

Life on the Edge: Foraging and Movement Behavior of Mice at Habitat Edges

An Honors Thesis for the Department of
Biology

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Abstract

Habitat edges are highly prevalent for any organism (plant or animal) that lives in a heterogeneous environment. These edges can have pronounced effects on animal behavior, but behaviors can also impact the edge. My senior thesis examined how foraging behavior of mice (*Apodemus flavicollis*, *Peromyscus maniculatus*, and *Peromyscus leucopus*) might vary along different edges and edge gradients. I used giving up densities and movement data to examine these impacts. The studies examined two edges - one in the mountains of Poland at treeline (forest turning to meadow) and the other in Harvard, Massachusetts with patches of forest surrounded by meadow. In Poland, I examined how foraging decisions, movement, and density might differ below treeline (forest habitat) and above treeline (meadow). I was unable to complete the work on foraging, but I found that density was generally higher in the forest while movement distances were longer in the meadow. This might have interesting consequences for seed dispersal by the seed caching yellow-necked mouse (*Apodemus flavicollis*). In Massachusetts, I examined how the distance to the edge of the forest and environmental factors might impact foraging decisions. While I found a strong effect of one environmental factor on foraging, it is in the opposite direction as that found in existing literature. This suggests that there is some other factor contributing to my results.

Introduction

Edges between habitats are ever-present characteristics that the majority of animals (and plants) will encounter at some point in their life history. The boundary between habitat and non-habitat can have highly influential effects on both individuals and species as a whole (Fagan, Cantrell, & Cosner, 1999). Dobson and Meagher (1996) found that bison that crossed out of the Yellowstone National Park boundary were frequently shot and killed for fear of spreading the disease *Brucella* to nearby cattle. However, the majority of edge-mediated effects are less drastic - red-backed voles will not cross from preferred forest habitat into clearcut areas because of a lack of food items in clearcut areas (Mills, 1995). While some of the most studied edge effects are changes in abundance or fitness (Ries, Fletcher, Battin, & Sisk, 2004), edge effects can also be observed as a change in behavior. This can be seen in increases in bird nest predation by raccoons, opossums, canids, and birds (Donovan, Jones, Annand, & Thompson, 1997), a decrease in plant visitation rates by native bee pollinators (Ricketts, et al., 2008), and in the voles mentioned above (Mills, 1995). While edge environments are frequently thought of as poor habitat with low quality food and high predation risk, there is also the possibility that animals can profit from living near the edge, choosing the habitat that is temporarily more beneficially in terms of food or shelter (Hansson, 1998).

For small, primarily woodland dwelling mammals such as *Apodemus flavicollis* (the yellow-necked mouse) or *Peromyscus spp.* (deer mice), habitat edges encountered are frequently those where forest becomes meadow or grassland. Small mammals seem to take advantage of both habitats when presented with an edge, as opposed to experiencing only deleterious edge effects. While mouse abundance was found to be higher in the forested (preferred) habitat than open areas, abundance was found to be even higher at forest edges than forest interiors (Garcia, et al., 1998; Hansson, 1998). Additionally, in Britain, the highest abundances of *A. flavicollis* were recorded in small woodland patches, where the ratio of edge to forest interior was the highest (Marsh & Harris, 2000). Seed predation rates by granivores is also impacted by the presence of an edge - seed removal rates were highest right at the edge between forest and grassland, and decreased strongly

within the first 25 meters of the forest (Kollmann & Buschor, 2002). These examples suggests robust, but highly localized edge effects.

Mice play an important ecological role as both seed predators and seed “farmers” (Zwolak & Crone, 2012). Although all small mammals examined in this study are primarily granivores (Abt & Bock, 1998; Page, Swihart, & Kazacos, 2001), they also cache seeds, hiding them underground for later consumption (Wróbel & Zwolak, 2013). If the mouse does not retrieve a seed from the cache, that seed has a higher probability of emerging as a seedling than it would if it was left on the surface (Zwolak, Bogdziewicz, Wrobel, & Crone, 2016). This creates a potentially mutualistic interaction between the plant and the granivore (Zwolak & Crone, 2012; Theimer, 2004).

The interaction between seed caching and habitat edges raises interesting questions about possible influences on mouse behavior. If a mouse moves and forages differently in the presence of a habitat edge - as suggested by Kollmann & Buschor (2002) and Mills (1995) - this could influence where seed caches are made. Over time, this behavior could affect the spatial distribution of the forest and the location of the edge itself. This thesis attempts to continue the search of how the edge impacts mouse behavior and how mouse behavior impacts the edge.

Chapter 1: Mouse Abundance and Space Use at Treeline in Bieszczady National Park

Introduction:

The presence of an alpine treeline presents a highly drastic habitat edge that can have a wide impact on the species that live in habitat on either side of treeline. There is no one factor that can be said to control the location of an elevational treeline; it is a combination of biotic and abiotic factors such as temperature, wind, soil conditions, water availability, and activity of herbivores (Korner, 1990; Stevens & Fox, 1991; Speed, Austrheim, Hester, & Mysterud, 2010). However, it is clear that at some elevation, there is an invisible boundary that prevents trees from growing beyond it, creating a grassland habitat. This boundary is also changing - moving to higher elevations - as the climate changes and warms which allows for seedling establishment in areas not previously possible (Illerbrun & Roland, 2011).

Treeline can also be pushed below its environmental boundary by the activity of herbivores. In alpine meadows, sheep graze heavily on saplings at treeline, which reduces recruitment of new trees, especially when sheep density is high (Speed, Austrheim, Hester, & Mysterud, 2010). Other large mammals, such as reindeer, moose, ibex, and elk, can also cause destruction of establishing trees at treeline (Holtmeierer, 2012). Overgrazing, trampling, or increasing soil erosion can cause this destruction. However, herbivores can also “benefit” treeline by helping a tree species reach its environmental boundary. Animals that play a role as seed dispersers can assist in transporting seeds across the current treeline to new habitat. This is the case with nutcracker birds (*Nucifraga caryocatactes*), which disperse and cache the seeds of stone pines, allowing for germination of stone pines above the current treeline (Holtmeierer, 2012). Seed caching behavior is also observed in *Apodemus flavicollis* (the yellow-necked mouse), a highly prominent rodent throughout the forests of Europe (Wróbel & Zwolak, 2013). While the role of scatterhoarding rodents in expanding treeline is not as well examined, it seems logical that if mice cache seeds above treeline, they would play a role in the maintenance/expansion of the alpine treeline.

The yellow-necked mouse is a primarily woodland rodent (Marsh & Harris, 2000), indicating that time spent in meadow habitat above treeline is most likely scarce.

Nonetheless, mice have been observed in meadows (Bergstedt, 1966), indicating that there is a potential for seed caching to occur in this environment as well. For seed dispersers, movement can strongly impact the scale of seed dispersal and consequently the structure of the plant community (Nathan & Mülle-Landau, 2000; Westcott & Graham, 2000). Thus, understanding movement behavior can provide clues as to where seeds might be dispersed, including in potentially new habitats.

In this study, I analyzed how the movement and density of *Apodemus flavicollis* differs above and below treeline to begin to predict how *A. flavicollis* behavior might impact tree dispersal at treeline. I used spatially explicit capture recapture models (SECR) to estimate the density and movement distances of *Apodemus flavicollis* in the meadow and forest habitat. I predicted densities would be higher in the forest as compared to the meadow, as the forest is the preferred habitat of the yellow-necked mouse (Marsh & Harris, 2000). Additionally, I expected movement distances to be higher above treeline (meadow) as compared to below treeline (forest) as animals tend to move faster (and thus farther in a shorter time period) when moving through non-habitat (Turchin, 1991). After analyzing patterns of movement, I speculate about how these patterns might impact seed dispersal and stability of treelines.

Methods:

Study Site

Research was conducted in Bieszczady National Park (southeastern Poland) in the Carpathian Mountains (see Fig. 1). The area is dominated by forest (84% forest cover; National Research Council, 1996) with an average annual precipitation of 800-1200 mm and an average annual air temperature of 4.9°C (Smietana & Wajda, 1997). Treeline in this area occurs between 1,050m and 1,200m (Jaworski, Kolodziej, & Porada, 2002). The highest peak located in the national park (Tarnica) is 1,346 m at the summit (Smietana & Wajda, 1997) and the lowest elevation in the park is below 650m (Jaworski, Kolodziej, & Porada, 2002).

Four experimental sites (160m x 80m) were established in Summer 2012 along the treeline gradient by Dr. Rafal Zwolak, Dr. Julia Witczuk, and their research groups (see Fig. 2). The longer axis of the site encompassed the habitat gradient, changing from forest to

krummholz to meadow with increasing elevation. Below treeline contains forested habitat primarily consisting of European beech trees with a mixture of fir and sycamore (National Research Council, 1996). The krummholz is considered the treeline boundary and contains beech trees and shrubs stunted by exposure to wind. Above the treeline is meadow habitat, consisting of grasses, raspberries, blueberries (*Vaccinium*), *Rumex hydrolapathum* (great water dock), forbs, and occasional ferns. Distances between each site were large enough to prevent movement of *A. flavicollis* between sites.

Small-Mammal Trapping:

Julia Witczku, Rafal Zwolak, and their research teams conducted all small-mammal trapping. Within each of the four sites described above, Zwolak and Witczuk established a grid with numbered flagging or wooden stakes, with points spaced 10m apart. 128 live traps were placed at each site along the grid, with each trap 10m away from the closest trap. In the evening (starting at 18:00), traps were opened and baited with oats. In the morning (starting at 8:00) traps were checked for small mammals. Animals were individually marked with a uniquely numbered ear tag and the species, sex, and trap location were recorded. Trapping occurred for four nights at each of the four sites, totaling 16 nights of trapping per trapping session. Trapping sessions occurred in June and September of both 2013 and 2014 (4 sessions). This resulted in 64 nights of small mammal trapping.

Apodemus flavicollis was the most abundant small-mammal species trapped across all years, totaling 38% of all captures. Other species captured included *Apodemus agrarius*, *Myodes glareolus*, *Microtus sp.*, *Pitymys subterraneus*, *Sorex araneus*, *Sorex minutus*, *Sorex sp.*, *Sorex alpinus*, *Sicista betulina*, *Micromys minutus*, *Muscardinus avellanarius*, *Glis glis*, *Mustela nivalis*, and *Mustela erminea*.

Mouse Species

The yellow-necked mouse (*Apodemus flavicollis*) is one of the most common small mammals in Central Europe (Niedzialkowska, Konczak, Czarnomska, & Jedrzejewska, 2010), and was the most common rodent captured at the study sites. Yellow-necked mice are primarily granivores, though they will also eat insects and some fungi and herbs (Drożdż, 1966). They have also been shown to both larderhoard and scatterhoard seeds,

including beech seeds (Wróbel & Zwolak, 2013). Yellow-necked mice have also been found to undergo drastic population fluctuations with the masting cycle seen in European beech trees (Zwolak, Bogdziewicz, Wróbel, & Crone, 2015) and alter their behavior with response to cloud cover and moonlight (Wróbel & Bogdziewicz, 2015).

Data analysis:

To determine how movement (σ) and density (D) of *A. flavicollis* varied between the habitats, I used the spatially explicit capture recapture (SECR) package in R. This package assumes that each individual occupies a home range centered at an unknown location (Efford M., 2004). “Detectors” (traps) are placed around the landscape at known locations. As the distance from the home range center increases, the probability of detecting the individual (g_0) decreases (Efford M., 2004). The relationship between distance and detection probability follows a half-normal distribution with variance equal to σ . As the density of the population increases, home ranges begin to overlap. An increase in σ indicates that animals move farther from their home range center. This metric (σ) has therefore been used as a measure of home range size (Efford, Dawson, & Robbins, 2004).

I analyzed home range sizes of female *A. flavicollis* as they are more resource driven in space use and overall more territorial than males (Ostfeld, 1990). Thus they have a better-defined home range, which allows for more accurate model fitting. To add in the habitat component of the analysis, I included a habitat mask that identifies the habitat type at each trap for each site. For each site, I fitted a model in which the probability of detection (g_0) was allowed to vary by “trap-happiness”, density varied with the habitat and trap session, and sigma (movement) varied with habitat. “Trap-happiness” refers to the notion that mice are more likely to be recaptured after an initial capture because the trap is identified as a safe place with food (Nichols & Pollock, 1983; Tanaka, 1980).

Because the density of mice varied across trapping sessions due to masting events (see Chapter 2, *Results and Discussion*), this effect had to be incorporated into an average density in each habitat for each site (see *Appendix* for detailed explanation of these calculations). I calculated an average density for each habitat by averaging across the densities in that habitat for each of the 4 trapping sessions. As an *ad hoc* standard error approximation, I used the standard error from each site for each habitat without

incorporating the effect of year; the effect of year did not have much influence on the overall standard error (unpublished analyses).

Results:

Density:

In three out of four of the trapping sites, the density of female *A. flavicollis* (in mice per hectare) in the forested habitat was significantly higher than the density in the meadow habitat (based on non-overlapping confidence intervals, see Fig. 3). In the fourth site (Wetlinska), the density was higher in the meadow (8.85 mice per hectare, 95% confidence intervals calculated as log-scale mean \pm 2 standard error, hereafter CI = 5.87-13.33) than in the forest (4.1 mice per hectare, CI = 2.61-6.42), but this difference was not significant (based on overlapping confidence intervals). Across the four sites, the difference in density between forests and meadows was marginally statistically significant (2-sample t-test, $t = 2.56$, $df = 4.18$, $p = 0.06$, see Fig. 3). However, because this test statistic is based on only 4 samples, I consider this to be an ecologically meaningful difference.

Movement:

In three out of the four trapping sites, home range size (σ) of female *A. flavicollis* was significantly higher in the meadow habitat than in the forested habitat (based on non-overlapping confidence intervals, see Fig. 4). This is the reverse effect as mouse density, which was generally higher in the forest than the meadow. The site that differs from the general movement trend is the same site as differed from the general mouse density trend, Wetlinska. At Wetlinska, σ was significantly higher in the forest (25.28 meters, CI = 23.10 - 27.66) than in the meadow (11.02 meters, CI = 9.21 - 13.20). Across the four sites, home range size did not differ between forests and meadows (2-sample t-test, $t = -1.20$, $df = 5.58$, $p = 0.28$, see Fig. 4). However, lack of a significant difference may reflect the low number of sites and low statistical power, not lack of an ecologically meaningful effect.

Discussion:

The patterns of *A. flavicollis* density and movement between the two habitats indicate a difference in habitat preference. In the meadow, mouse density is very low while movement distances are large, suggesting that mice that find themselves in the meadow are likely to move farther distances. The low density in the meadow also suggests that few mice have established territories in this habitat. In contrast, the high density and short movement distances in the forest confirm that this is the preferred habitat of *A. flavicollis*, as has been suggested previously (Marsh & Harris, 2000; Montgomery, 1978). There are likely many (at times overlapping) territories in the forest, and mice are not traveling large distances in an attempt to leave the habitat. This habitat preference is most likely related to food abundance since, as primarily granivores, *A. flavicollis* eats the seeds that fall from forest trees (Abt & Bock, 1998; Drożdż, 1966).

It is currently unclear why one site had the opposite results for both density and movement between the two habitats. No obvious physical differences exist between this site and the three other trapping sites - they are located at the approximate same elevation and have similar percentages of meadow and forest on the grid. Wetlinska had the highest number of *A. flavicollis* captured as compared to the other sites, but followed the trend of more captures in the forest than the meadow (Table 1). The difference in new captures between the forest and meadow suggest that differences in capture probabilities between the two habitats could be included in future models. Further examination of the site and model with comparison to the other locations should be undertaken to determine what might be causing this difference.

The high amount of movement in the meadow raises interesting questions regarding the impact of *A. flavicollis* on treeline. Since the mice are moving much larger distances in the meadow than in the forest, any seeds that they carry with them in the meadow to be cached would have a much wider dispersal area than those cached in the forest. If the environmental conditions above treeline are favorable to seed germination and growth, it is possible that this high dispersal distance could result in expansion of the forest up the mountain, especially since seed predation rates by rodents can be higher closer to the forest edge (Kollmann & Buschor, 2002). The mutualistic relationship

between seed predators/farmers and seed germination is heavily context dependent (Theimer, 2004), but the possibility of directed dispersal of seeds to new environments would support this mutualism. However, this proposal still has many unknowns, such as if mice are transporting seeds across treeline and how mice forage in the meadow. These questions could begin to be answered through a successful experiment as explained in Chapter 2, as well as through seed tracking studies and examining beech germination success above the current treeline.

Figures: Chapter 1

Table 1. The number of captures in each habitat split by site.

Site	Total Captures ^a				New Captures ^b			
	Meadow	Krummholz	Forest	Total	Meadow	Krummholz	Forest	Total
Bukowe Berdo	38	19	38	95	20	4	15	39
Wetlinska	62	88 ^c	72	226	33	34	28	95
Rozsypaniec	67	39	84	190	32	14	29	75
Carynska	36	17	96	149	20	7	43	70
Total	207	163	290	660	105	59	115	279

^a Number of captures and recaptures. ^b Number of initial captures only.

^c This number is high because Wetlinska has the widest krummholz habitat of all sites.



Fig. 1. Field site located in Bieszczady National Park, Poland. Location of Bieszczady National Park in Poland (left). Location of 4 mountain field sites in Bieszczady National Park (right).

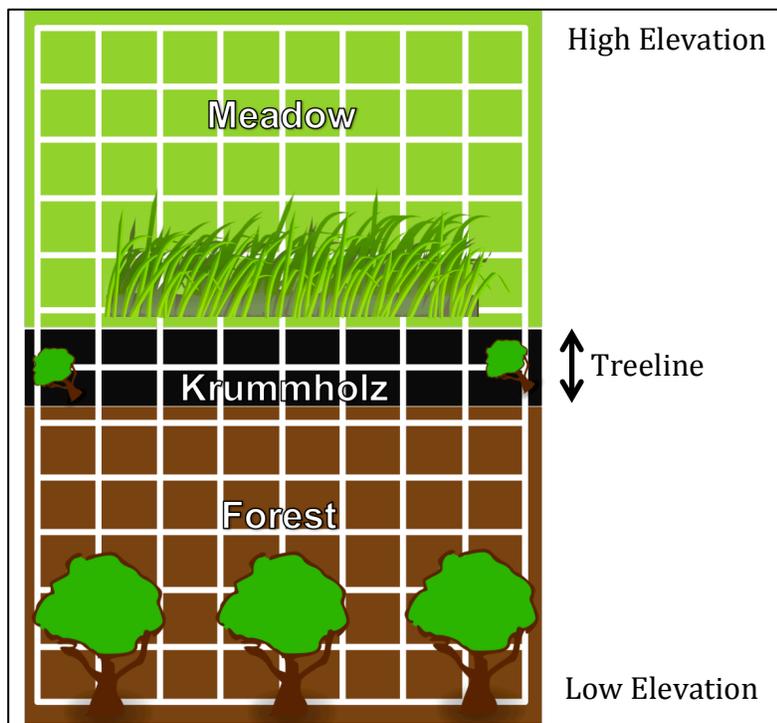


Fig. 2. Example of field site layout in Bieszczady National Park, Poland. Habitat is forest at low elevations, transitioning to Krummholz (stunted trees) and finally meadow at high elevations. Grid points are spaced 10m apart.

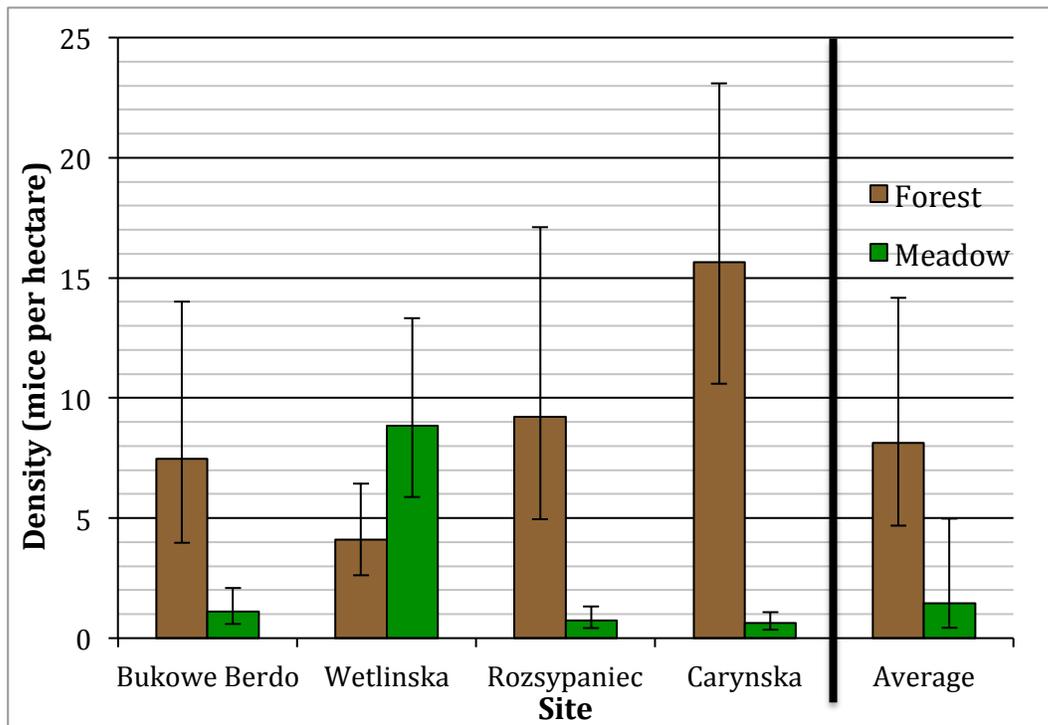


Fig. 3. Density of female *A. flavicollis* mice (averaged across trapping sessions) at each of the trapping sites and an average across all sites. Error bars for all sites indicate 95% confidence intervals calculated as log-scale mean \pm 2 standard error. Error bars for average density indicate \pm 2 standard error.

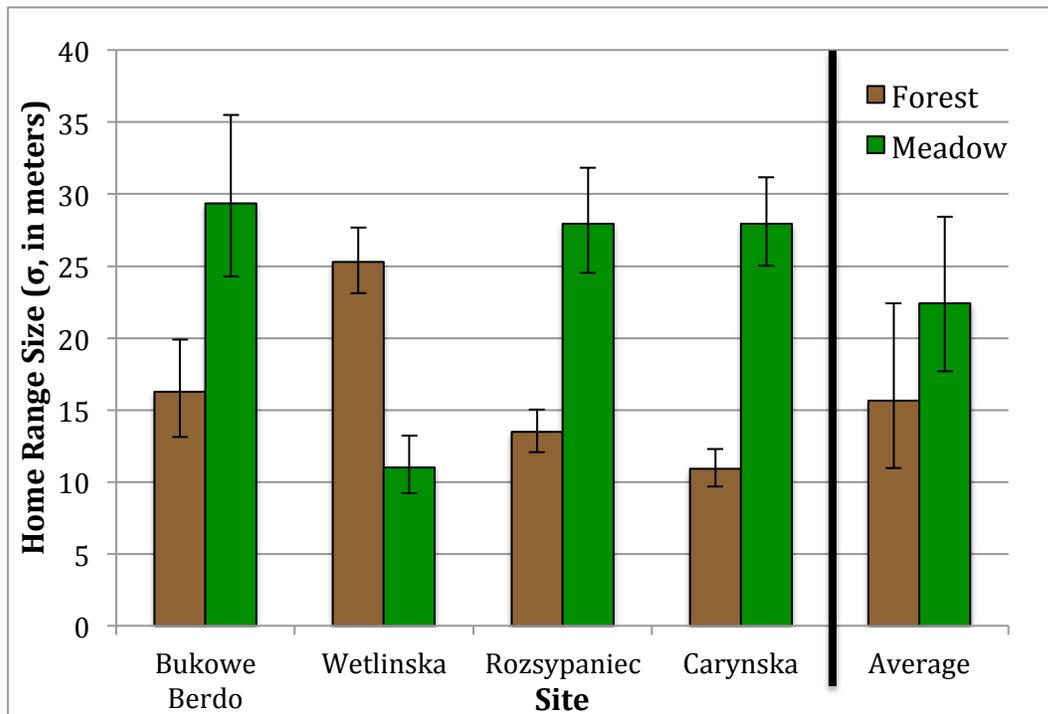


Fig. 4. Home range size (σ) of female *A. flavicollis* at each of the trapping sites and an average across all sites. Error bars for all sites indicate 95% confidence intervals calculated as log-scale mean \pm 2 standard error. Error bars for average indicate \pm 2 standard error.

Chapter 2: Giving up Densities of Mice in the Forest and Meadow at Treeline

Introduction:

The ability for mice to act as regulators of treeline via seed dispersal depends not only on mouse movement habits but also on how mice forage above treeline as compared to below treeline. If mice move through the meadow without spending time in this habitat foraging, the capacity for mice to expand treeline would be limited.

The potential for small-mammals to push treeline higher is not commonly studied. Impacts of small-mammals on treeline have frequently focused on the role of some small mammals (e.g. lemmings and voles) as herbivores (Grau et al., 2012; Olofsson, Oksanen, Callaghan, Hulme, Oksanen, & Suominen, 2009; Olofsson, Hulme, Oksanen, & Suominen, 2004; Gough, Ramsey, & Johnson, 2007; Munier, Hermanutz, & Jacobs, 2010), which would result in a stationary or receding treeline. Seed predation by small-mammals at or above treeline has also been shown to prevent treeline expansion (Castro, Gomez, Garcia, Zamora, & Hodar, 1999; Garcia, 2001). Other work regarding treeline and small-mammals focuses on how vegetational changes with altitude impact species composition and abundance (Ferro, 2013; Ulateig, 2010) as opposed to causation in the opposing direction. The impact of granivore seed dispersal on treeline is infrequently considered or discounted at best (Holtmeirer, 2012).

However, examining mouse caching and foraging behavior can serve as a proxy for how mice might expand treeline. A preference for forested habitat by *A. flavicollis* (Marsh & Harris, 2000; Montgomery, 1978) would suggest that they would stabilize treelines by preferentially caching seeds within the forest. However, mice have been observed in meadow habitat (Bergstedt, 1966) and a high amount of seeds cached near shrubs (Jansen & Nielsen, 1986; Vander Wall, 1997; Gomez, Puerta-Pinero, & Schupp, 2008) such as those found in krummholz or meadow habitat would suggest that mice help treelines advance. Before we can determine if seeds are cached above treeline, we must first identify if mice will forage in the meadow habitat above treeline and how the costs and benefits of foraging in the meadow compare to those in the forest.

In this study, I attempted to use the technique of giving-up densities to investigate foraging preference and behavior between the meadow and the forest. This technique measures the density of food resources within a patch at which the costs of continued foraging outweigh the benefits, and an individual “gives up” on foraging in that patch. By comparing the giving up densities between the two distinct habitats, I would be able to better understand foraging in the meadow versus the forest and begin to determine the impact of *A. flavicollis* on treeline. I predicted that while the giving up density would be much lower in the forest than the meadow (i.e. the forest is the preferred foraging habitat), foraging would still occur in the meadow. I also hypothesized that the frequency of foraging would decrease with increasing distance from treeline.

Methods:

Giving up densities

Giving up densities (GUDs) are a commonly used technique to identify animal foraging preferences. GUDs are defined as “the density of resources within a patch at which an individual ceases foraging” (Brown, 1988). As an animal forages in the patch, the density of resources in the patch decreases, decreasing the benefit gained as the animal must search harder for each remaining food item (Orrock, Danielson, & Brinkerhoff, 2004). At a given point, the costs of continued foraging in the patch (e.g., predation, not engaging in other activities) outweigh the benefits of continued foraging, and the individual stops foraging in the patch – i.e. gives up (Brown, 1988). The density of resources in the patch at this point is the giving up density. Assuming other factors are constant, a lower giving up density (i.e. more foraging items removed) in one habitat indicates a higher preference for foraging in that habitat over the other. I elected to use this method as it would provide a metric for foraging preference above and below treeline.

All fieldwork occurred at the same four field sites on the same grids described in Chapter 1, in Bieszczady National Park. My plan was to establish 3 transects within each site along the changing habitat gradient following the grid described above. I placed seed trays 10m apart from each other along each transect, with 48 trays placed in total at a site. The number of trays placed in each habitat was proportional to the size of the habitat (>20 in forest, ~3 in krummholz, >20 in meadow). Trays used were standard petri dishes

(100mm x 15mm) with no lid, filled with 20 sunflower seeds and sand. Sunflower seeds (unroasted and unshelled) were elected as the foraging item as mice willingly eat them and they are easy and inexpensive to procure. Twenty seeds were placed in the tray in the evening and I filled the tray to the rim with sand, mixing it to ensure an even distribution of seeds.

Filled seed trays were placed on the transects around dusk (starting at 18:00) and collected in the morning (starting at 08:00). GUDs would have been determined by counting the number of seeds remaining in each tray in the morning. If the project had been carried to completion, trays would have been set out for two nights at each of the four sites, for a total of 8 nights of data collection. This plan was changed based on very low mouse abundance and activity (see *Results and Discussion*, below).

Results and Discussion:

Data collected after the one night of placing seed offerings at one site indicated that it would not be feasible or productive to continue this experiment. All seed offerings showed little to no signs of disturbance, and I could not conclude that where trays were disturbed, the disturbance was caused by mouse foraging activity. Thus, the project was halted after one night.

The lack of foraging observed was primarily caused by a population crash of *A. flavicollis* and other small mammals in the area (see Fig. 5). Small mammal trapping occurred during the same time period (again led by Zwolak and Witckuz) at the same sites (see Chapter 1), and only one yellow-necked mouse was caught over the 16 total nights of trapping (4 nights at each site) in June 2015. This lack of mice further confirmed that I would be unable to conclude that any foraging activity observed was mice as opposed to insects or other granivores.

The population dynamics of *A. flavicollis* in this area appear to follow the dynamics of populations under the influence of masting. The phenomena of masting occurs when forest trees of the same species (in this situation beech) produce abundant amounts of fruit (beech nuts) all in the same year, followed by year(s) of little to no fruit production (Hilton & Packham, 2003). This pattern typically follows an irregular cycle. For granivores, in mast years there is abundant food available, while in non-mast years food can be severely

limited. This results in population spikes in the year following a mast year, and a population crash in the year following a non-mast year (Zwolak, Bogdziewicz, & Rychlik, 2016). At the study site, a beech mast occurred in the fall of 2013 (personal communication, Zwolak). This resulted in the huge population increase observed in June 2014 (see Fig. 5). However, since a beech mast did not occur again in 2014, food supply became severely limited and the population crashed, resulting in only one mouse capture during the trapping session of June 2015 (see Fig. 5).

Based on the habitat-specific differences in density and movement (described in Chapter 1), if this experiment had been successful I predict I would have seen much lower giving up densities (higher foraging) in the forested habitat than in the meadow. The low density and large movement distances in the meadow suggest that the meadow is not a preferred habitat of *A. flavicollis*, so I would expect any foraging that occurs in the meadow has a high cost associated with it and thus a high giving up density. However, I would still expect some foraging to occur in the meadow, as mice are present in this habitat (albeit at low densities; see Chapter 1). Finally, I would expect there to be a spatial gradient of foraging in the meadow, with higher foraging (lower giving up densities) closer to the forest edge and foraging decreasing with distance into the meadow. Ideally, this study would be repeated when the population has recovered to confirm or refute these hypotheses. A multiyear study could identify how foraging in each habitat might be impacted by masting.

Figures: Chapter 2

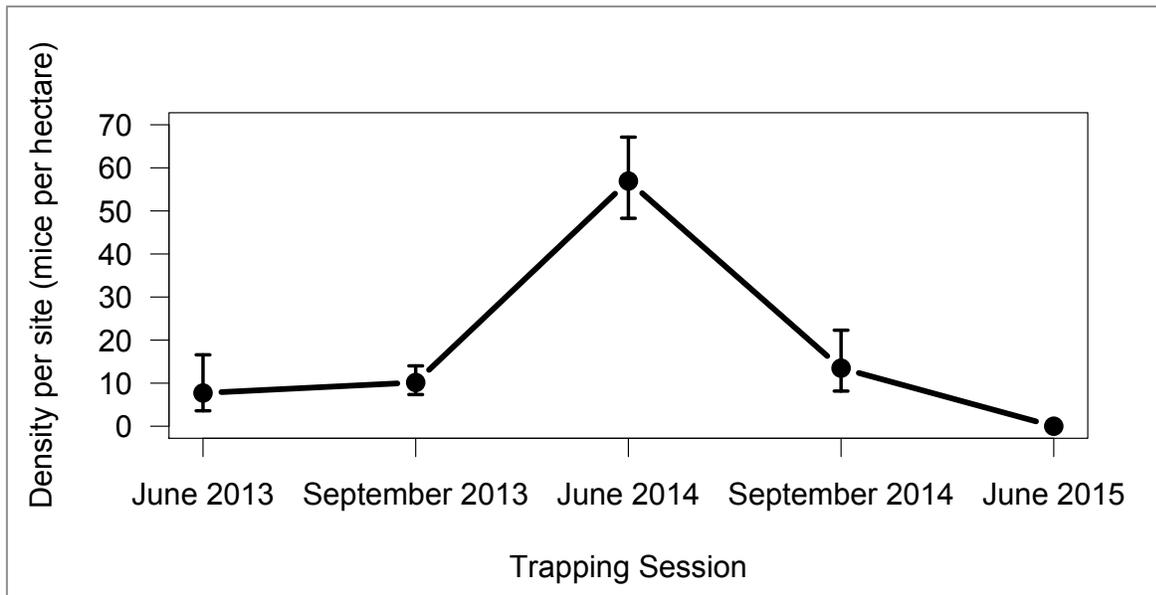


Fig. 5. Estimated density of female *Apodemus flavicollis* mice across the trapping session using spatially explicit capture recapture models. Data includes capture-recapture data from all four sites combined. Models were fit to all sites and both habitat types, using the SECR package in R as explained in Chapter 1. Error bars for all sites indicate 95% confidence intervals calculated as log-scale mean \pm 2 standard error. No error bars are present in June 2015 as only one mouse was captured during this session.

Chapter 3: Giving up Densities of Mice in Forest Patches in Central Massachusetts

Introduction:

While alpine treeline provides a good example of a clear edge with pronounced edge effects, the transition from forest to meadow without an altitude component is more commonly studied and also has widespread impacts on the surrounding environment. Natural forest edges are typically not a sharp boundary, there is usually an “edge zone” where the microclimate and community structure differs from the interior of the forest (Matlack, 1993). In this edge zone, shrub cover, light, and temperature decrease with increasing distance into the forest (Matlack, 1993). It stands to reason that if the forest to habitat edge is more of a gradient in terms of microhabitat and vegetation, then the effects of the edge on animal behavior could also be described as a gradient. This gradient can be seen through effects on animal abundance, where the number of species, species diversity, and overall abundance increased as distance from the edge into the forest increased (Stevens & Husband, 1998).

In this study, I investigated how foraging of woodland mice (*Peromyscus spp.*) might change in relation to distance into the forest and environmental variables. I used the technique of giving up densities (see Chapter 2) to examine foraging patterns at different edge distances. I expected foraging to decrease with increasing distance from the edge, as seed predation rates have been found to be higher in an edge environment (Kollmann & Buschor, 2002). In addition to edges, I analyzed the effects of lunar illumination as a predictor of GUD. I expected foraging to be altered by the presence of indirect predation cues such as moon illumination (Fanson, 2010).

Methods:

Study Site:

Research was conducted at the Williams Property in Harvard, Massachusetts on a small area of land primarily used for recreation purposes (see Brown and Crone, 2015). The site is approximately 10.5ha and consists of large areas of meadow and a few scattered forest patches (Brown & Crone, 2015). Average air temperature is 47°F (8.3°C) and

average annual precipitation is 48 inches (1220mm; USA.com). The forest in the area is primarily composed of oak trees with some maples and pines (Hall, Motzkin, Foster, Syfert, & Burk, 2002).

I established two experimental patches in late August 2015. The smaller patch measured approximately 20m x 16m, while the larger site consisted of two adjacent rectangles measuring 28m x 20m and 12m x 16m (see Fig. 6). The patches were both forest habitat but were surrounded on all sides by meadow habitat. I created a grid on both patches using flagging with points spaced 4m apart. The two patches were approximately 50m apart from each other.

Mouse Species:

Two mouse species, *Peromyscus maniculatus* (deer mouse) and *Peromyscus leucopus* (white-footed mouse), are present in the study region (Lindemann, Harris, & Keller, 2015; Choate, 1973). Both *P. leucopus* and *P. maniculatus* are primarily granivores, though they will also eat lepidopterous larvae and other plant matter (Whitaker, 1966). *P. maniculatus* is more commonly found in open areas while *P. leucopus* generally inhabits wooded areas (Whitaker, 1966) but can also be considered a habitat generalist (Lindemann, Harris, & Keller, 2015).

To verify that only mice were removing seeds, I placed wildlife cameras around the two patches prior to and during the experiment. At night, I only observed mice (*Peromyscus spp.*). The two *Peromyscus* species cannot be distinguished from photographs, and I was unable to perform trapping at the sites to identify specimens to species.

Giving up densities:

The same technique of giving up densities as described in Chapter 2 was utilized in this experiment. Foraging dishes (standard petri dishes with no lid) that had been filled with a mixture of 20 sunflower seeds and sand were placed at each point along the grids described above. The distance to the edge for each dish was found by measuring the closest distance from the tray to the forest-meadow edge. Filled dishes were placed on the landscape at dusk (starting at 19:00) and collected and counted at dawn (starting at 05:30) for six continuous nights in late August. Care was taken to ensure that dishes were put out

and collected before squirrels became active (daylight hours), as they would readily forage on any food available during the day (personal observation). During the experiment, nightly temperatures remained fairly constant around 66°F (19°C) and there was no precipitation recorded in the area at any point of the study period (The Weather Company, 2016). A full moon occurred on the fourth night (August 29th) of the study.

This study was originally designed to investigate the effect of protection from predation on the giving up densities as well as the distance from the forest edge. Thus, three different types of covers (“treatments”) were designed in an attempt to prevent predation from aerial predators, terrestrial predators, or both and were placed over trays for the duration of the study in a pseudo-random fashion. Additionally, percentage of microhabitat cover was measured as this can be an indirect predation cue (Fanson, 2010). However, as there was no effect of treatment or microhabitat on giving up densities ($\Delta\text{AIC} > 10$ for all models including treatment and microhabitat), I elected to pool results across treatments and microhabitats and focus on the effect of edge and moon.

Data Analysis:

Data were analyzed using binomial generalized linear mixed-effects models with the number of seeds eaten at a tray indicating a success and the number of seeds remaining at a tray indicating a failure. I performed a model selection analysis in which I explored a range of predictor variables to determine which predictors had significant impacts on the giving up density. Due to a limited sample size, I primarily examined predictor variables one at a time, keeping single predictor variables in the model if they had a significant effect. The predictor variables I explored included phase of the moon, distance to the forest edge, and temperature (scaled so the average nightly temperature during the experiment was 0°). Models included random effects of tray location on grid (tray ID) and a unique tray identifier (each tray treated uniquely regardless of night, unique ID) to account for over-dispersion (Elston, Moss, Boulinier, Arrowsmith, & Lambin, 2001). I determined the best-fit model by using AIC (Akaike information criterion) (Bolker, 2008).

Results:

Model Selection:

Our best model of giving up density (GUD) included two-way interactions of distance from the edge and the moon phase, and nightly average temperature and the moon phase. The best model also included random effects of the tray ID and the unique ID (see Table 2).

Distance to Edge and Moon:

I found a slightly significant (Type II marginal hypothesis test, $X^2= 3.77$, $df= 1$, total observations= 255, $p= 0.0523$) interaction between the distance from the tray to the forest edge and the phase of the moon, but no significant edge effect alone (Type II marginal hypothesis text, $X^2=0.070$, $df= 1$, $p= 0.7914$). Overall, foraging increased as moon illumination increased (Fig. 7). However, the effect of distance changed depending on the phase of the moon. When the moon was not full (i.e. August 26, 27, and 31), the lowest proportion of seeds removed was recorded at trays 1 meter from the forest edge (6% on August 26, 95% Confidence Intervals (hereafter CI) = 3 - 15%) while 44% of seeds were removed from trays 15 meters into the forest (CI = 17 - 75%). However, during the full moon there was no significant difference between seed removal at different distances from the edge (99% for 1 meter from edge, CI = 98-100%; 90% for 15 meters from edge, CI = 72-99%). Thus, the decrease in giving up density with increasing moon illumination was greater for trays that were closer to the edge of the forest (1 meter) than those further inside the forest (15 meters).

Temperature and Moon:

The average nightly temperature over the course of the study was 66.0°F (18.9°C), with the highest average nightly temperature (70.7°F; 21.5°C) on August 31st and the lowest average nightly temperature (61.8°F, 16.6°C) on August 28th. Increasing temperature significantly decreased GUD (Type II marginal hypothesis test, $X^2= 9.94$, $df= 1$, total observations= 255, $p= 0.0016$, see Fig. 8) and there was a slightly significant interaction between temperature and the phase of the moon (Type II marginal hypothesis test, $X^2= 3.71$, $df= 1$, total observations= 255, $p = 0.0541$).

Discussion:

In this study, the effects of edges on mouse giving up densities were much smaller than the effects of illumination. The forest patches I used were small, with no trays further than 15m from the forest edge. Thus, the interior of my patches would still be considered the edge in other studies using giving up densities to examine edge effects (Jacob & Brown, 2000; Morris & Davidson, 2000; Wolf & Batzli, 2004). The presence of edges results in decreased foraging as they are seen as “riskier” habitat than the forest interior by small-mammals (Morris & Davidson, 2000; Wolf & Batzli, 2004).

The positive relationship between nightly temperature and foraging activity is consistent with other examinations of activity in small mammals (Fanson, 2010; Vickery & Bider, 1981; Kotler, Brown, & Mitchell, 1993). This relationship is suspected to be a result of less energy required for thermoregulation at higher temperatures leading to a reduction in foraging costs (Fanson, 2010).

Results regarding illumination were less consistent with other studies. In this study, mice increased foraging as moonlight illumination increased. Most other studies have found that, overall, mice are less active during the full moon than at other moon phases. This change in activity is thought to be a result of increased predation threat with increased illumination, as the illumination increases the ability of predators to detect prey (Prugh & Golden, 2014). A reduction in *Peromyscus* activity during the full moon has been identified via sand transects (Vickery & Bider, 1981), tracking (Wolfe & Summerlin, 1989), and capture probabilities (Wróbel & Bogdziewicz, 2015). Mice have also been observed to shift activity from open areas to covered areas during moonlit periods (Wolfe & Summerlin, 1989). In contrast, Barry & Francq (1982) and Orr (1959) found no effect of moonlight on activity levels.

The reduction of activity has also been noted when using giving up densities, with a lower proportion of seeds eaten during the full moon (Fanson, 2010; Orrock, Danielson, & Brinkerhoff, 2004; Prugh & Golden, 2014). This is the exact opposite as what I observed in this study, where a higher proportion of seeds (almost 100%) was eaten during the full moon. Additionally, Bowers & Dooley (1993) observed that not only did *Peromyscus leucopus* reduce foraging during the full moon, but activity at the edge of patches was more

reduced than activity in the interior of the patch. While I did not find a significant impact on the distance from the forest edge on foraging during the full moon, the present trend indicates that foraging was greater closer to the habitat edges as opposed to the interior of the forest.

The most likely explanation for the increase in foraging observed during the full moon is due to a change in density in the forest patches used. In open habitats such as a meadow, predation risk for small mammals is generally higher due to the lack of protective cover (Orrock, Danielson, & Brinkerhoff, 2004). Thus, as increased moonlight increases predation risk, animals move from open, meadow habitats to more covered, forested habitats (Brown, Kotler, Smith, & Wirtz, 1988). So, if mice move into forested patches from the meadow during a full moon, this would increase the density of mice in the forest patch during this time. This increase in density could result in a perceived increase in foraging activity and a higher proportion of seeds removed, as more animals are foraging in a constant number of trays. This is one flaw in using a giving up density as a proxy for foraging activity, as it cannot account for fluctuations in animal density over a study period. It is possible that these density changes do not affect all portions of the forest patch equally - if animals move from the meadow to the forest during the full moon but remain at the forest edges rather than move fully into the center of the patch, this might result in the slight trend observed of slightly higher foraging 1 meter from the edge as compared to 15 meters.

To determine if changes in animal density across the habitat are causing a perceived increase in foraging activity, small mammal trapping could be performed in both the meadow and forest habitat during the same lunar cycle as used in this experiment. This would allow for identification of how density changes throughout the lunar period, using the data analysis described in Chapter 2. It would also be interesting to perform this experiment again, but place foraging trays in both the forest and the meadow. If this were done tangentially with trapping to control for density, this would allow for identification of how foraging itself changes across the habitat gradient and lunar cycle.

In conclusion, this study demonstrated that overall the effect of lunar illumination was larger than the effect of the habitat edge, but there was a marginally significant interaction between the two effects. The increase in foraging observed during the full

moon is likely a result of an increase in local mouse density. Integration of these methods and results into the meadow and larger forest patches could be undertaken for future work.

Figures: Chapter 3

Table 2. AIC and dAICc of Tested Models for Giving up Densities in Massachusetts.

Model Name	Predictor Variables	Random Effects	AIC ^a	dAICc ^b	df ^c
m0	None	None	4709.5	3406.4	1
m1	Moon	None	4549.7	3246.6	2
m2	Moon*Distance to Edge	None	4506.5	3203.5	4
m3	Moon*Distance to Edge	Tray ID	3015.4	1712.5	5
m4	Moon*Distance to Edge	Tray ID; Unique ID	1312.4	9.6	6
m5	Moon*Distance to Edge Moon*Temperature (scaled)	Tray ID; Unique ID	1302.6	0.0	8

^a Akaike Information Criterion; ^b Difference in AICs corrected for small sample size;

^c Degrees of Freedom

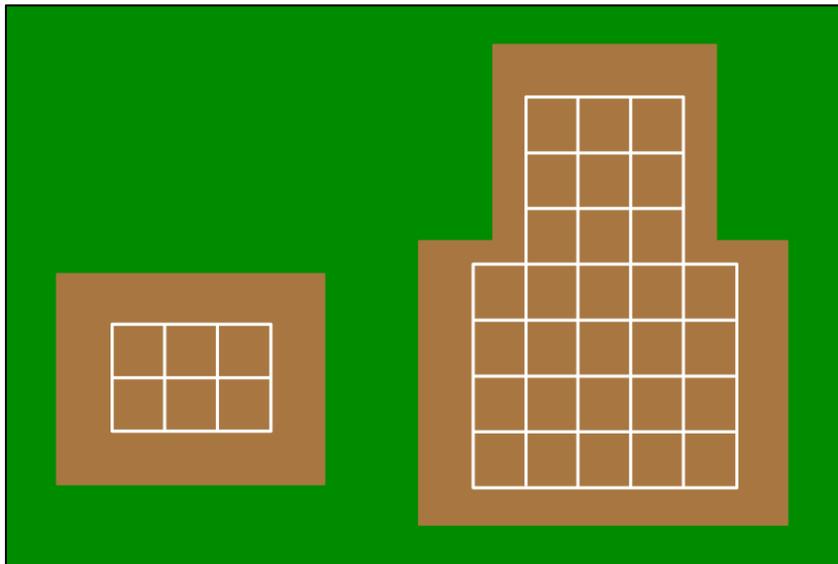


Fig. 6. Field site setup in Harvard, Massachusetts. Brown represents two forest patches surrounded by meadow (green). Grid was set up inside forest patches with points spaced 4m apart. The two patches were approximately 50m apart.

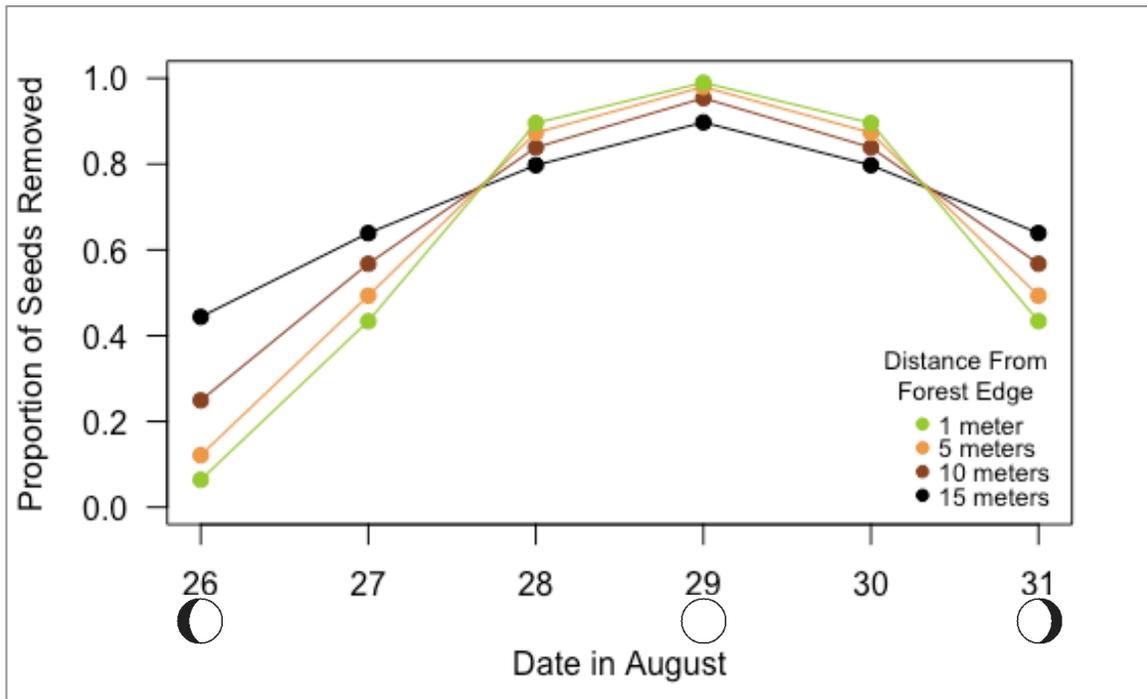


Fig. 7. Effect of distance from the forest edge on the estimated proportion of seeds removed (eaten) from foraging trays over the study period in August. A full moon occurred on August 29th; August 26th and 31st were waxing and waning gibbous moons, respectively.

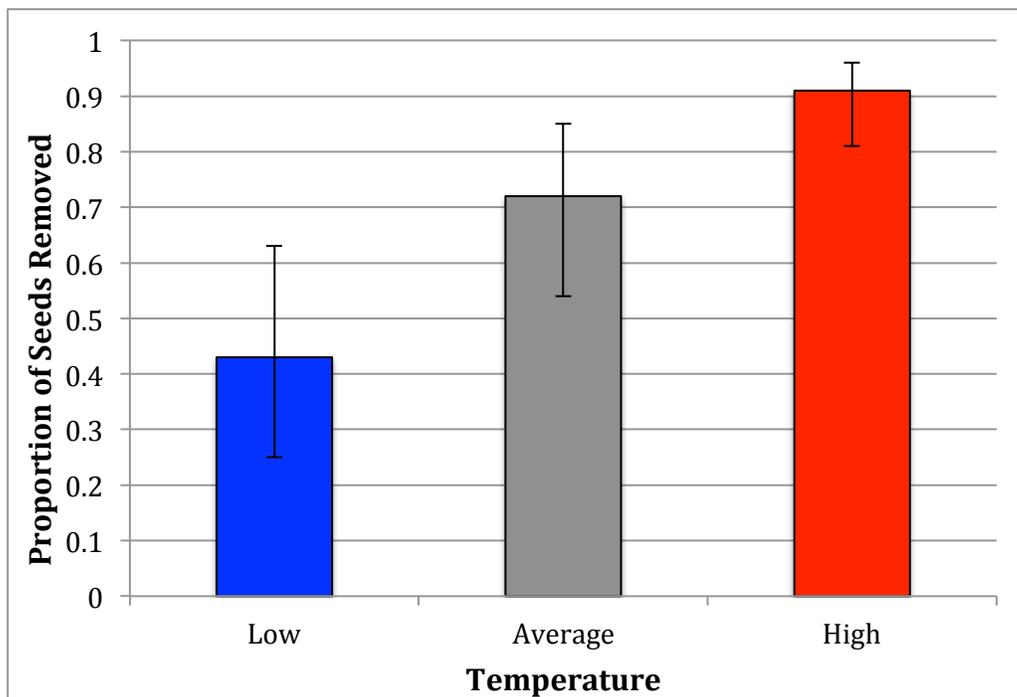


Fig. 8. Effect of temperature on the estimated proportion of seeds removed (eaten) from foraging trays. Temperature indicates the highest (70.7°F; 21.5°C), lowest (61.8°F; 16.6°C), or average (66.0°F, 18.9°C) nightly temperature recorded during the study period (from The Weather Company, 2016). Effect is examined at the average lunar illumination over the study period. Error bars indicate 95% confidence intervals calculated as log-scale mean \pm 2 standard error.

Conclusion

This thesis supports the effect of habitat edges on the behavior of small mammals and suggests that small mammals might also strongly impact the edge. In addition to changing abundance patterns (Garcia et al., 1998; Hansson, 1998) and seed removal rates (Kollmann & Buschor, 2002), my work indicates that the habitat edges can impact movement, density, and foraging behavior in mice. Combined with the dual role of mice as seed predators and seed farmers (Zwolak & Crone, 2012), this suggests mice can play an important ecological role as mediators of habitat edges.

To fully identify how mice might impact treeline, three characteristics of mice and seeds must be identified: how much do mice leave the forest to go into the meadow, how far do mice move when they are in the meadow, and what is the germination success of seeds in the meadow? In Chapter 2, I was unable to determine how *Apodemus flavicollis* might allocate foraging behaviors between the forest and the meadow due to a crash in the population. However, based on spatial analysis of densities from past trapping, I expect that mice spend more time foraging in the forest as compared to the meadow, but with some foraging occurring in the meadow above treeline. Combined with the results from Chapter 1 that *A. flavicollis* moves greater distances in the meadow, this would indicate that it is possible for mice to cache seeds in the meadow far away from parent plants. Repeating the experiment performed in Chapter 2 in a year of higher population densities could further identify how time allocation varies above and below treeline.

To complete the examination of mice as drivers of treeline placement, the survival of seeds above and below treeline could be compared. If seeds above treeline can germinate, this would suggest that the current treeline is below its environmental boundary and would lend further support to mice as potential drivers of treeline. Seed tracking experiments could also be performed to identify the rate at which seeds are transported from the forest into the alpine meadows.

The meadows above treeline in Bieszczady National Park are prized for their beauty, rare wildflowers, and attraction to tourists. Thus, as climate change creates environments hospitable to higher elevation treelines, *A. flavicollis* could play a role in the shrinking of

these alpine meadows. Should management practices be considered to keep the desired meadows in place?

My work on foraging in Harvard, Massachusetts identified interesting interactions between the forest edge, changes in density, and the lunar phase. I observed that the distance to the forest edge had a smaller impact on mouse foraging than the effect of moon illumination. This is likely caused by the use of small forest patches, where the interior of my patch is frequently still the edge of other studied patches (Morris & Davidson, 2000; Wolf & Batzli, 2004). While many studies have indicated a decrease in foraging and activity during the full moon (Bowers & Dooley, 1993; Fanson, 2010; Orrock, Danielson, & Brinkerhoff, 2004; Prugh & Golden, 2014), I found that foraging increased during the full moon. This could be attributed to an increase in density as *Peromyscus spp.* concentrate in the forest during the full moon instead of the more dangerous meadow. This suggests that mice can easily move across the edge and select the more beneficial or less costly habitat for foraging. Small-mammal trapping and giving up densities in both habitats over a lunar month could confirm the influence of density on foraging.

This thesis adds to the body of literature investigating the effects of habitat edges on mammals. Understanding these effects is increasingly important as humans lead to increased habitat fragmentation and thus an increase in the amount of habitat edges that exist.

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Appendix: Determining Average Density of Mice with Effect of Year

The calculations that follow were repeated for each of the four sites. To incorporate the effect of year on density, I extracted the density for each year and each habitat from the SECR models, and then averaged the densities within the habitat. In the models run, the first trapping session (June 2013) and forest habitat were set as the baseline values. Thus, to determine the density in the other sessions in the forest, the coefficient for the session desired was added to the baseline density. For example, to determine the density in the forest for September 2013, the equation was: Baseline Density + Coefficient for Density September 2013 = Overall Density September 2013. I repeated this process for all sessions (see Table A1). I then found the average value for the density in the forest across all sessions.

For the meadow habitat, I used the same equation but added the coefficient for density in the meadow. For example, to determine the density in the meadow for September 2013, the equation was: Baseline Density + Coefficient for Density September 2013 + Coefficient for Density in Meadow = Overall Density in Meadow for September 2013. I repeated this process for all sessions (see Table A1). Again, I then found the average value for the density in the meadow across all sessions. All values were finally back-transformed from a log-scale.

Table A1. Calculating Average Density of Mice with Effect of Year with values from example Bukowe Berdo Site

Session	Habitat	Equation	Values	Result
June 2013 (Baseline)	Forest (Baseline)	Baseline + 0 + 0	1.52 + 0 + 0	1.52
September 2013	Forest	Baseline + Coef Sep 13 + 0	1.52 + 0.18 + 0	1.70
June 2014	Forest	Baseline + Coef June 14 + 0	1.52 + 1.44 + 0	2.96
September 2014	Forest	Baseline + Coef Sep 14 + 0	1.52 + 0.34 + 0	1.86
Average	Forest	(June 13 + Sep 13 + June 14 + Sep 14)/4	(1.52 + 1.70 + 2.96 + 1.86)/4	2.01
June 2013 (Baseline)	Meadow	Baseline + 0 + Coef Meadow	1.52 + 0 + (-1.90)	-0.38
September 2013	Meadow	Baseline + Coef Sep 13 + Coef Meadow	1.52 + 0.18 + (-1.90)	-0.2
June 2014	Meadow	Baseline + Coef June 14 + Coef Meadow	1.52 + 1.44 + (-1.90)	1.06
September 2014	Meadow	Baseline + Coef Sep 14 + Coef Meadow	1.52 + 0.34 + (-1.90)	-0.04
Average	Meadow	(June 13 M + Sep 13 M + June 14 M + Sep 14 M)/4	(-0.38 + (-0.2) + 1.06 + (-0.04))/4	0.11