

POST-DISPERSAL SUGAR MAPLE (*ACER SACCHARUM*) SEED  
PREDATION BY SCIURIDS AND OTHER SMALL MAMMALS IN A NORTHERN  
HARDWOOD FOREST

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This is dedicated to my family and friends for their unwavering support.

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## INTRODUCTION

Seeds are important food resources for many small mammal species (Snyder 1982; Steele 1998). To maintain a more constant food supply, small mammals often store seeds, referred to as seed caching or hoarding behavior. Also, during periods of abundant food but adverse weather, food hoarders can avoid harsh conditions by relying on their stored food supply (Vander Wall 1990). Caching also allows individuals to benefit from a short-term rich food patch for a longer period. An individual can first satisfy its current energy demands, then store some items from the energy-rich patch, and consume those items at a later time after the patch is depleted (Clarke and Kramer 1994a).

### *Caching Behavior*

The main purposes of food hoarding are to delay consumption of food items and to discourage others from consuming the stored food because burying makes the food items more difficult for naïve foragers to locate (Vander Wall 1990). Small mammals can scatter hoard seeds by storing small amounts of food in relatively widely-dispersed, small storage sites, or they can larder hoard them by concentrating food in piles (Clarke and Kramer 1994a; Vander Wall 1990).

Although scatter hoarding and larder hoarding represent two extremes on a continuum of hoarding behavior (Vander Wall 1990), studies have shown that some species employ both hoarding techniques (Clarke and Kramer 1994b; Hurly and Lourie 1997). Both methods have advantages and disadvantages. Larder hoarding concentrates

food into one or a small number of places and facilitates relocation. Also, if a competitor discovers the larder hoard and pilfers from it, the proportion lost from that hoard will be smaller than the proportion lost from a scatter hoard although the absolute number of lost food items may be more (Clarke and Kramer 1994a). However, because a larger cache of seeds emits a stronger odor, larger caches are also more susceptible to pilferage (Abbott and Quink 1970). To reduce the likelihood that other seed predators will locate and pilfer the seeds, the hoarder can scatter hoard by widely dispersing smaller concentrations of the food items, using memory to relocate the caches (Stapanian and Smith 1984). This type of caching should also be favored when organisms cannot effectively protect a high concentration of stored food items at one site from competitors (Vander Wall and Joyner 1998). However, if a scatter hoard is discovered, a larger proportion (although perhaps a smaller number) of food items will be lost than from a larder hoard.

A small mammal decides to eat or store a seed based on comparing the seed's present value with the seed's future value. The present value is the energy that the small mammal can gain by eating the seed immediately. The future value is the small mammal's net energy gain by storing and later eating the seed, after accounting for the energy spent caching the seed and the risk of losing the cache. If the animal decides that the present value is greater and eats the seed, then it has acted as a seed predator. However, if the animal decides that the future value is greater and stores the seed, the relationship becomes more complicated. If the animal caches the seed, then eventually relocates the cache and consumes the seed, then it has acted as a seed predator. However, if it stores the seed in a shallow cache without other seeds and fails to revisit the cache (e.g. forgetting the cache location), the seed has the opportunity to germinate and

establish a seedling. If this occurs, then the animal has acted as a seed disperser (Gendron and Reichman 1995; Fig. 1).

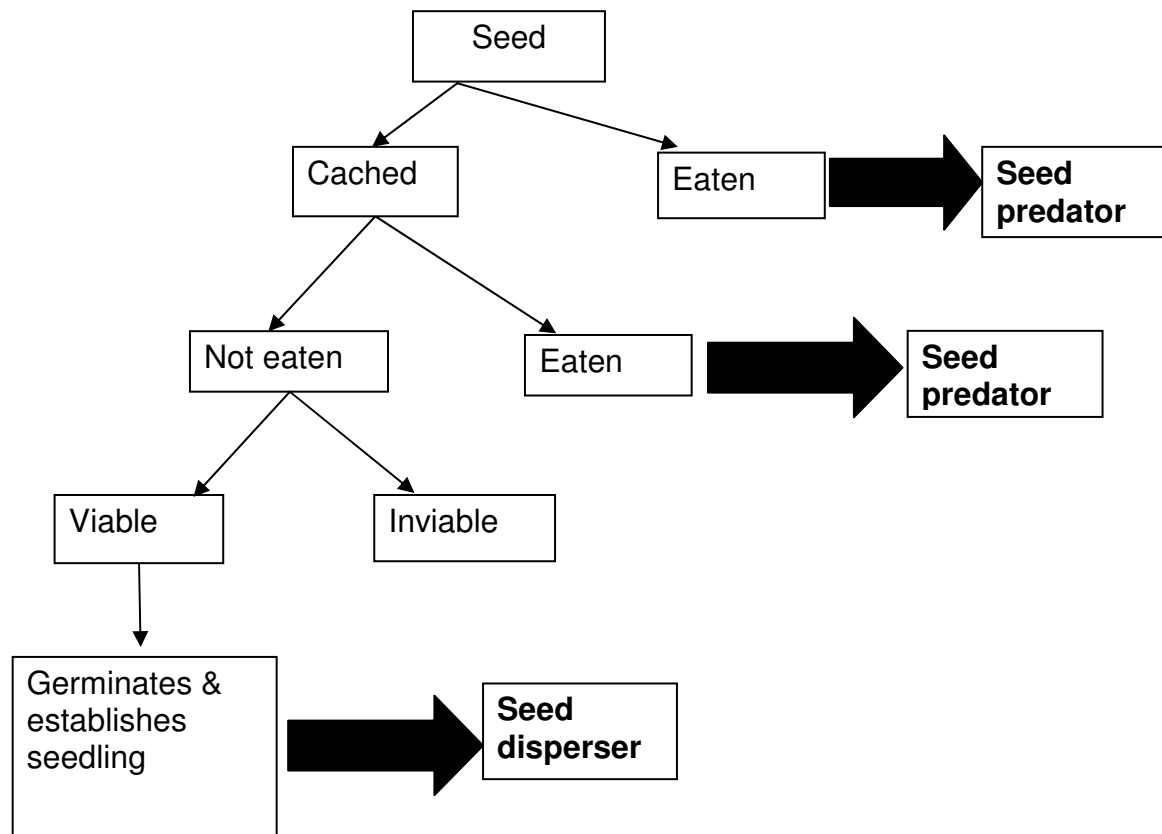


Figure 1. Decisions made by a small mammal upon encountering a seed and corresponding consequences for the seed (simplified from Vander Wall 2004).

Caching behavior also varies over time, even within a year. Animals often store food to ensure over-winter survival. For example, red squirrels (*Tamiasciurus hudsonicus*) create caches in summer and fall for use in the winter and spring (Benhamou 1996), and their over-winter survival and fecundity in the subsequent spring partially depend on the extent of their caches (Benkman et al. 1984). Eastern chipmunks (*Tamias striatus*) also cache in the late summer and fall to survive the winter (Snyder 1982).

### *Seed Dispersal vs. Seed Predation*

The seed-caching behavior of small mammals may benefit the tree whose seeds are being cached. For wind- and animal-dispersed plant species, small mammals disperse seeds farther from parent plants than can be achieved by wind dispersal alone (Vander Wall 1992). The plant benefits because seed survival increases with distance from parental plants (Houle 1995). Furthermore, seed hoarders benefit by burying seeds away from the parental plant and remembering where the seeds are buried because competitors for seeds are more likely to find seeds buried closer to the parental plant (Tamura et al. 1999). Naïve foragers will then have difficulty locating the seeds (Jacobs and Liman 1991). Moreover, the act of seed burial benefits the plant by reducing the likelihood of seed predation and by providing a necessary step for the germination of some seeds (Chambers and MacMahon 1994; Vander Wall 1992) although other seeds, like those of sugar maple (*Acer saccharum*), can germinate above the soil without burial (Barnes and Wagner Jr. 2004). Furthermore, the caches themselves are not stationary but are dynamic storage sites where food items within a cache can be redistributed into newly-made or other previously existing caches (Steele et al. 2001). As a result, seeds are more evenly distributed in a habitat, which could increase the chances of seed deposition in favorable microhabitats for establishment (Vander Wall and Joyner 1998).

Despite these potential benefits to plant species, small mammal activity may also reduce seed abundance through seed predation. Red squirrels have been found to be important seed predators of white spruce (*Picea glauca*; Peters et al. 2003) and southwestern white pine (*Pinus strobiformis*; Samano and Tomback 2003) in western North America and hickory nuts (*Carya glabra*; Sork 1983) in eastern North America.

Their seed predation can have marked effects on natural forest regeneration (Sork 1983). Heavy seed predation can make a common plant species rare over time by reducing seed abundance (Janzen 1971).

Seed dispersal and predation constitute two extremes of a behavioral continuum as individuals within the same population can act as either dispersers or predators (Janzen 1971). However, knowing whether small mammals eat or cache more seeds of a specific species remains important, particularly to inform managers, and the predominant effect of small mammals on sugar maple (*Acer saccharum*) seeds is unknown. By predominantly caching or eating seeds, forest-dwelling small mammals may have net effects on forest regeneration. First, they could positively affect regeneration by enhancing seed dispersal when storage sites are not revisited. Second, they could negatively affect forest regeneration by reducing seed abundance through seed predation (Janzen 1971). However, the redistribution of food within a cache into newly-made or other previously-existing caches (Steele et al. 2001) introduces further complexity, depending on the fate of the redistributed seeds.

#### *Studying Caching Behavior*

Why is it important to study seed caching behavior? Today, the area of forests in the United States comprises ca. three-quarters of the original area covered (303 million ha vs. 404 million ha) 400 years ago (prior to European settlement; Smith et al. 2002). Currently, the United States is the second largest producer of wood products in the world and the leading consumer of forest products. Furthermore, timber demand is at record levels and is expected to increase (Haynes 2003).

For each of these pressures on, and changes in, forest ecosystems, research that focuses on natural processes that may affect regeneration rates could inform managers of additional considerations. One limiting factor for forest stand regeneration is the species richness of the existing seed bank. This seed bank can be altered by small mammals through their caching behavior (Burt 1957).

### *Sciurids*

Based on food preferences, sciurids (limited in this discussion to eastern chipmunks, *Tamias striatus*, and red squirrels, *Tamiasciuris hudsonicus*) can have important impacts on seed fates of tree species found in the northern hardwood forests (Côté and Ferron 2001; Kurta 1995), like those present at the University of Notre Dame Environmental Research Center (UNDERC). This property straddles Vilas County, Wisconsin and Gogebic County, Michigan. Both eastern chipmunks and red squirrels have been trapped at various sites at UNDERC (K. Francl, personal communication) and could potentially overlap considerably in their food resources (Ivan and Swihart 2000). Grey squirrels (*Sciurus carolinensis*), least chipmunks (*Tamias minimus*), northern flying squirrels (*Glaucomys sabrinus*), and southern flying squirrels (*Glaucomys volans*) were other potential sciurid seed predators. Northern flying squirrels tend to rely on fungi as their main food source over the summer with few, if any, seeds in their diet (Weigl 1978) and so were excluded as potential seed predators.

Eastern chipmunks inhabit deciduous forests in the United States from Minnesota eastward through Maine and southward to the Gulf states. They inhabit a variety of habitats, from open shrubby areas to mature forests. To survive harsh winters, chipmunks generally larder hoard seeds in their burrows and undergo bouts of

hibernation in their underground burrows from late fall to early spring although they may go aboveground during favorable weather. When they are not hibernating in the winter, they feed on stored seeds (Snyder 1982).

Red squirrels inhabit the boreal forests of Canada and the northern United States, from Alaska to the Atlantic Ocean and south along the Appalachian, Cascade, and Rocky Mountain ranges. In particular, they prefer coniferous forests with large supplies of conifer seeds, fungi, and heavy canopy cover because these areas provide foraging opportunities and protection from predators. They are granivores with a primary diet of conifer and maple seeds in forests like those present at UNDERC but can be opportunistic when mast food is absent (Steele 1998).

Eastern chipmunks and red squirrels are diurnal and solitary rodents. Both species maintain and defend territories (Vander Wall 1990). Red squirrels defend average areas of  $7600 \pm 800 \text{ m}^2$  (Steury and Murray 2003) while chipmunks defend areas of  $978 \pm 856 \text{ m}^2$  on average (Mares et al. 1982). In general, red squirrel densities range from 0.3 - 2.0 squirrels/ha (Steele 1998) whereas chipmunk densities vary much more widely from 0.3 - 37.6 chipmunks/ha (Snyder 1982). However, they exhibit similar caching behaviors.

Squirrels are useful for studying the impacts of seed-caching behavior on forest regeneration and plant community composition (Steele and Koprowski 2001), and chipmunks may have marked effects on the seeds of various plant species. Red squirrels largely larder hoard but scatter hoard in eastern portions of their range (Goheen and Swihart 2003; Hurly and Lourie 1997). Like squirrels, chipmunks both scatter hoard and larder hoard seeds. In particular, juvenile eastern chipmunks tend to scatter hoard more

than adults, and females with young tend to scatter hoard more than other adults (Clarke and Kramer 1994b). Red squirrels and eastern chipmunks are also important seed predators of red maple (*Acer rubrum*), white pine (*Pinus strobus*), and red oak (*Quercus rubra*; Plucinski and Hunter 2001). In the northern hardwood forests where sugar maples dominate, the predominant effects of chipmunks and squirrels on sugar maple seeds are unknown.

#### *Other Mammalian Seed Predators*

In addition to sciurids, other forest-dwelling small mammals could potentially be important seed predators. Based on their diets (Kurta 1995), deer mice (*Peromyscus maniculatus*), meadow jumping mice (*Zapus hudsonius*), southern red-backed voles (*Myodes gapperi*), white-footed mice (*Peromyscus leucopus*), and woodland jumping mice (*Napaeozapus insignis*) were potential seed predators at my sites.

#### *Questions*

My study addressed the following questions:

1) Are seeds provided later in late summer more likely to be cached? Small mammals begin building food stores for winter during the late summer (Hurly and Lourie 1997). Thus, seeds provided later in the summer should have a larger proportion cached if the availability coincides with the onset of creating caches to survive the winter.

2) Are small mammals more effective seed predators or seed dispersers? I measured the proportion of seeds eaten to explore the predominant effect of small mammals on post-dispersal (i.e. after dispersing via wind from the parent tree) sugar maple seeds during the summer months in UNDERC forests where sugar maples are a dominant canopy species. A larger proportion of seeds eaten suggests that small

mammals are more effective seed predators while a larger proportion cached suggests that they are more effective seed dispersers. Examining these patterns provided insights into the net impact that small mammals have on the seeds and potentially on regeneration (although this was not directly assessed).

3) Do areas with a higher biomass experience more seed predation? Biomasses rather than densities should more accurately reflect the contributions of each seed predator species because small seed predators may have relatively high densities but contribute relatively little to biomass and therefore have comparatively smaller effects on seed resources. More specifically, sciurids are important seed predators of other tree species (Plucinski and Hunter 2001). Looking at how sciurid biomass affects seed predation addresses whether sciurids are important seed predators of post-dispersal sugar maple seeds.

Although small mammal abundances (and therefore biomass) can vary greatly from year-to-year (Moses and Boutin 2001), sites with high relative small mammal densities should maintain higher densities relative to other sites, even if absolute densities are lower. For example, small mammals at UNDERC had lower densities during the summer of 2005 than that of 2006; however, comparing eastern chipmunk capture data between the two summers at the same sites, the site with the highest density in the summer of 2005 maintained the highest density in the summer 2006 although the specific densities differed.

4) How does biomass vary with plant community composition and habitat structure? If higher biomasses result in a higher proportion of seeds eaten, I would further explore which habitat measures affect biomasses. If small mammals and, in

particular, sciurids are important sugar maple seed predators, then examining how habitat features and plant community composition affect their biomasses can identify areas where heavy predation on sugar maple seeds can be expected.

5) Is sciurid biomass related to the biomass of other potential small mammal seed predators (non-sciurid biomass)? Sciurid biomass could increase or decline with increasing non-sciurid biomass, which might indicate how sciurids and non-sciurids respond similarly or differently to their environments. This relationship could also potentially affect seed predator biomass.

## MATERIALS AND METHODS

### *Study Sites*

Experiments were conducted in the northern mesic hardwood forests of UNDERC in the Upper Peninsula of Michigan (ca. 46° 13' N, 89° 32' W), which consists of 3055 ha with ca. 80% forest. This property was clearcut around 1900 and selectively logged from ca. 1950 -1960, with the last recorded incidence occurring in 1968. Since the cessation of logging, the upland forests are mainly stands dominated by late-successional sugar maple with a mixture of stands dominated by early-successional trembling aspen (*Populus tremuloides*) and balsam fir (*Abies balsamea*). I selected eight sites on UNDERC property containing a mixture of deciduous (specifically sugar maple) and coniferous trees for my seed fate experiment (see Appendix 2) and named them after nearby landmarks: Beaver Bog, Cranberry Bog (Cranberry), Ed's Bog, Kickapoo Lake (Kickapoo), Long Lake, Northeast (NE) Gate, Palmer Lake (Palmer), and North Tenderfoot Creek (Tenderfoot).

### *Trapping*

To identify seed predators and calculate seed predator biomasses, I established a 4500-m<sup>2</sup> (45 m x 100 m) trapping grid at each site. This plot size was deemed appropriate based on the average territory size for red squirrels, which have the largest documented home range of the potential seed predators in the region. Within each site, I established four 100-m transects spaced 15 m apart (0, 15, 30, 45 m). Sherman live traps were placed on the ground every 10 m, and three evenly-spaced Tomahawk live traps

were placed along each transect. I used rolled oats and peanut butter as bait in the traps. The location, species, gender, age (juvenile vs. adult), and weight of captured individuals were recorded. I then marked each captured individual with a numbered metal ear tag (No. 1, National Band and Tag Co., Newport, KY). Once per month for June and July of 2006, I trapped at each site for five consecutive nights (totaling 10 total nights per site).

Using the capture data, I summed the average weight of captured individuals from each species to estimate the total biomass of seed predators (seed predator biomass) for each site. Because biomass calculations for each seed predator species were based on captures, species that were present but not captured were underrepresented. However, assuming this trend is consistent across sites, I could use biomass as a relative estimate. I also estimated sciurid biomass for each site, summing the weights of captured eastern chipmunks and/or red squirrels. One grey squirrel was captured during the summer of 2006 at one site (Palmer) and was included in the sciurid biomass calculation. However, its inclusion did not affect trends. The non-sciurid biomass equaled the difference between total seed predator biomass and sciurid biomass. To obtain seed predator densities for each site, I calculated the total # captured individuals/4500-m<sup>2</sup> and extrapolated that value to individuals/ha.

All methods and procedures were in compliance with the University of Notre Dame's Institutional Animal Care and Use Committee standards.

#### *Habitat Measures*

Because the species composition and size distribution of trees in each of the study areas could affect the food types and quantities available to small mammals and thereby affect their densities and biomass, I measured the abundance and density of tree species

and tree size for at 20 points per site. Within 5 m x 5 m plots every 20 m along my trapping transects, I identified to species all the trees with DBH > 5 cm (diameter at breast height – DBH; Brooks et al. 1998) and recorded their DBH. I further separated sugar maples into immature (DBH < 20 cm) and mature (DBH ≥ 20 cm) because a DBH of 20 cm approximates the age at which sugar maples first produce seeds (Burns and Honkala 1990; Houle 1992; Houle and Payette 1991).

To measure seed fall as an estimate of seed availability, I placed tin cans (ca. 15 cm diameter x 20 cm) on the ground in each trapping grid during June and August over the 14 d period that the track boards were in place. Cans were placed at 0, 50, and 100 m along the first and third transects and at 33, 66 m along the second and fourth transects, totaling 10 points per site. I then totaled the number of seeds collected from the 10 cans from June and from August at each site and then extrapolated density estimates to # seeds/ha.

The biomass of small mammal species could be affected by more than the composition and sizes of trees and seed availability; therefore, I measured other habitat characteristics. Within the 5 x 5 m plots, I also recorded snag and downed log densities for snags and logs with ≥ 50% of their material within the plot. Snags serve as potential seed storage sites for small mammals (Mahan and Yahner 1996) and were defined as either leaning or standing dead trees or stumps. Logs consisted of any downed piece of wood along which any small mammal could potentially travel. Neither snags nor logs were quantified by size, with minimum size for inclusion subjectively determined.

I estimated ground cover by the point-quarter method (Cox 1996) at 10 random points for each site. Using this method, I located an individual shrub below which a

small mammal could be concealed (thereby providing cover) and measured its basal area and designated four quadrants around that shrub (the point). For each quadrant, I located the nearest individual shrub ( $\leq 3$  m of the point) which could provide cover and recorded its basal area and its distance to the point, hereafter referred to as the nearest neighbor distance. If no cover was within 3 m, I assigned a value of 3 m. Although this potentially truncated my distribution, only ca. 10% (33/320) of the measured distances were assigned this value, and removing these values did not affect results.

Because vertical vegetation structure within a habitat affects species richness (Morris 1979), I measured vertical diversity (i.e. vertical distribution of vegetation) and canopy cover. In addition, I selected 30 random points within each site and calculated the relative vertical diversity across sites through the use of a range pole (Franel and Schnell 2002). At each point, I measured the presence of vegetation in 0.5-m increments along a 6.5-m tall pole (plus a category for hits above 6.5 m; 14 increments) and estimated canopy cover using a spherical densiometer (Forestry Suppliers Inc., Jackson, MS). I calculated the Levins index of vertical diversity.

$$L = \sum 1/d_i^2$$

where  $d_i = \#$  of vegetation hits at the  $i^{\text{th}}$  0.5 m increment/total # hits possible (30; Franel and Schnell 2002). Soil moisture was measured using a Kelway Soil Moisture Tester (Kel Instruments Co., Inc, Japan) at the same 30 random points for each site. To account for potential variation, soil moisture readings were taken three times during June and July of 2006. The 30 values from each site and each time were averaged, and I then obtained an overall site average by averaging the three values from different times at each site.

### *Seed Tagging*

To study post-dispersal seed fates, I glued 1.9 cm wire brads to the winged part of commercially-purchased sugar maple seeds (Catalpa Tree Seed Company, Medford, NJ). Because sugar maple seeds were obtained from a non-local source, I microwaved them for 45 sec to make them inviable. Seeds were placed on track boards to identify visitors to the boards. The wire brads were marked with a unique color band to indicate June or August and the board on which the seed was placed.

### *Lab Study*

Because tagging the seeds with wire brads was modified from a method using nails to tag acorns (Sork 1984; Steele et al. 2001), I conducted a study in summer 2005 to determine whether the wire affected the preferences of eastern chipmunks and red squirrels for the seeds. I successfully tested 10 eastern chipmunks; however, I only tested one red squirrel due to low trapping success. Individuals were housed in 10-gal aquaria with 12:12 light-dark cycles and at room temperature (Goheen et al. 2003). Food was withheld from test individuals for 12 h prior to the trial (Briggs and Vander Wall 2004). I presented each individual with each of three groups of four sugar maple seeds in random order: seeds with color-coded wire brads, seeds with wire brads without color-coding, and seeds without wire brads. Seeds were presented for 140 min, with observations made every 20 min. The amount of time for individuals to eat each seed type did not vary among the three groups (one-way ANOVA:  $F_{2,117} = 0.138$ ,  $p = 0.87$ ). Moreover, the first two test subjects were presented with un-microwaved seeds, and they took similar amounts of time to eat the seeds. Thus, microwaving the seeds did not appear to have an effect.

### *Pilot Study*

During the summer of 2005, I trapped for small mammals for 5 consecutive nights at each site using the previously described setup and conducted basic vegetation surveys. Using a 5-m radius circular plot, ten points per trapping grid were sampled for tree species composition and sapling density. Any tree with a diameter at breast height (DBH) > 5 cm was included in the species composition.

For my track board methods, at each site, I placed ca. 100 tagged seeds on track boards (ca. 0.067 seeds/m<sup>2</sup>) under nylon mesh bird netting, which excluded and protected other seed predators (e.g., birds and deer) from the potential harm of consuming the metal attached to the seeds (Sork 1984). Track boards were placed at 50-m intervals halfway between the second and third transects in trapping grids at each site (3 boards/site) and were checked once every 2-3 days. Track boards were in place for two periods to observe whether patterns change over the summer: June 29 – July 13 (June) and July 26 – August 7 (July).

To test ways of recording small mammals tracks, I painted carbon black ink (Dick Blick Art Materials, Galesburg, Illinois) around the outer 10 cm of each board for June and dusted the boards with talcum powder for July, but neither method was successful.

To relocate removed seeds, I used a Fisher 1225-X metal detector (Fisher Research Laboratory, Los Banos, California) after each 14-d period. Once a seed or wire brad was relocated, I noted from which track board and the month it originated and whether it was eaten or cached.

These methods were implemented at 4 of my 8 sites: Kickapoo, Long Lake, Northeast Gate, and Palmer. Because trends were difficult to detect with the small number of sites, the findings were used to identify which methods to use and what

additional information needed to be collected for the experiment conducted in the summer of 2006, and the results are not reported herein.

### *Post-Dispersal Seed Fate Experiment*

During the summer of 2006, I placed  $100 \pm 2$  tagged seeds on each of three track boards for each site (total addition of  $0.067 \pm 0.001$  seeds/m<sup>2</sup>, mean  $\pm$  1 SE, over each 4500-m<sup>2</sup> study area). Each 60 cm x 60 cm styrene track board had one track plate taped to each of the four sides, totaling four plates per track board. Each track plate consisted of one 14 cm x 22 cm acetate sheet with a mixture of 80% ethyl alcohol, 15% graphite powder, and 5% mineral oil. A thin layer of this mixture was applied with a foam paintbrush and allowed to dry (Connors et al. 2005).

This method allowed for a relative visitation index as I could not determine how many individuals of each species visited the boards nor how many seeds an individual manipulated. The main purpose of the track plates was to identify which species at each site likely interacted with the seeds. The proportions of tracks left by each species on the track boards appeared to correspond to their respective proportions of capture because a paired t-test found no difference between the mean proportion of tracks and the mean proportion of captures across sites ( $p = 0.696$ ).

Boards were checked once every 2-3 days and were in place for two periods to observe whether patterns change during summer 2006: June 14/15 – June 28/29 (June) and August 9/10 – August 23/24 (August). Because other studies have found that the majority of seeds were removed within the first two weeks (Plucinski and Hunter 2001; Vander Wall 1992; Whelan et al. 1991), I determined that 14 d allowed ample time for seed removal.

To relocate removed seeds, I used a Fisher 1225-X metal detector (Fisher Research Laboratory, Los Banos, California) after each 14-d period. Once a seed or wire

board was relocated, I noted from which track board and month it originated and whether the seed was eaten, uneaten or missing. Because the majority (> 50%) of removed seeds were found within 3 m of the board, I did not quantify the distance from seeds to the board.

Track boards were spaced 50 m apart down the middle of each trapping grid. The seed density provided on the track boards should not have artificially augmented food resources because an average of  $53.8 \pm 8.9$  (mean  $\pm$  1 SE) seeds/m<sup>2</sup> were available according to my seed fall data. For eastern chipmunks, which appear to have the smallest documented home range size out of the potential seed predators, the seed addition increased seed density, on average, by 0.31 seeds/m<sup>2</sup>. Based on my lowest collected seed density of 11.3 seeds/m<sup>2</sup>, the seed addition was equivalent to 2.7% of the natural seed availability. While piling the seeds may have attracted small mammals more than scattered seeds, at least one board per site was used by more than one species, and thus more than one individual, as evidenced by the tracks recorded on the track plates.

### *Statistics*

Questions 1, 2, 3 - ANCOVA determined whether the proportion of seeds eaten varied between June and August, between sites, and with the biomass of seed predators. A separate ANCOVA also determined whether the proportion of seeds eaten varied between June and August, between sites, and with seed predator densities.

Some wings were found without seeds attached (hereafter referred to as seedless wings). In the field, the seed coats of eaten seeds remained intact and tended to be left on or near the board with wings intact, so removed wingless seeds were not likely consumed. Instead, animals likely carried the seeds away from the board after clipping

off the wings, so the proportion of seedless wings represented the proportion of cached seeds in my analyses. A Student's t-test determined if the mean proportion of seedless wings differed between June and August.

To test if sciurid biomass affected the proportion of eaten seeds, I used a linear regression to relate the proportion of seeds eaten to sciurid biomass. I also performed linear regressions with the proportion eaten and eastern chipmunk or red squirrel biomasses. I also examined the effects of time period and site on total seed fall, using a t-test and a one-way ANOVA respectively.

Question 4 - To examine whether seed predator and, in particular, sciurid biomasses varied with plant community composition, I used habitat measures as independent variables and seed predator biomass, non-sciurid biomass, and sciurid biomass, respectively, as the dependent variable in a forward stepwise linear regression. Due to low capture success, I used chipmunk presence/absence data to analyze their relationship with vegetation characteristics. A forward stepwise discriminant function analysis determined which vegetation characteristics best predicted the presence of chipmunks, which were present at four out of the eight sites. The estimates for the proportions of canopy cover, deciduous trees, soil moisture, and sugar maples were arc-sine transformed to normalize the data. A similar analysis could not be performed for red squirrels because they were present at too many sites, i.e. six out of the eight. Linear regressions examined relationships between vegetation variables to see if any vegetation measures affected other measures.

Question 5 - A linear regression between sciurid and non-sciurid biomasses tested whether sciurid biomass was related to the biomass of other potential small mammal seed predators (non-sciurid biomass). A linear regression between eastern chipmunk biomass and red squirrel biomass also tested whether the two biomasses were related to each other.

All analyses were run in SYSTAT Version 10.0 (Systat Software, Inc., San Jose, CA). Due to the small sample size ( $N = 8$  sites), I accepted  $p \leq 0.10$  as statistically significant.

## RESULTS

### *Trapping*

Over 4134 trap-nights, a total of 264 captures of 117 individuals were recorded (Table A.1), with recaptures accounting for 55.7% of captures. Twenty eastern chipmunks were captured at three out of the eight sites (although they were present at four based on observation), and six red squirrels were trapped at four sites (although they were present at six based on observation). Densities and biomasses of individual seed predator species and total seed predator biomass for each site are listed in Table 2 using species codes listed in Table 1. Least chipmunks and southern flying squirrels were not captured at any sites. White-footed and deer mice (listed as *Peromyscus* spp.) accounted for 56.1% of captures followed by eastern chipmunks with 16.3% and southern red-backed voles with 9.5%.

### *Post-Dispersal Seed Fate Experiment*

Questions 1 and 2- While I successfully located seeds removed from the boards, I failed to find any cached seeds. Overall, I successfully recovered  $92.2 \pm 0.01\%$  (mean  $\pm 1$  SE) of the seeds. The fates of the remaining seeds were unknown. A higher proportion of seeds cached were found in June ( $0.020 \pm 0.007$ ) than in August ( $0.007 \pm 0.004$ ;  $t = 2.20$ ,  $df = 14$ ,  $p = 0.045$ ). Because of the low average proportion of seeds cached overall, this measure was not further analyzed. Natural seed fall ( $53.8 \pm 35.6$  seeds/m<sup>2</sup>) did not vary between June and August ( $p > 0.40$ ), by site ( $p > 0.30$ ), or with any vegetation measure ( $p > 0.10$ ).

TABLE 1.  
 FAMILY, SCIENTIFIC NAME, COMMON NAME, AND SPECIES CODES FOR  
 SEED PREDATORS CAPTURED AT EIGHT MIXED CONIFEROUS AND  
 DECIDUOUS SITES AT UNDERC, 2006.

Family	Scientific name	Common name	Code
Dipodidae	<i>Napaeozapus insignis</i>	Woodland jumping mouse	NAIN
Dipodidae	<i>Zapus hudsonius</i>	Meadow jumping mouse	ZAHU
Muridae	<i>Myodes gapperi</i>	Southern red-backed vole	MYGA
Muridae		White-footed mouse or deer	
	<i>Peromyscus</i> spp.	mouse	PE sp.
Sciuridae	<i>Sciurus carolinensis</i>	Eastern gray squirrel	SCCA
Sciuridae	<i>Tamias striatus</i>	Eastern chipmunk	TAST
Sciuridae	<i>Tamiasciurus hudsonicus</i>	Red squirrel	TAHU

TABLE 2.  
INDIVIDUAL SEED PREDATOR DENSITIES AND BIOMASS AND TOTAL SEED  
PREDATOR BIOMASS FOR EACH OF EIGHT MIXED CONIFEROUS AND  
DECIDUOUS FOREST SITES AT UNDERC, 2006.

Site	Species	Density (per ha)	Biomass (g)	Total Biomass (g)
Beaver Bog	NAIN	4.44	47.00	571.90
	PE sp.	24.44	216.90	
	TAHU	4.44	308.00	
Cranberry	MYGA	11.11	80.00	558.83
	PE sp.	26.67	199.83	
	TAHU	2.22	119.00	
	TAST	4.44	160.00	
Ed's Bog	MYGA	8.89	80.50	723.29
	NAIN	2.22	8.00	
	PE sp.	33.33	347.79	
	TAHU	4.44	272.00	
	ZAHU	2.22	15.00	
Kickapoo	MYGA	8.89	63.00	2205.00
	NAIN	2.22	23.00	
	PE sp.	66.67	514.29	
	TAHU	2.22	182.00	
	TAST	26.67	1422.71	
	MYGA	15.56	168.25	
Long Lake	PE sp.	6.67	73.50	241.75
	NAIN	4.44	37.00	
NE Gate	PE sp.	11.11	79.58	131.58
	ZAHU	2.22	15.00	
	PE sp.	28.89	229.63	
Palmer	SCCA	2.22	525.00	1974.29

Species codes listed in Table 1.

Question 3 - The proportion of seeds eaten (the proportion eaten) did not differ between June and August ( $F_{1,7} = 2.71$ ;  $p = 0.144$ ), between sites ( $F_{6,7} = 1.76$ ;  $p = 0.234$ ) or with seed predator density ( $F_{1,7} = 2.28$ ;  $p = 0.175$ ). However, the proportion eaten varied with seed predator biomass ( $F_{1,7} = 9.35$ ;  $p = 0.018$ ) with no significant interactions ( $p > 0.10$ ).

More specifically, the proportion eaten increased with increasing seed predator biomass ( $r^2 = 0.490$ ,  $p = 0.053$ ) and with increasing sciurid biomass ( $r^2 = 0.445$ ,  $p = 0.070$ , Fig. 2). The proportion of seeds eaten also increased with increasing chipmunk biomass ( $r^2 = 0.445$ ,  $p = 0.071$ , Fig. 3). However, red squirrel biomass was not related to the proportion of eaten seeds ( $p > 0.9$ ).

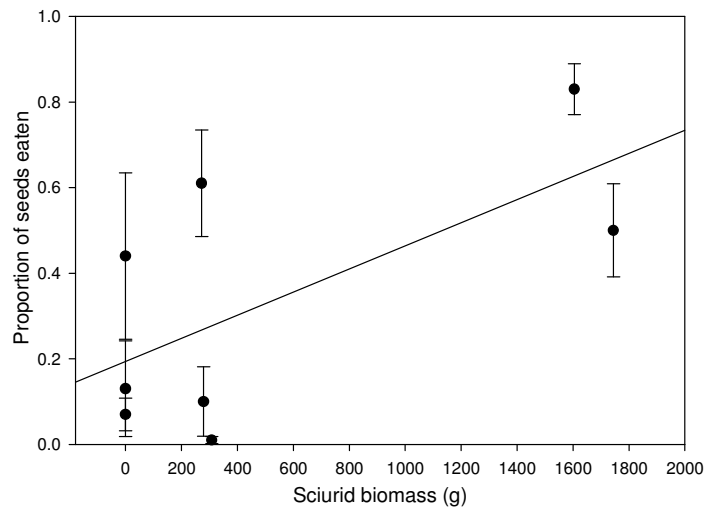


Figure 2. A plot of sciurid biomass (sum of the weights of eastern chipmunks and red squirrels and one grey squirrel) against the proportion of seeds eaten across eight mixed deciduous and coniferous forest sites at UNDERC, 2006. The proportion of seeds eaten increased with sciurid biomass ( $r^2 = 0.445$ ,  $p = 0.070$ ).

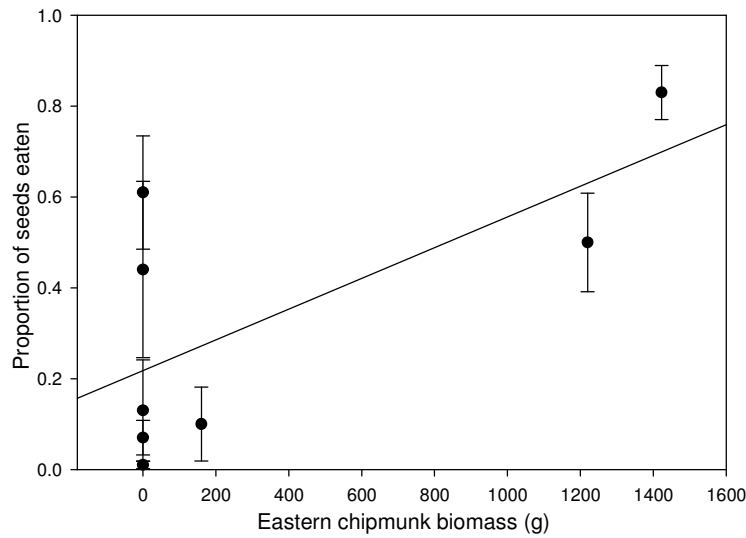


Figure 3. A plot of eastern chipmunk biomass against the proportion of seeds eaten across eight mixed deciduous and coniferous forest sites at UNDERC, 2006. The proportion of seeds eaten increased with eastern chipmunk biomass ( $r^2 = 0.445$ ,  $p = 0.071$ ).

Question 4 - Seed predator biomass increased with proportion of deciduous trees, soil moisture, and snag density but decreased with increasing Levins index across sites ( $r^2 = 0.962$ ,  $p = 0.018$ , Table 3). Non-sciurid biomass increased with increasing distance to the nearest neighbor (a measure of ground cover) and soil moisture but decreased with increasing Levins index across sites ( $r^2 = 0.980$ ,  $p = 0.001$ , Table 4). Sciurid biomass also increased with increasing soil moisture ( $r^2 = 0.774$ ,  $p = 0.004$ ).

TABLE 3.

FORWARD STEPWISE REGRESSION RESULTS FOR VEGETATION  
 CHARACTERISTICS AND SEED PREDATOR BIOMASS FOR EIGHT MIXED  
 CONIFEROUS AND DECIDUOUS SITES AROUND UNDERC PROPERTY, 2006.

a) Regression Coefficients

Effect	Coefficient	P(2 Tail)
Constant	-6800.9	0.006
Asn proportion deciduous	3053.9	0.030
Asn soil moisture	6937.6	0.004
Snag density	78.9	0.097
Levins index	-0.3	0.141

b) Analysis of Variance

Source	Sum-of-Squares	df	F-ratio	P
Regression	4,432,310	4	19.2	0.018
Residual	173,111	3		

ASN indicates the variable was arcsine transformed. Coefficients for the significant characteristics (a) and the overall regression ANOVA table (b) are provided ( $r^2 = 0.96$ ).

TABLE 4.  
FORWARD STEPWISE REGRESSION RESULTS FOR VEGETATION  
CHARACTERISTICS AND NON-SCIURID BIOMASS FOR EIGHT MIXED  
CONIFEROUS AND DECIDUOUS SITES AROUND UNDERC PROPERTY, 2006.

a) Regression Coefficients

Effect	Coefficient	P(2 Tail)
Constant	12.73011	0.87153
Distance to nearest neighbor	324.09495	0.00016
Asn soil moisture	212.62886	0.09977
Levins index	-0.15917	0.00083

b) Analysis of Variance

Source	Sum-of-Squares	df	F-ratio	P
Regression	162,148	3	65.6	0.001
Residual	3293.7	4		

ASN indicates the variable was arcsine transformed. Coefficients for the significant characteristics (a) and the overall regression ANOVA table (b) are provided ( $r^2 = 0.98$ ).

Discriminant function analysis identified immature sugar maple density, downed log density, snag density and percent soil moisture as the distinguishing factors between sites with and without chipmunks. Based on these four measures, the analysis successfully classified 100% of the sites as with (4/4) and without chipmunks present (4/4). In particular, sites with chipmunks had higher immature sugar maple density, higher density of snags, lower density of downed logs, and higher soil moisture. Downed log density was negatively related to immature sugar maple density and soil moisture ( $r^2 = 0.901$ ,  $p = 0.003$ ).

Question 5- Non-sciurid biomass increased with increasing sciurid biomass ( $r^2 = 0.782$ ,  $p = 0.004$ , Fig. 4). Eastern chipmunk biomass and red squirrel biomass were not related ( $p > 0.9$ ).

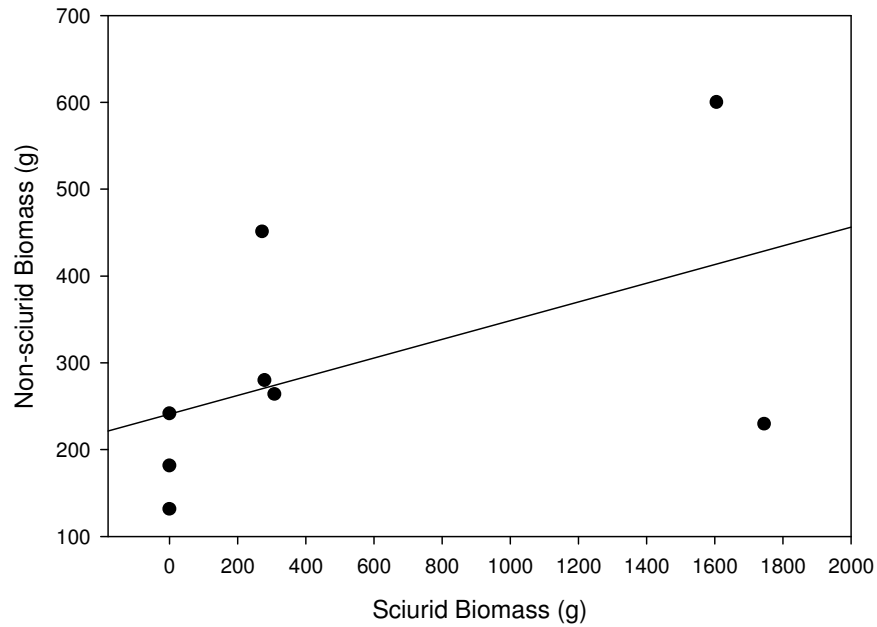


Figure 4. A plot of eastern chipmunk biomass against the proportion of seeds eaten across eight mixed deciduous and coniferous forest sites at UNDERC, 2006. The proportion of seeds eaten increased with eastern chipmunk biomass ( $r^2 = 0.445$ ,  $p = 0.071$ ).

## DISCUSSION

### *Question 1*

Fewer seedless wings were left on the boards in August than in June, suggesting that the proportion cached was lower in August. Even though fewer seedless wings were found in August than in June, seedless wings on average accounted for less than 2% of the seeds on the boards. Thus, caching had little overall effect on seed fates over the course of this study. This finding is consistent with observations from a predation experiment on red maple seeds conducted in late spring (Beckage and Clark 2005).

Seed predators may have experienced a greater food shortage in August than in June. Although the relative food availability as estimated by seed fall did not vary, the small mammal population size may have been augmented in August due to the dispersal of juvenile eastern chipmunks. Juveniles of females impregnated in early April would likely disperse around the end of June or early July (Snyder 1982). Particularly at the Kickapoo and Palmer sites for this study, the number of unique captured individuals increased from 7 to 19 individuals, and juveniles increased from 0 to 8 between early June and early July. Another possibility is that individuals learned to locate boards in June and used them more in August. However, this explanation is unlikely as Northeast Gate had few seeds eaten for both months in summer 2006 despite also being used in summer 2005 as part of a pilot study. Thus, the most likely explanation is that, because small mammals build their winter caches in late summer and fall (Kemp and Keith 1970), the seed fate experiment concluded before small mammals began hoarding for the winter.

### *Question 2*

These findings suggest that small mammals during the summer months serve as seed predators of post-dispersal sugar maple seeds rather than seed dispersers. In general, small mammals should favor eating seeds over caching them because caching provides food for later consumption and energy gain whereas eating provides immediate energy. Thus, caching should only be favored over eating in the relatively rare instances when immediate energy is not required. Before the onset of caching for the winter (i.e. the likely time period of the seed fate experiment), small mammals do not rely on caches in the summer because deciduous areas have high food availability during that time (Kemp and Keith 1970), and eating the seeds should then also be more frequent.

### *Question 3*

A higher biomass of seed predators requires a larger supply of seeds. This explains why the proportion of seeds eaten increased with seed predator biomass. However, Reed et al. (2004) found that seed predation was not affected by rodent abundance. That abundance does not correspond directly to biomass explains this apparent contradiction as small mammals may achieve high abundance but contribute relatively little to consumptive biomass. The finding that seed predator density had no effect on the proportion of seeds eaten further supports this idea. While smaller-bodied small mammals have a faster metabolic rate (Vaughan et al. 2000) and thus must eat a larger proportion of their body weight, the absolute amount they eat relative to larger-bodied small mammals may still be less. Thus, biomass better indicates the relative contribution of potential small mammal seed predators to seed predation and should be used in future seed predation studies.

Consistent with the trend for seed predator biomass, the proportion eaten also increased with increasing sciurid biomass. The finding that eastern chipmunks and red squirrels are seed predators more than seed dispersers of sugar maple seeds during the summer months was consistent with findings from other studies. Red squirrels are considered major seed predators of southwestern white pine seeds in western North America, removing as much as 83% of cones (Benkman et al. 1984). Furthermore, eastern chipmunks and red squirrels may be important seed predators of red maple, white pine, and red oak seeds (Plucinski and Hunter 2001). In addition, chipmunks and squirrels are considered seed predators because they store seeds in places that prevent germination such as hollow logs and burrows (Sork 1983).

More specifically, the proportion of seeds eaten was unaffected by red squirrel biomass but increased with sciurid biomass and, in particular, eastern chipmunk biomass. This suggests that eastern chipmunks likely have a larger impact than red squirrels, which is consistent with the preference of eastern chipmunks for deciduous forests (Snyder 1982) and the preference of red squirrels for coniferous forests (Steele 1998). Alternatively, eastern chipmunk biomass varied more than red squirrel biomass across my sites, so the effects of red squirrel biomass on the proportion of seeds eaten were more difficult to detect.

#### *Question 4*

The biomass of seed predators increased with a higher density of snags and more deciduous trees but less vertical diversity. The decreasing vertical diversity is consistent with the increasing proportion of deciduous trees. This preference for more deciduous trees is consistent with the finding from Chambers and MacMahon (1994) that rodents

are important predators of large-seeded deciduous tree species. Thus, small mammal seed predators should prefer areas where more food resources are available. Because snags can serve as potential food storage and nest sites (Mahan and Yahner 1996), areas with more snags should support a higher biomass of small mammals. Consistent with their preference for deciduous tree seeds, seed predator biomass increased with increasing soil moisture because the higher moisture content in these areas may aid the olfactory sense used by small mammals to locate seeds (Vander Wall 1991). Similarly, non-sciurid biomass increased with increasing nearest neighbor distance (i.e. lower ground cover density) and decreasing vertical diversity. Both of these trends are consistent with areas with more deciduous trees.

Consistent with the trend for seed predator biomass, sciurid biomass and non-sciurid biomass also increased with increasing soil moisture. More specifically, higher soil moisture along with higher immature sugar maple density, higher density of snags, and lower density of logs best predicted chipmunk presence. The higher immature sugar maple density may indicate, as previously mentioned, the preference of chipmunks for deciduous forest. Overall, these trends were as expected except for the trend for the density of logs. The presence of eastern chipmunks in areas with lower densities of downed logs contradicts expectations if chipmunks use logs as travel routes (Zollner and Crane 2003). However, Dueser and Shugart (1978) also found more chipmunks in areas with lower densities of woody stems on the ground. Because chipmunks only use logs with diameters larger than 5 cm (Zollner and Crane 2003), smaller logs included in this measurement could instead act like dense understory vegetation to inhibit the visual signals that chipmunks use for communication (Svendsen and Yahner 1979). Including

only logs  $\geq 5$  cm in diameter may reveal a different trend. However, because log size was not quantified in this study, this explanation could not be tested. Downed log density also was inversely related to soil moisture. Thus, the relationship with downed log density may actually reflect the preference of chipmunk for areas with higher soil moisture (Svendsen and Yahner 1979). Future studies should compare chipmunk biomass between coniferous stands with few and many large trees and deciduous stands with few and many large trees to determine whether chipmunks predominantly select habitats based on forest type or tree size.

That the trends found for vegetation characteristics that best predicted chipmunk presence were consistent with trends for increased seed predator and sciurid biomasses further emphasize the importance of eastern chipmunks as seed predators of post-dispersal sugar maple seeds. Preliminary findings from this study suggest that areas with eastern chipmunks lose about 50% of their sugar maple seeds to predation during the summer.

#### *Question 5*

Sciurid biomass and non-sciurid biomass exhibited a strong positive relationship. This strong relationship suggests that sciurids and non-sciurids responded similarly to their environment. Eastern chipmunks and non-sciurids appear to prefer areas with more deciduous trees and higher soil moisture, and the relationship between sciurid and non-sciurid biomass may reflect these preferences.

## CONCLUSION

One limiting factor for forest stand regeneration is the species richness of the existing seed bank, which can potentially be altered by small mammals through their caching behavior. According to the current study, this is unlikely during the summer months as caching was a relatively rare event. More likely, small mammals affect plant recruitment patterns through their seed predation. Small mammal seed predators and, in particular, sciurids may affect the distribution and abundance of sugar maples because a higher proportion of seeds were eaten with higher seed predator and sciurid biomasses. These findings are supported by several studies identifying rodents as the main post-dispersal seed predators with important effects on plant recruitment (Edwards and Crawley 1999; Hulme 1993; Peters et al. 2004). While a higher proportion of sugar maple seeds were eaten with increasing sciurid biomass, this trend is mainly driven by chipmunk biomass. This suggests that eastern chipmunks are important predators of sugar maple seeds.

Because forests recovering from human activities like timber harvests actively undergo secondary succession, knowing that sciurids and other small mammals act primarily as seed predators of late-successional species such as sugar maple during the summer months offers additional considerations for restoration strategies. In particular, managers looking to regenerate sugar maples should measure eastern chipmunk biomasses to best estimate seed loss due to predation. Furthermore, the varying seed supply of sugar maples influences the post-dispersal fates of their seeds (Houle 1992) and

thereby their subsequent establishment patterns. Thus, consistent with suggestions from Kellman (2004), large-scale seed application might be most effective for regenerating sugar maples because providing large quantities of seeds satiates predators and allows some seeds to escape and potentially establish seedlings. However, this strategy would require further testing as artificially augmenting the food supply could attract transient individuals from surrounding territories (Koford 1992) or cause eastern chipmunks to contract their home ranges (Mares et al. 1982) and thereby support larger sciurid populations, which may negate intended food supplementation effects. An alternative but more labor-intensive strategy would be to maintain smaller sciurid populations. This would also require further testing as red squirrels, for example, can locate and takeover vacant territories shortly after the territory owner is removed (Boutin et al. 1993).

To determine if the predominant effect of the small mammal community on sugar maples changes over time, future studies should track seed fates during the other seasons to determine if caching ever exceeds predation, particularly in the fall when the most caching occurs. Studying predation on sugar maple seeds at different times throughout the year could also indicate the times of lowest predation, during which time seeds would have the highest chance of survival. Monitoring how the biomass of eastern chipmunk populations change throughout the year affect the proportion of sugar maple seeds eaten would also provide more accurate predictions of seed loss due to predation by eastern chipmunks. Red squirrels may also be important predators of sugar maple seeds, but more comparisons need to be made between the proportion eaten at sites with and without red squirrels, in particular at sites without eastern chipmunks.

## APPENDIX A

TABLE A.1.

CAPTURE SUCCESS (CAPTURES/TRAP-NIGHT) OF POTENTIAL SEED PREDATORS AT EACH OF EIGHT MIXED CONIFEROUS AND DECIDUOUS SITES WITH PROVIDED UTM (NAD27, ZONE 16N) LOCATIONS AROUND UNDERC PROPERTY, 2006.

Site	UTM - N	UTM - E	MYGA	NAIN/ZAHU	PE sp.	SCCA	TAHU	TAST
Beaver Bog	5124050	305776	0	0.004	0.021	0	0.004	0
Cranberry	5123548	304001	0.009	0	0.023	0	0.002	0.004
Ed's Bog	5143644	306772	0.008	0.004	0.029	0	0.004	0
Kickapoo	5121677	307259	0.008	0.002	0.058	0	0.002	0.023
Long Lake	5122919	307921	0.014	0	0.006	0	0	0
Northeast Gate	5125904	306423	0	0.006	0.009	0	0	0
Palmer	5119765	308183	0	0	0.026	0.002	0	0.026
Tenderfoot	5125459	304436	0	0.002	0.017	0	0	0

Species codes listed in Table 1.

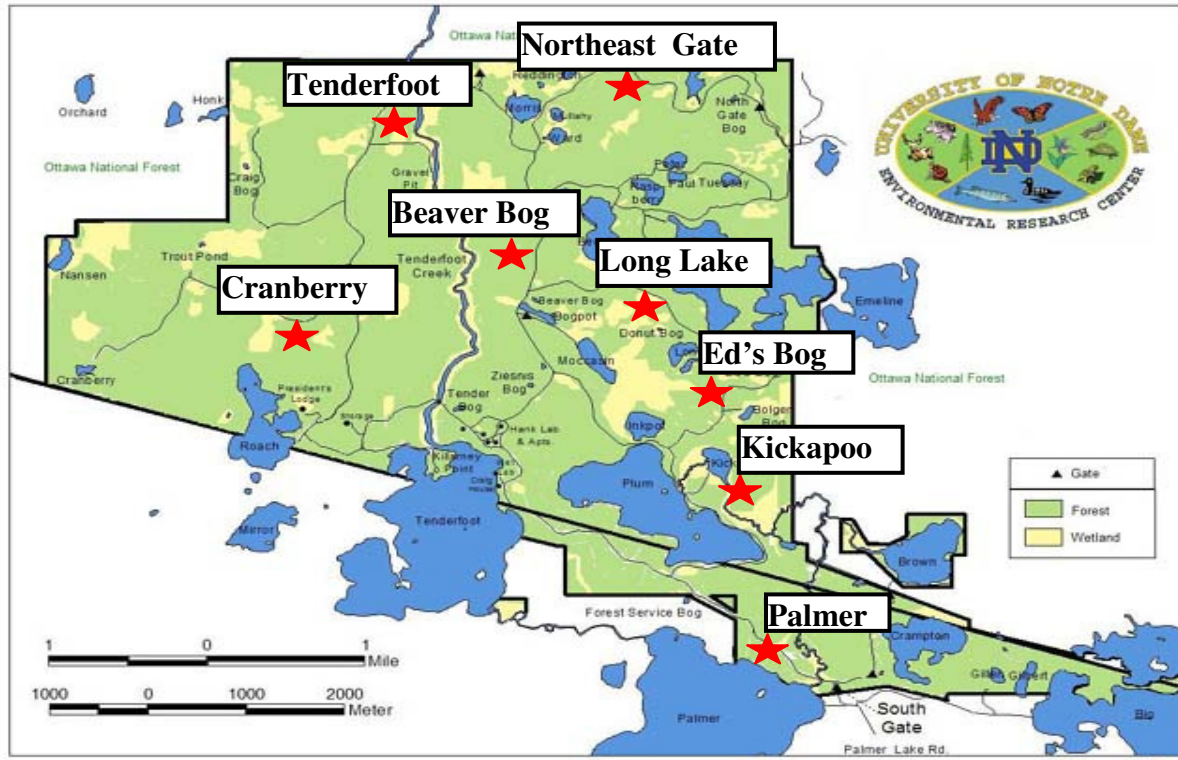


Figure A.1. Layout and names of the eight mixed coniferous and deciduous sites on UNDERC property, surveyed in 2006 (map courtesy of K. Francl, 2006). GPS coordinates provided in Table A.1.

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