 0.000001$). In addition, differences between arboreal and terrestrial feeding were dependent upon treatment ($F_{1, 48} = 35.479$, $p < 0.000001$), with control showing significant differences between arboreal and terrestrial GUDs, but removal showing no differences.

RM-ANOVA was then utilized to analyze differences between each site. Removal sites (Site 3, Site 4, and Site 5) could not be analyzed by this method because their standard errors of the mean all equaled 0 due to an absence of variation. Alternatively, RM-ANOVA was conducted to determine differences in paired arboreal and terrestrial GUDS among only the three control sites (Site 1, Site 2, and Site 6) (Fig. 5). There was no significant difference in differences between arboreal and terrestrial GUDs between sites ($F_{2, 23} = 0.474$, $p = 0.629$).

Simple correlations were run to determine whether any other factors, such as weather, could have been affecting GUDs. Mean terrestrial GUDs by night were not correlated with precipitation (cm) ($r = 0.320$, $p = 0.536$), temperature (˚C) ($r = -0.695$, $p =$

0.125), phase of moon (% illumination) (r = 0.606, p = 0.203), or sustained wind speed (kmph) (r = 0.237, p = 0.651). Likewise, mean arboreal GUDs by night did not correlate with precipitation (cm) (r = 0.294, p = 0.572), temperature (˚C) (r = -0.747, p = 0.088), phase of moon (% illumination) (r = 0.733, p = 0.098), or sustained wind speed (kmph) (r = 0.124, p = 0.815). RM-ANOVA was also run over arboreal and terrestrial GUDs for all sites between nights which received rain and nights which did not, showing no significant difference between nights with and without rain ($F_{1, 48}$ = 0.947, p = 0.335).

DISCUSSION

With all tested abiotic variables of weather and environmental conditions showing no significant correlations to explain the variation between sites, and with sites within each treatment showing no significant differences, treatment was accepted as the driving factor behind the differences between arboreal and terrestrial GUDs. Terrestrial GUD did increase as predicted, from an average of 8.83 ± 0.70g to 20.00 ± 0.00g, however, so did arboreal GUD, from an average of 14.80 ± 0.71g to 20.00 ± 0.00g. Therefore, the hypothesis was not supported. Beyond the refutation of the hypothesis, neither arboreal nor terrestrial feeder was ever foraged by *P. m. gracilis* over all removal sites and nights tested.

One first question arises in the background of these conclusions and observations: if *Peromyscus maniculatus* does spend as much time on the ground as in trees (Kurta 1995), then why were terrestrial GUDs significantly lower than arboreal GUDs for all control sites and on average? A possible explanation to this question lies in the theory of predator facilitation, which states that one type of predator (e.g. avian predators) drives

prey into one type of response, and another type of predator (e.g. terrestrial predators)

drives the prey into another, opposite response, making it vulnerable to the former

predator while safe from the latter predator, and vice versa with the former response. The

prey ought to choose the response which provides protection from the more lethal of the

two types of predators, while remaining vulnerable to the less lethal of the two predators

(Korpimaki 1996). Following this line of thought, the response of *P. m. gracilis* to its

aerial predator in northern hardwood forests, owls, ought to be to hide among the

branches of thickly foliated trees, such as *A. saccharum* (sugar maple). Mustelids of

northern hardwood forests: weasels, fishers, and martens, are all apt climbers, however

(Kurta 1995). The inability to escape mustelids in the tree would most likely drive the

mouse to the ground, for safety from mustelids in the possibility for escape. Since the

GUDs were so much higher on the ground than in the trees in control sites, it was thus

concluded that mustelids were perceived as a bigger threat to *P. m. gracilis* than owls.

Due to their high metabolic demands, mustelids, even in small numbers, can have quite a

substantial effect on less aggressive small mammal populations, especially *Peromyscus*

species (Derting 1989).

      Another, more obvious question is then more easily explained with this

knowledge: why was there such a drastic change in foraging of *P. m. gracilis* after the

removal of CWD and MWD? Often, seemingly small changes in habitat composition or

arrangement can produce very large increases or decreases in the costs of predation of

some activities (Brown and Kotler 2004). Because *Peromyscus* species may use woody

debris for cover from both arboreal and terrestrial predators (Loeb 1999) and as quiet

travel routes along the forest floor (Barnum et al. 1992), the removal of such woody

debris would severely increase predation risks to both aerial (owls) and terrestrial (mustelids) predators. These increases in predation risks may very well have caused the cost of predation alone (either to aerial or terrestrial costs of predation, or the combined costs of both) to greatly outweigh any energetic benefit afforded by foraging within the sites with CWD and MWD removed.

Finally, the topic of disturbance must be addressed. With such a drastic change to the habitat as removing all fallen pieces of wood greater than 3cm in diameter, disturbance would have been heavy and could very well have been operating in the displacement of the *Peromyscus* populations. The logical question which follows then is: how do *Peromyscus* spp. respond to disturbance? In a two year study in which 50% of CWD in 60m x 60m plots was removed and then added to other 60m x 60m plots, with still other 60m x 60m plots remaining unaltered as controls, live trapping was conducted before and directly after (within less than 24 hours) manipulations to test the effects of disturbance on mammal communities. *Peromyscus* spp. actually showed significantly higher population densities after removal manipulations than in controls (Osbourne, unpublished). Although the mice may have been using traps as artificial cover in sites with less woody debris, the same could be argued for the possibility of mice to take refuge from predators within the enclosed feeders in this experiment. With these results taken into consideration, the absence of all feeding within removal sites could almost definitely not be attributed to disturbance.

From the analysis of this study, the role of woody debris as a facilitator of both arboreal and terrestrial foraging in northern hardwood habitats is a vital one. Without woody debris, and even with substantial amounts of leaf litter and understory growth,

foraging was halted entirely. More in-depth analyses are required, however, in order to

make more universally applicable conclusions. These extensions include, but are not

limited to: increasing sample size of sites tested, addition of variation in stand

compositions (i.e. mixed and coniferous habitats), extending pre-baiting periods, and

observing plots over longer data collection periods (e.g. collecting data for 1 week per

site rather than 1 day). At the very least, though, dependence upon woody debris and its

importance to *P. m. gracilis* foraging patterns was positively demonstrated in this study.

WORKS CITED

Barnum, S. A., C. J. Manville, J. R. Tester, and W. J. Carmen. 1992. Path selection by *Peromyscus leucopus* in the presence and absence of vegetative cover. *Journal of Mammalogy* 73:797-801.

Bowman, J. C., D. Sleep, G. J. Forbes, and M. Edwards. 2000. The association of small mammals with course woody debris at log and stand scales. *Forest Ecology and Management* 129:119-124.

Brown, J. S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral Ecology and Sociobiology* 1: 37-47.

Brown, J. S. 1992. Patch use under predation risk: I. Models and predictions. *Annales Zoologici Fennici* 29:301-309.

Brown, J. S. 1999. Vigilance, patch use and habitat selection: Foraging under predation risk. *Evolutionary Ecology Research* 1: 49–71.

Brown, J. S. and B. P. Kotler. 2004. Hazardous duty pay and the foraging cost of predation. *Ecology Letters* 7:999-1014.

Derting, T. L. 1989. Prey selection and foraging characteristics of least weasels (*Mustela nivalis*) in the laboratory. *American Midland Naturalist* 122(2):394-400.

Gilliam, J. F. and D. F. Fraser. 1987. Habitat selection under predation hazard: a test of a model with foraging minnows. *Ecology* 68:1856–1862.

Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack, Jr., and K. W. Cummins. 1986. Ecology of course woody debris in temperate ecosystems. *Advances in Ecological Research* 15:133-302.

Korpimaki, E., V. Koivunen, and H. Hakkarainen. 1996. Microhabitat use and behavior of voles under weasel and raptor predation risk: predator facilitation? *Behavioral Ecology* 7(1)30-34.

Kotler, B. P., J. S. Brown, and A. Bouskila. 2004. Apprehension and time allocation in gerbils: the effects of predatory risk and energetic state. *Ecology* 85(4):917-922.

Kurta, A. 1995. Mammals of the Great Lakes Region. University of Michigan Press, Ann Arbor, Michigan.

Loeb, S. C. 1999. Responses of small mammals to course woody debris in a southeastern pine forest. *Journal of Mammalogy* 80(2):460-471.

MacArthur, R. H. and E. R. Pianka. 1966. On optimal use of a patchy environment. *The American Naturalist* 100:603-609.

Molles Jr., M. C. 2008. Ecology: Concepts and Applications. McGraw-Hill, New York, New York.

Moore, J. E., A. B. McEuen, R. K. Swihart, T. A. Contreras, and M. A. Steele. 2007. Determinants of seed removal distance by scatter-hoarding rodents in deciduous forests. *Ecology* 88(10):2529-2540.

Osbourne, J. D. Unpublished. Effects of edge and course woody debris on small mammal communities in riparian and upland habitats in northern West Virginia. Thesis submitted to Davis College of Agriculture, Forestry, and Consumer Sciences, West Virginia University.

Sih, A. 1980. Optimal behavior: can foragers balance two conflicting demands? *Science* 210:1041-1043.
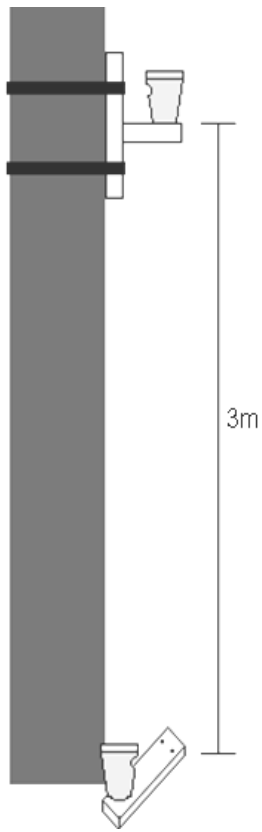
FIGURES
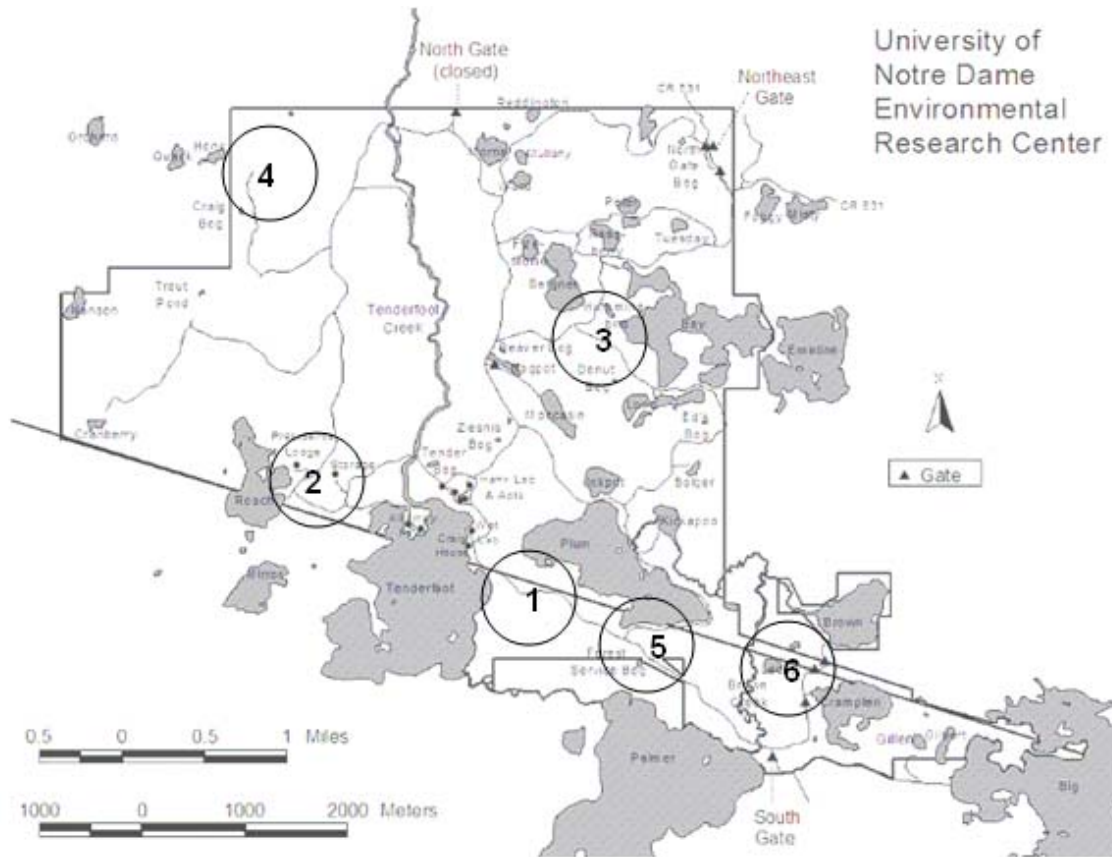
**Figure 1.** *Map of UNDERC property with study sites numbered and circled.*
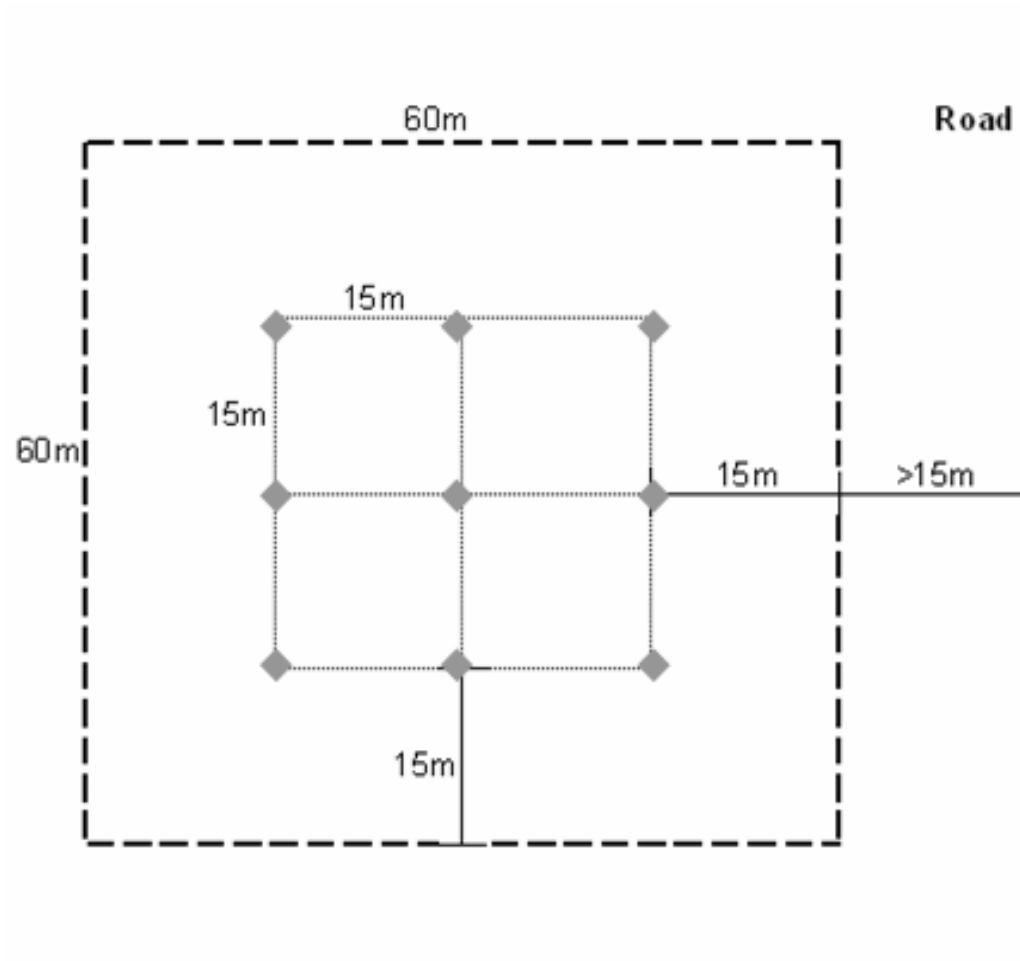
Figure 2. *Diagram of an experimental plot utilized in this study.* The outer, heavy dashed line denotes the edges of the 60m by 60m plot from which all woody debris was removed for experimental treatment. The inner, lighter dashed lines represent the 30m by 30m feeding grid, with each pair of feeders represented by a gray diamond. No feeder was within less than 15m from the edge of the cleared plot in experimental sites, and no 60m by 60m plot was within 15m of any road.

Figure 3. *Paired feeder set-up*. Vertical distance between arboreal feeder (above) and terrestrial feeder (below) is 3m.
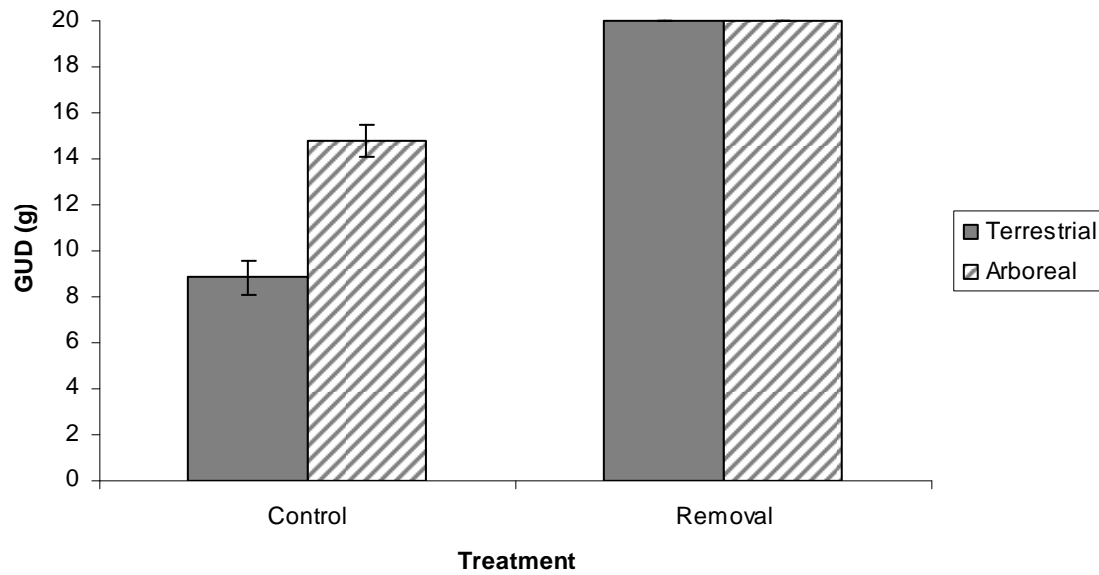
Figure 4. *Mean giving-up densities (±SE) for pairs of terrestrial and arboreal feeders between treatments.* GUDs were significantly different between treaments, with control showing more feeding than removal ($F_{1, 48} = 232.219$, $p < 0.000001$) and between feeder, with terrestrial feeder showing more feeding than arboreal ($F_{1, 48} = 35.479$, $p < 0.000001$).
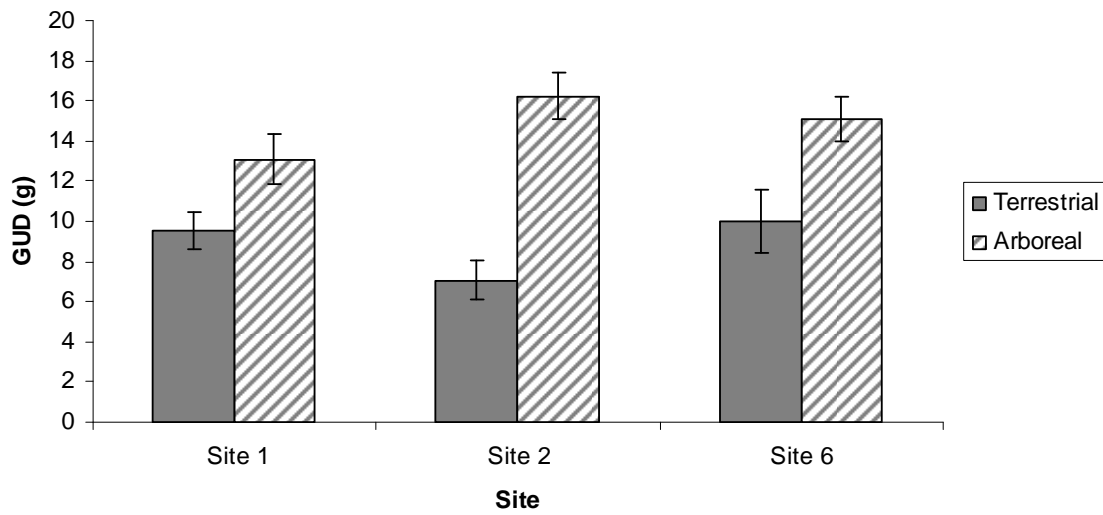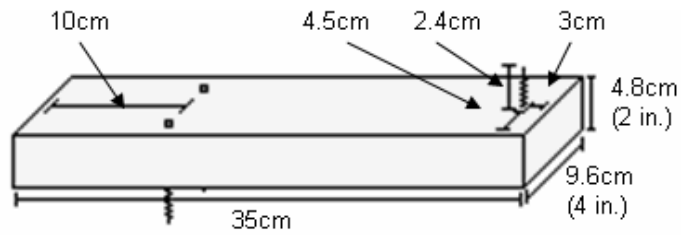
Figure 5. *Mean giving-up densities (±SE) for pairs of terrestrial and arboreal feeders across all control sites.* There was no significant difference in arboreal and terrestrial GUDs between control sites ($F_{2, 23}$ = 0.474, p = 0.629).

APPENDIX A – Dimensions of feeders and feeding cups.

Appendix A1. *Dimensions of arboreal feeder.*
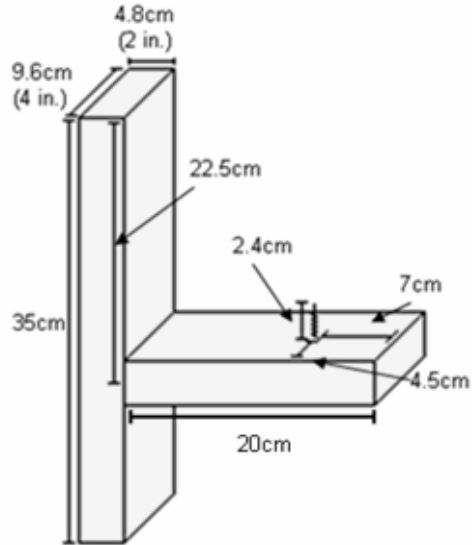
Appendix A2. *Dimensions of terrestrial feeder.*

Appendix A3. *Dimensions of feeding cup.*