

Implications of the Lunar Cycle on Rodent Foraging in Multiple Habitats

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Abstract

Giving Up Densities (GUDs) can be used to determine perceived predation threats by optimal foragers in a multi-predator environment. The marginal value theorem, upon which GUDs are based, assumes that resources are distributed patchily throughout the environment and that a forager randomly encounters them. If the marginal value of the resource at the current patch falls below the marginal value of the resources in surrounding patches, then the forager will abandon the patch. Levels of illumination can alter the perception of visual cues about predation, which in turn affects the marginal value of resources since exposed brightly lit areas are less appealing to foragers.

This study was conducted along a riparian zone, with sections of thick riparian cover and more sparse grassland vegetation. The data suggest that moonlight has no effect on GUDs in the areas of riparian cover, however in open grassland areas, GUDs decrease with increased darkness. Open grassland areas are perceived as safer during periods of low illumination, with fewer seeds remaining in these trays. Reduction in seed shells remaining in trays and the overall higher number of seeds removed from trays on nights later in the summer likely indicate that throughout all habitats, seed resources in the entire environment were becoming limited.

Introduction

Optimal foraging theory is one of the most widely studied theories in ecology due to its application to a broad array of species and systems. The basic principles behind optimal foraging theory state that a foraging animal should maximize their energetic intake when consuming food resources, while at the same time minimize their energetic costs. The value of a food source

therefore is equal to the energetic gain from the resource divided by all the costs associated with obtaining the food (MacArthur and Pianka 1966).

If resources are distributed patchily throughout the environment and a forager encounters them, they will feed on a patch until the energetic gain falls below the costs to find a new patch (MacArthur and Pianka 1966). Patches that are perceived as more favorable will be used for a longer period of time. To quantify the point at which a resource patch is abandoned, Brown (1988) used the idea of Giving Up Densities (GUDs). If the marginal value, based on energetic cost analysis, of the resources around the patch is greater than the marginal value of those within the current patch, then the forager leaves the patch. This can be quantified through the use of feeding trays and measuring the amount of resources left in the tray (e.g., Brown 1988, Bowers 1988, Kotler et al 1991).

Whereas the energetic gain from a food resource may be considered fairly simply, the potential costs due to foraging are often many-fold and not straightforward. Some costs include the time required for handling, or the time involved in searching and finding the resource. These times translate into missed opportunity costs, where the forager could be putting energy into other activities ranging from reproduction to defending their territory. Again, the marginal value of the resource must be greater than that of the search and handling time necessary to exploit the surrounding environment. Brown (1988) also incorporates predation into the cost analysis, since one must put more energy into reproduction to increase or maintain one's fitness, also necessitating a need for higher marginal values in the current patch compared to the rest of the environment. Competition would function similarly since there is an energetic cost to fighting and increased vigilance.

Many times, even a perceived threat is enough to alter a forager's behavior and reduce the marginal value of resources. The presence of predators can be detected by prey through a variety of different sensory cues. Past experiments have examined effects of predator scent cues or auditory cues around select feeding trays. By playing a predator's call around trays examined the behavioral response of rodent foragers. Visual sensory cues are another potentially huge impact on the behavior of foragers and often stems from increased illumination from moonlight. Past studies (e.g., Kotler et al. 1991, Bowers 1988) have examined moonlight effects on foraging behavior to make conclusions about perceived predation threats. They found that on bright nights, GUDs were higher (a more risky landscape) than on dark nights. In addition, on dark nights GUDs were lower (less risky) in open habitats than in closed habitats. On dark nights, avian predators, which hunt mainly in open areas, lose the ability to visually locate prey, while ground predators in closed habitats, such as snakes, do not experience this decline in hunting ability. Darkness, then becomes a limiting resource for foragers.

Evidence from marine systems (Gerrish et al.) suggest that there is a threshold level of darkness that elicits distinct behavioral responses. In a rodent foraging system, it may be the case that the light cast by a half moon elicits the same response as that of the full moon. Previous work with moonlight and GUDs examine only periods of intense lunar activity, at either the new moon or full moon. If indeed there is a threshold level, the whole lunar cycle must be examined. Furthermore, past experiments have been primarily conducted in arid or semi-arid desert habitats. This study will be conducted in adjacent riparian and grassland areas. There are very strong multi-predator effects in this landscape, which may trigger a shift in habitat use with a change in darkness. I believe that although variation in moonlight may not affect GUDs within a dense riparian zone due to cover, foragers will make an apparent shift from more covered areas

to more open areas as darkness increases throughout the lunar cycle. Of particular interest is the level of illumination that causes the switch in foraging location based on perceived predation threats at different times in the lunar cycle.

The forager I will be concentrating on during this experiment is the Deer Mouse (*Peromyscus maniculatus*). This rodent has dentition adapted for seed predation and can be found from drier shrub habitats to denser, moist riparian zones. In an unpublished study, Williams (2006) trapped 80 individuals of the species in “Dense Riparian” habitat and 104 individuals in “Riparian Grassland” habitat, along similar sections of Mission Creek on the National Bison Range. This indicates that the Deer Mouse will forage in both of my habitat types. In addition, Williams did not trap any other granivorous rodents in that study, eliminating any interspecies interactions.

As mentioned earlier, I expect multi-predator effects to play a significant role in the study and they can be broken down into two main groups. Aerial predators, which I would expect to have a greater impact in open areas are mainly comprised of owls. Present in the region and habitat types are the Barn Owl, Great Horned Owl, Northern Saw-whet Owl and the Long-Eared Owl. While these species locate prey by auditory means to an extent, they are also greatly reliant on visual cues. To a much lesser extent, harriers and some hawks may play a predation role around sunrise and sunset. The second group, ground predators, includes both snakes and mammalian predators. The main snake threat to rodent foraging is the Rubber Boa and to a lesser extent the Prairie Rattlesnake, which was visibly seen active at one of the study sites. Mammalian predators are abundant in the riparian zone, as many find it ideal habitat for residency, while others use riparian areas as corridors for movement. These predators include the Long-tailed Weasel

(*Mustela frenata*), Red Fox (*Vulpes vulpes*), Raccoon (*Procyon lotor*), Striped Skunk (*Mephitis mephitis*), Badger and Coyote (*Canis latrans*) (Montana Field Guide).

Methods

This study was conducted on the National Bison Range in Charlo, MT during the span of a full lunar cycle (new moon to new moon) during July 2008. Three sites were selected along Mission Creek, each with a riparian, grassland and transition habitat type. The different habitats were in close enough proximity so that a foraging Deer Mouse could forage between all three in a given night, being within their home range. Experimental sites were pre-baited for three days prior to the official start of the experiment, since there is a lag time in the rodent response to resource addition, altering marginal values throughout the landscape. Sampling took place for three consecutive nights, beginning on July 6 and extending through August 2. Every fourth night was taken off, giving a total of 21 experimental nights.

A 3x3 grid of feeding trays was placed in each habitat type at each of the three sites. Trays measured 15"x10.25"x.75 , were separated by 25m, and were each filled with a liter of sand. On each experimental night, 2.5 ± 0.02 g of unshelled striped sunflower seeds were placed in each tray. To decrease the marginal value of seeds within each tray, 1 tbsp of seeds were scattered in a 1 m circle around each tray. The following morning, uneaten seeds and seed fragments remaining in each tray were sifted out, collected and weighed. Seeds were placed in trays beginning a half hour before sunset and ending a half hour after sunset, plus or minus five minutes. Seed collections occurred at a similar time scale, but around sunrise. To account for seeds consumed, the mass of shell fragments were weighted according to the amount of seeds consumed in the tray.

Sunrise, sunset, moonrise and moonset data were collected from www.wunderground.com for Charlo, MT and percent illumination of the moon was obtained from the Naval Observatory website. Using these times, minutes of complete darkness were determined as well as minutes of moon illumination. These two times were combined along with percent illumination to obtain a “Darkness Value.”

$$\text{Darkness Value} = \text{Minutes of Complete Darkness} + \\ (100\% - \text{Percent of Disc Illuminated}) * \text{Minutes of Moon Illumination}.$$

To characterize the habitat surrounding each tray, percent vegetation cover, vegetation height and number of burrows were measured. Percent cover was determined from the average of three densiometer readings, and vegetation height was an average of six heights, representing the tallest plants within 1 m of the tray. These values when multiplied together gave “Vegetation Value.” Both the number and location of burrows were recorded and combined, weighting burrows closer to the tray more heavily, to give “Foraging Pressure.”

$$\text{Forage Pressure} = 5 * (\# \text{ burrows} < 1 \text{ m from tray}) + \\ 3 * (\# \text{ burrows from 1-3 m}) + (\# \text{ burrows from 3-5 m}).$$

Results

The riparian zone had a much greater percent cover and vegetation height than the grassland or transitional zones (Fig 1a and 1b). At Site 3, the transition appears to be much more similar to

a riparian habitat than a grassland habitat. Also, most of the burrows were found in the grassland, with the exception being the shockingly high foraging pressure in the transition at Site 1 (Fig 1c).

GUDs, averaged from all 9 sub-sample trays in a given night, for each habitat treatment and also by site over the summer shows differing patterns (Fig 2). In the grassland, at Sites 2 and 3, GUDs are relatively low and there is an observed peak where GUD increased around the time of the full moon. At Site 1, this relationship is not as pronounced and for almost all the experiment nights had much higher GUDs. For the transition zones at Site 1 and 2, GUDs follow a similar pattern to those in the grassland. However, for the more vegetated Site 3, the overall trend is a steady decrease in GUD over time, with no apparent peak around the full moon. GUDs in the transition zone in site 3 closely resemble those observed in the riparian zone, where there is a steady decline in GUDs over time. Also notable in this figure is the sharp decrease in GUDs, for all habitats, around night 18 or shortly thereafter. In general, GUDs for all habitat types are decreasing over time.

Comparing GUDs versus the Darkness value (Fig 3), three downward sloping trend lines were also seen for each habitat type, although the riparian regression line was the only one that wasn't significant. As the darkness resource is increasing, GUDs are decreasing, however, it is not clear now whether the decrease in GUDs is due to the experimental day and progress into the summer, or to the increasing level of darkness, or both. By running a multiple regression between GUDs and the night number and darkness level, it was seen that progression into the summer was significant in explaining the decline of GUDs for all three habitats (Riparian: $p < 0.001$; Transition: $p = 0.026$; Grassland: $p = 0.078$). Darkness level was not significant for the riparian ($p = 0.143$) however, in the transition ($p = 0.075$) and grassland ($p = 0.021$) it could also partially explain the decline in GUDs.

After running an Analysis of Covariance test (ANCOVA) with categorical variables of site and treatment and covariates of night of experiment and darkness level, it's seen that both site and treatment, as well as the interaction term between them, are significant. Breaking the data down visually into separate habitats and sites and plotting GUDs versus Darkness Level (Fig 4), one sees that for the riparian zone, none of the regressions are significant and they don't explain the data very well. In the transition zone, the regression for Site 3 is significant ($p=0.016$), for Site 2 is marginally significant ($p=0.084$) and for Site 1 is possibly approaching significance ($p=0.188$). For the grassland, all three regressions for the sites were highly significant (Site 1: $p=0.02$; Site 2: $p<0.001$; Site 3: $p=0.003$). Again, a multiple regression was ran because it was unclear whether the Darkness Level or just the night of the experiment in the summer caused the trends in GUDs. In the riparian zones, the night of the experiment was significant in explaining the decline of GUDs, whereas in the transition and grassland, the relationship was explained by both variables.

The second part of the experiment was looking at the empty shell fragments that were left in the feeding trays. Figure 5a shows the regressions for mass of empty shells versus night of the experiment, while Figure 5b has the regression with darkness as the x-variable. The regressions using night of the experiment are significant, except in the transition zone, while the regressions based on the level of darkness are not significant. Running a multiple regression with these variables, a similar result is seen where night of the experiment seems to be the only factor explaining the negative trend in empty shell masses (Table 2). Running an ANCOVA with site and treatment as factors and night and darkness level as covariates, I found significant differences between sites ($p<.001$) and treatment ($p<.001$).

Regressions were also run for GUD against vegetative cover or foraging pressure (Fig 6). Since the sites were found to be different, analysis was done by site, but insignificant regressions resulted for both vegetative cover and foraging pressure as the independent variables.

Discussion

Examining GUDs across all the nights of the experiment (Fig. 2), one sees a general trend that GUDs are decreasing. This is likely due to the fact that the surrounding environmental landscape is being depleted of resources as the summer progresses. If there are fewer resources available, but the seeds in the trays are introduced nightly at a constant value, then their marginal value increases over time and the rodents will abandon the patch at lower GUDs. In the grassland, it is interesting to see a peak or an increase in GUDs around the nights of the full moon, at least for Sites 2 and 3. Site 1 however, does not seem to follow this pattern and has significantly higher GUDs than the other two sites. Physical differences between the sites could account for this result. At Site 1, the grassland zone is at a similar elevation to the transition and riparian areas, but at the other two sites, the grassland is on a ridge above the other habitats. This lack of elevation change could lead to more riparian predators moving into the grassland making this zone extremely vulnerable to predation. Sullivan et al. (2001) found a similar result in response to topography and an elevation gradient.

Transition sites 1 and 2 act similar to the grassland habitats, which likely relates to their physical characteristics of percent cover and vegetation height which are more similar to those in the grassland than riparian areas. A difference however, is seen in Site 3, which physically appears more like a riparian zone. On the riparian graph, no peak is seen around the full moon as GUDs decline over time. It is interesting to note, however, that on all three graphs around night 18 or shortly thereafter, GUDs dramatically decrease. This indicated that the surrounding

landscape has become extremely depleted since the rodents are willing to forage for longer periods in the tray. On nights 16 and 17, which were not used as experimental nights, there were nights of intense wind and isolated storms throughout the area. Deer mice preferentially forage on *Tragopogon dubious* and dandelion species, whose seed heads are easily dispersed by wind. After these storms, rather than food resources being clumped together and found easily, resources are scattered throughout the landscape, increasing the marginal value of seeds within the feeding trays.

These results correspond to what Kotler et al. (1991,1993) and Bowers (1988) have found in previous studies. In the riparian zone, cover is great so light penetration from the moon on bright nights does not have as great of an effect. In open areas, the effect of moonlight is much greater. It would also be of interest to see whether the patterns observed, follow for the more open trays in the riparian habitat.

For empty shells, the results indicate that night of the experiment is the variable that is accounting for decreasing masses of shells and not that darkness is causing this decrease. As the summer continued, the resources in the surrounding environment were diminished leading to increased marginal values of the seeds in the trays. However, it seems that it was not cost effective to consume these seeds on the spot. Rather, the data suggest that as the experiment ran for a longer period of time, rodents were more likely to quickly build seed caches and then resume foraging, looking for another resource patch. This behavior would happen across all habitat types, as our results show. During vegetation surveys, many seed caches were come across, however, there is no way to assign them a creation date or the rate at which they add seeds to the cache over time. Darkness would not have an impact for different reasons. In the riparian zone, the effect of moonlight is again minimized due to vegetative cover, meaning that

on bright nights and dark nights, foragers could potentially spend equal amounts of time in the tray. In the grassland however, one may initially expect to see an increase in seed shells with an increase in darkness. This is not the case, however, because although there is a reduced threat of predation on dark nights it is not eliminated. The fact still remains that the forager is exposed and will opt to seek shelter when they can. This means that the rodents are most likely gathering the seeds that they can, then taking them to a nearby covered location. Evidence from the field supports this idea as there were several trays in an open area that had a large quantity of shells underneath an area with slightly more cover. The forager does not necessarily have to consume the seeds on the spot and may opt to set aside some resources in caches.

From the ANCOVA using Site and Treatment as factors and Night and Darkness as covariates, there were significant differences between both sites and treatments. The grassland had a significantly lower mass of shells in the tray than riparian areas and the differences between sites can be attributed to the overall trend of a site toward more covered riparian habitat or open grassland habitat.

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The 2008 UNDERC-West class

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Figures and Tables

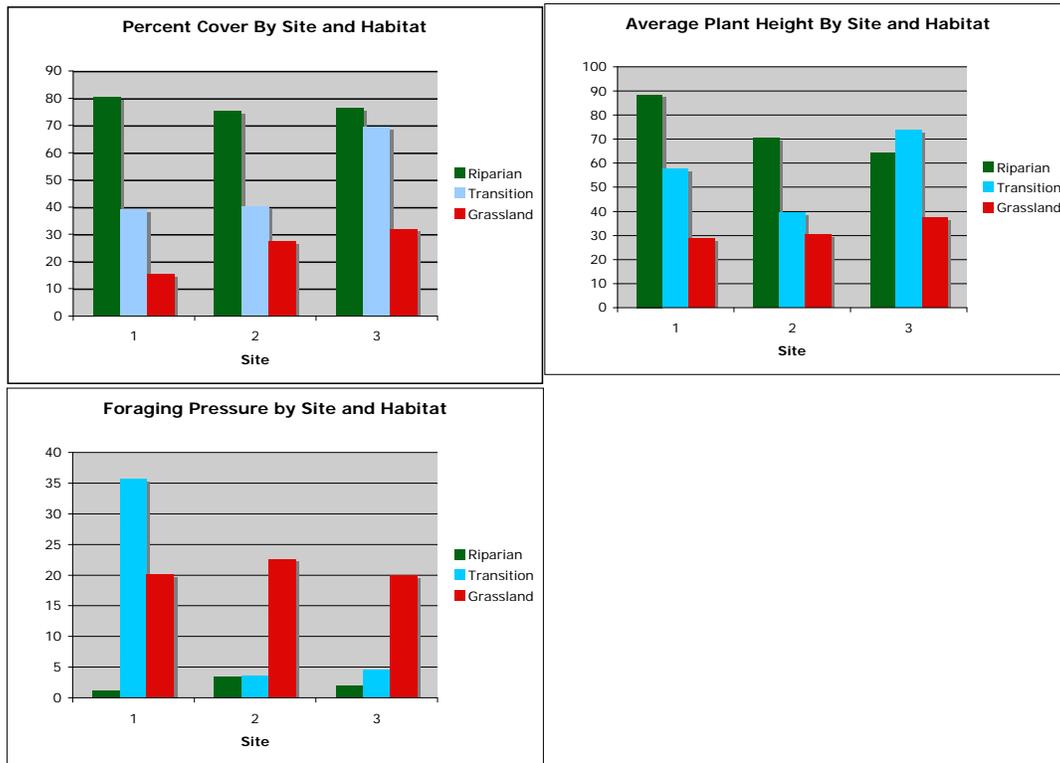


Figure 1. (a) Percent Cover, (b) Average Height, and (c) Foraging Pressure by Site and Habitat.

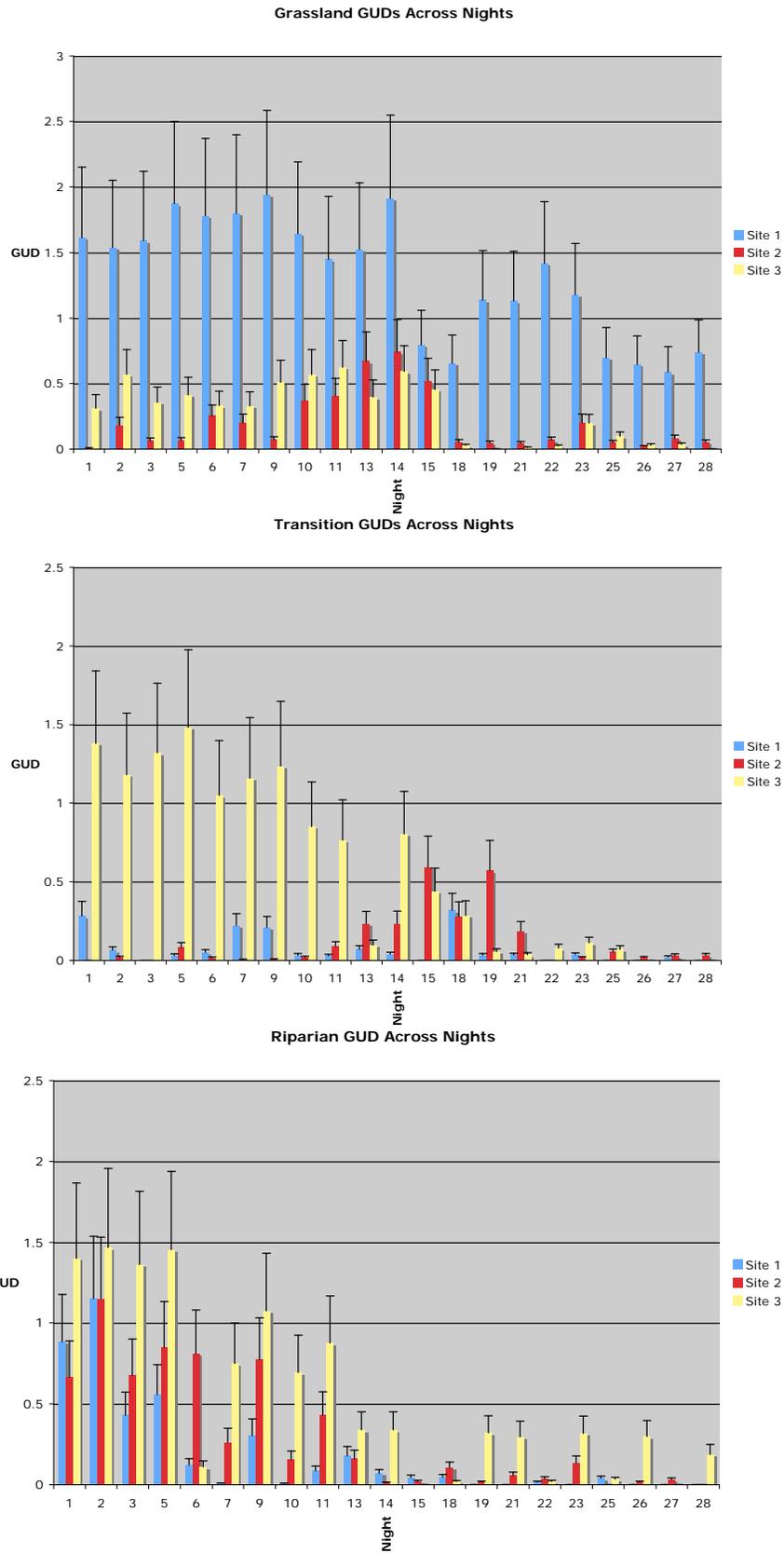


Figure 2. GUDs by Habitat and Site across the 28 days of the lunar cycle (new moon to new moon)

GUDs Vs Adjusted Time of Darkness:

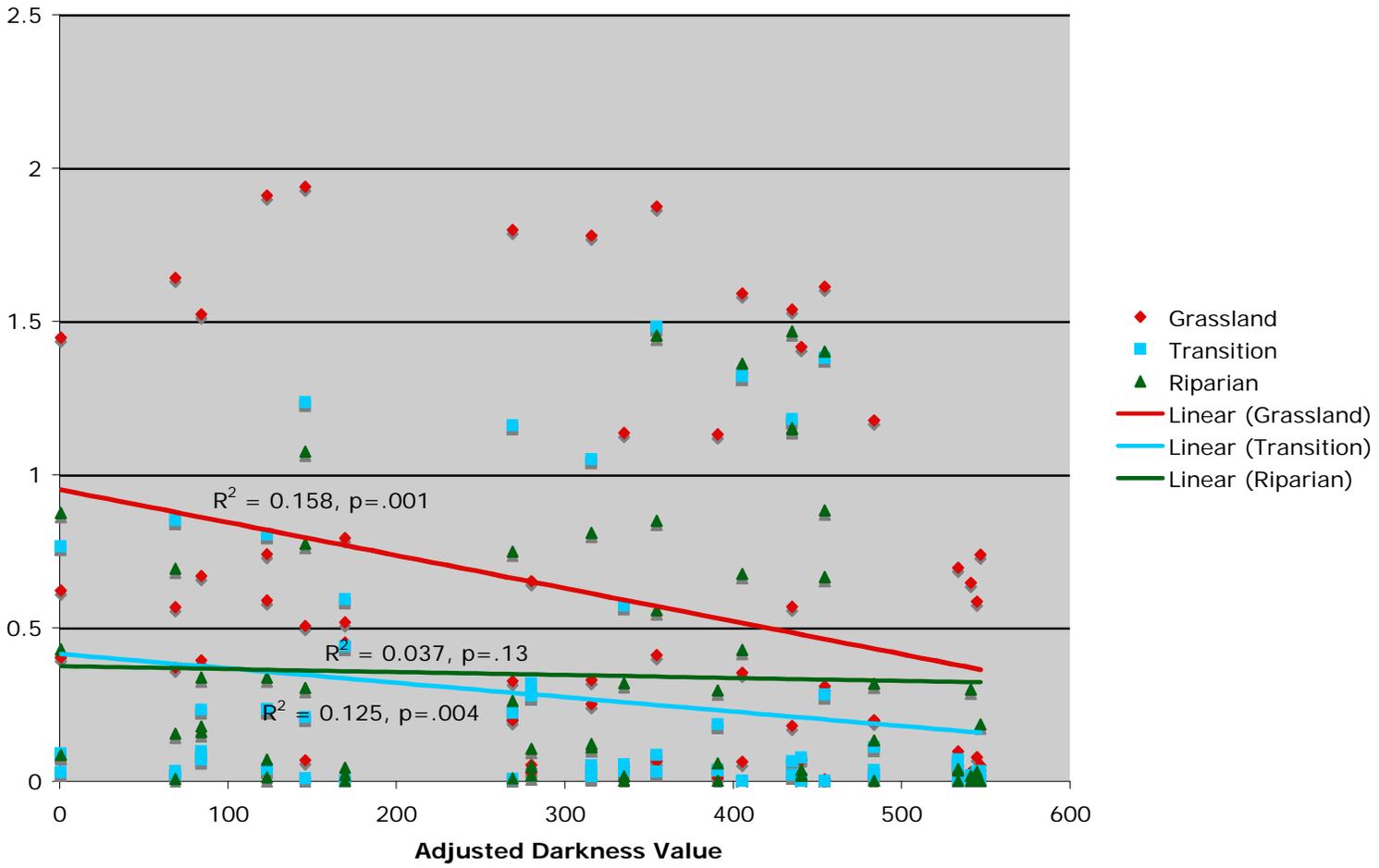


Figure 3. GUDs by Habitat Type versus Darkness

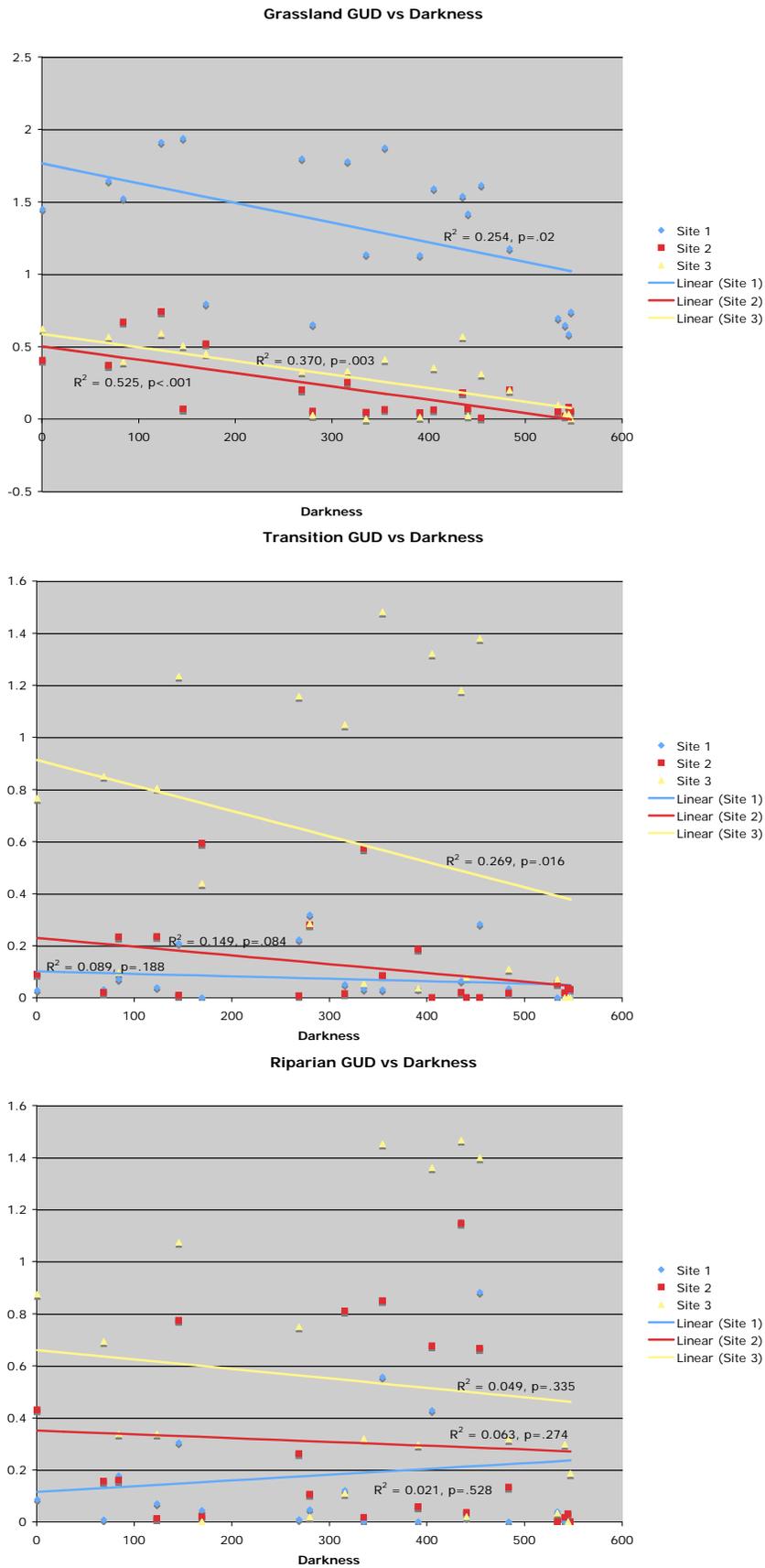
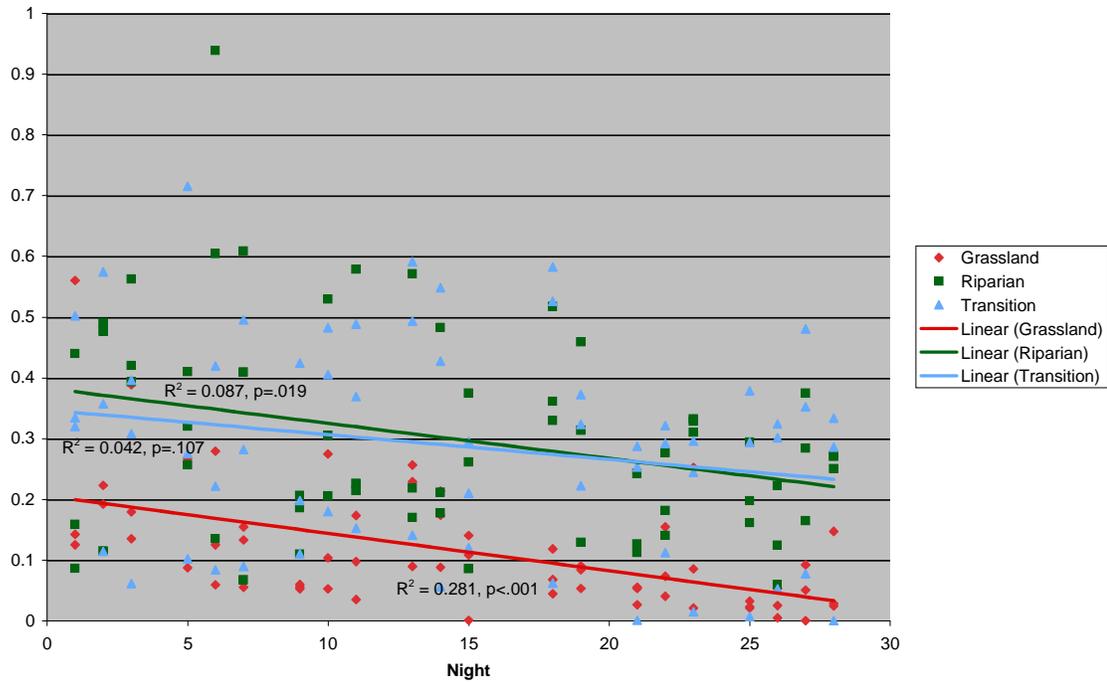


Figure 4. GUDs by Habitat Type and Site versus Darkness.

Mass of Empty Shells vs Night



Mass of Empty Shells vs Darkness

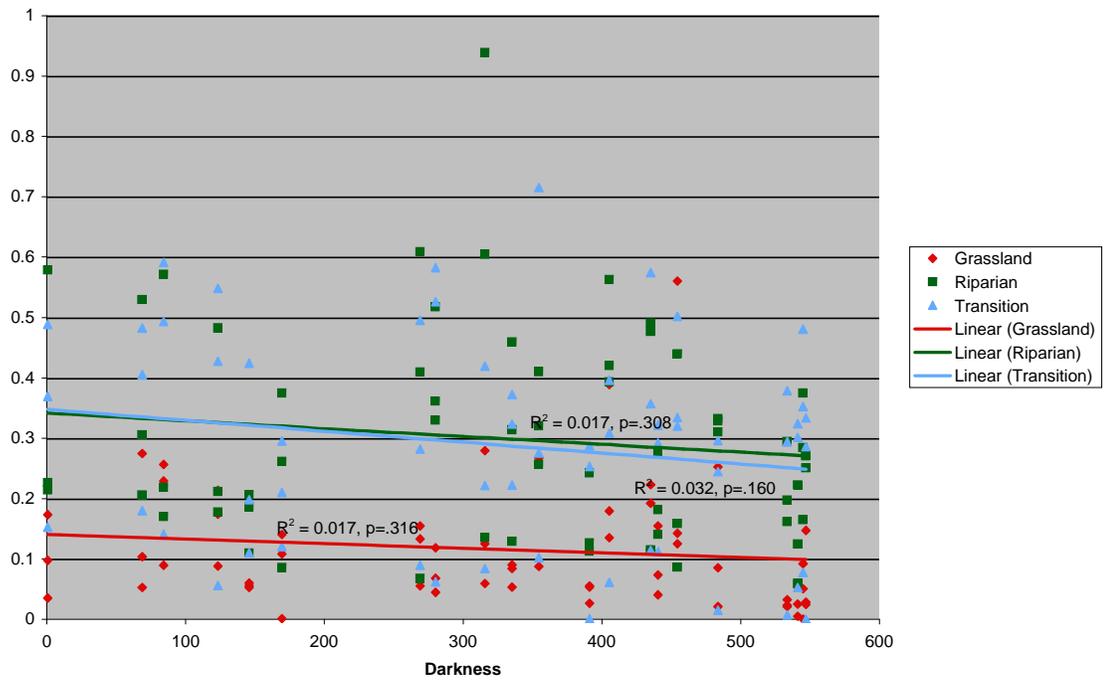


Figure 5. (a) Regression of Empty Shell Masses by Habitat versus Night. (b) Regression of Empty Shell Masses by Habitat versus Darkness.

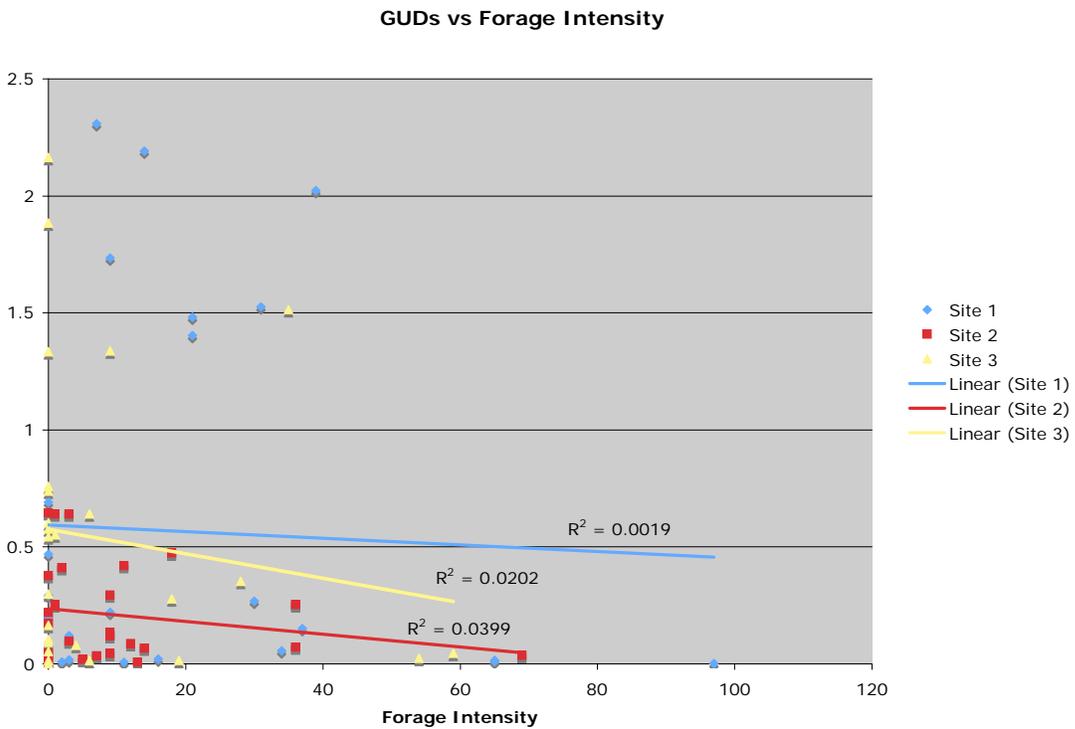
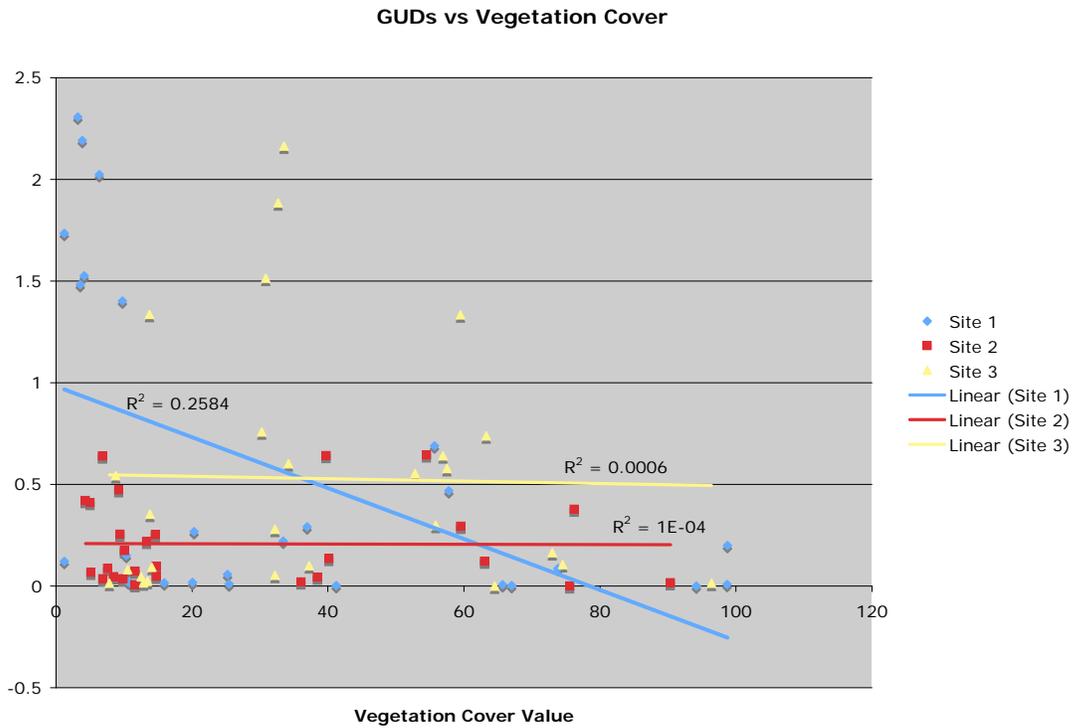


Figure 6. (a) GUD versus Vegetation Cover Value by Site. (b) GUD versus Forage Intensity Value by Site.