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Postdispersal Sugar Maple (*Acer saccharum*) Seed Predation by Small Mammals in a Northern Hardwood Forest

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ABSTRACT.—Small granivorous mammals may have marked effects on plants through their seed predation. Using live-trapping efforts and tagged sugar maple (*Acer saccharum*) seeds in 2006 at eight mixed forest sites in the northern Great Lakes region, we asked: (1) Were small mammals seed dispersers or predators at these sites? (2) How did seed predator (*i.e.*, all granivorous small mammals) and sciurid (chipmunks and squirrels only) biomasses affect the proportion of seeds eaten? (3) How did habitat structure affect seed predator biomasses? We found that small mammals, particularly eastern chipmunks (*Tamias striatus*), were predators of sugar maple seeds as the proportion of seeds eaten and seed predator biomasses were positively related. We also found a larger seed predator biomass and the presence of eastern chipmunks in areas with higher proportions of deciduous trees. Our findings have important implications for forest regeneration, as seed predators may negatively impact restoration efforts.

INTRODUCTION

Seeds are important food resources for many small mammal species (*e.g.*, Snyder, 1982; Steele, 1998). A small mammal decides to eat or store a seed by comparing the seed's present value with the seed's future value (Fig. 1). 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 determines that the present value is greater and eats the seed, then it has acted as a seed predator. However, if the animal determines that the future value is greater and stores the seed in a shallow cache and fails to revisit the cache, 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).

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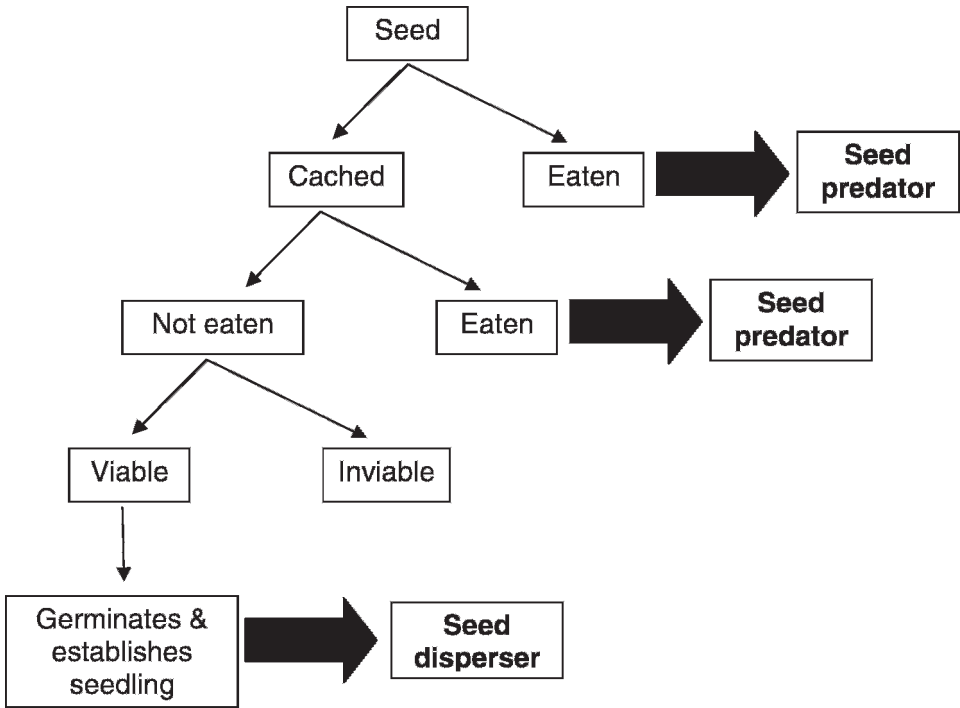


FIG. 1.—Decisions made by a small mammal upon encountering a seed and corresponding consequences for the seed (modified from Vander Wall, 2004)

MAMMALIAN SEED PREDATORS

Small mammal seed predation may reduce seed abundance—even to the extent that a common plant species could become rare over time (Janzen, 1971). Rodents have been found to remove up to 89% of antelope bitterbrush (*Purshia tridentata*) seeds (Vander Wall, 1994). Moreover, small mammals such as eastern chipmunks (*Tamias striatus*) and deer mice (*Peromyscus maniculatus*) predate heavily upon dogwood (*Cornus* spp.) and cherry (*Prunus* spp.) seeds and are considered the most important predators of these seeds (Whelan *et al.*, 1991). Red squirrels (*Tamiasciurus hudsonicus*) have been found to be important seed predators of white spruce (*Picea glauca*) and southwestern white pine (*Pinus strobiformis*) in western North America and hickory nuts (*Carya glabra*) in eastern North America (Sork, 1983; Peters *et al.*, 2003; Samano and Tomback, 2003). In particular, red squirrels have been found to remove over 50% of white spruce seeds despite an 80% reduction in density (Peters *et al.*, 2003). In the northeastern United States, red squirrels and eastern chipmunks are influential seed predators of conifers, red maple (*Acer rubrum*), white pine (*Pinus strobus*) and red oak (*Quercus rubra*; Plucinski and Hunter, 2001). In particular, Plucinski and Hunter (2001) found that 50–80% of red maple seeds were removed after 21 d when only smaller rodents (*e.g.*, white-footed mice; *Peromyscus leucopus* and southern red-backed voles; *Myodes gapperi*) were allowed access compared to 90–100% removal when eastern chipmunks and red squirrels were allowed access. In northern Great Lakes region, we suspect that these two sciurids can have marked impacts on seed fates in northern hardwood forests (Kurta, 1995; Côté and Ferron, 2001). Based on their diets (Kurta, 1995), deer mice, white-footed

mice, meadow jumping mice (*Zapus hudsonius*), woodland jumping mice (*Napaeozapus insignis*) and southern red-backed voles were other potential seed predators within our study area.

QUESTIONS ADDRESSED

Using sugar maples (*Acer saccharum*), a dominant canopy species in northern hardwood forests in the northern Great Lakes region, our study addressed the following questions:

- (1) Are small mammals more effective seed predators or seed dispersers? We compared the proportion of sugar maple seeds eaten to the proportion of seeds cached to explore the predominant effect of small mammals on postdispersal (*i.e.*, after dispersing via wind from the parent tree) sugar maple seeds during the summer months in a northern hardwood forest. Because seed germination and seedling establishment were not assessed in this study, a larger proportion of seeds eaten would suggest that small mammals were more often seed predators, whereas a larger proportion cached would suggest that they were more often seed dispersers. Examining these patterns provided insights into the net impact of small mammals on seed fates.
- (2) Do areas with higher biomasses of seed predators and, in particular, sciurids (limited in this study to red squirrels and eastern chipmunks) 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, may have comparatively smaller seed predation effects.
- (3) Do seed-predator and, in particular, sciurid biomasses vary with habitat structure? If small mammals and specifically 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.

MATERIALS AND METHODS

STUDY SITES

We studied caching behavior in the northern mesic hardwood forests of University of Notre Dame Environmental Research Center (UNDERC) in the Upper Peninsula of Michigan and northern Wisconsin (ca. UTM NAD27, Zone 16 N, 5122300 N, 303900 E, Vilas County, Wisconsin and Gogebic County, Michigan) which consists of 3055 ha with ca. 80% mature second-growth forest. This property was clearcut ca. 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*). We selected eight sites on UNDERC property, each containing a mixture of deciduous (predominantly sugar maple) and coniferous trees, for the seed fate experiment (named after nearby landmarks; *see* Hsia, 2007 for specific locality information): 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, we established a 4500-m² (45 m × 100 m) trapping grid at each site. Within each site, we established four 100-m

transects spaced 15 m apart. Sherman live traps were placed on the ground every 10 m, and three evenly-spaced Tomahawk live traps were placed along each transect. We used rolled oats and peanut butter as bait. We marked each captured individual with a numbered metal ear tag (No. 1, National Band and Tag Co., Newport, KY). Once in Jun. and once in Jul. of 2006, we trapped at each site for five consecutive nights (totaling 10 total nights per site).

Using the capture data, we summed the average weight of captured individuals (to account for recapture weight differences) from each species to estimate the biomass of seed predators (seed predator biomass) for each site. We also estimated sciurid biomass for each site, summing the weights of captured eastern chipmunks and/or red squirrels. The non-sciurid biomass equaled the difference between total seed predator biomass and sciurid biomass. To obtain seed predator densities for each site, we calculated the total number of captured individuals/4500-m² and extrapolated that value to individuals/ha.

HABITAT MEASURES

Within 5 m × 5 m plots every 20 m along our trapping transects, we noted whether a tree (diameter at breast height [DBH] > 5 cm) was deciduous or coniferous (Brooks *et al.*, 1998). We then determined the proportion of deciduous trees at each site. We also separated sugar maples into immature (DBH < 20 cm) and mature (DBH ≥ 20 cm; Burns and Honkala, 1990; Houle and Payette, 1991). Within these plots, we also recorded snag and downed log densities for snags and logs with ≥ 50% of their material within the plot. Snags were defined as either leaning or standing dead trees or stumps with diameter > 2 cm. Downed logs consisted of any downed piece of wood (diameter > 2 cm) along which any small mammal could potentially travel.

We estimated ground cover by the point-quarter method (Cox, 1996) at 10 random points for each site. Using this method, we located an individual shrub below which a small mammal could be concealed (thereby providing cover) and designated four quadrants around that shrub (the point). For each quadrant, we located the nearest individual shrub (≤ 3 m of the point) which could provide cover and measured its distance to the point, hereafter referred to as the nearest neighbor distance. If no cover was within 3 m, we assigned a value of 3 m. Although this potentially truncated the distribution, removing these values did not affect our results. We selected 30 random points within each site and calculated the relative vertical diversity across sites using a range pole (Francl and Schnell, 2002). At each point, we measured the presence of vegetation in 0.5-m increments along a 6.5-m tall pole (plus a category for hits > 6.5 m; 14 increments). From these measures, we calculated the Levins index of vertical diversity for each site (Levins, 1968). We measured percent soil moisture three times during Jun. and Jul. of 2006 using a Kelway Soil Moisture Tester (Kel Instruments Co., Inc, Japan), which measured on a scale of 0–100% in 10% increments, at the same 30 random points per site, and calculated an overall average percent soil moisture across all three samples for each site.

POSTDISPERSAL SEED FATE EXPERIMENT

During the summer of 2006, we glued 1.9-cm wire brads to the winged part of commercially-purchased sugar maple seeds (Catalpa Tree Seed Company, Medford, NJ). The wire brads were marked with a unique color band to indicate Jun. or Aug. and the board on which the seed was placed (modified from Steele *et al.*, 2001). We microwaved them for 45 s to make them inviable. Neither tagging nor microwaving the seeds affected their consumption (Hsia, 2007).

We then placed 100 ± 2 tagged seeds on each of three 60 cm × 60 cm styrene boards for each site (total addition of 0.067 ± 0.001 seeds/m² [mean ± 1 SE] for 4500-m² study area).

To relocate removed seeds, we used a Fisher 1225-X metal detector (Fisher Research Laboratory, Los Banos, California). Because we were unable to relocate any cached seeds and because small mammals eat both tagged and untagged seeds without removing the wings of the seeds (J. Hsia, pers. obs.), the proportion of seedless wings represented the proportion of cached seeds in our analyses. Boards were checked once every 2–3 d and were in place for two periods: 14/15 Jun.–28/29 Jun. (June) and 9/10 Aug.–23/24 Aug. (August). Styrene boards were spaced 50 m apart down the middle of each trapping grid.

STATISTICS

Question 1.—Because comparing the proportion of seeds eaten to that of seeds cached indicated whether small mammals were more often seed predators or dispersers, respectively, data were not analyzed statistically.

Question 2.—We used an ANCOVA (covariate = seed predator biomass) to measure how the response variable of the proportion of seeds eaten varied with the main effects of month, sites and seed predator biomass. A separate ANCOVA tested whether the response variable of the proportion of seeds eaten varied with the main effects of month, sites and seed predator densities. We used a linear regression to relate the proportion of seeds eaten to sciurid biomass. We also performed separate linear regressions with the proportion eaten and eastern chipmunk or red squirrel biomasses.

Question 3.—We selected habitat measures as independent variables and seed predator biomass, non-sciurid biomass or sciurid biomass, respectively, as the dependent variable in a forward stepwise linear regression. Percent soil moisture and the proportion of deciduous trees were arcsine-transformed to ensure normality. A forward stepwise discriminant function analysis determined which vegetation characteristics best predicted the presence of eastern chipmunks, which were present at four out of the eight sites. Linear regressions examined relationships between vegetation variables to determine if any vegetation measures affected other measures.

We performed all statistical analyses in SYSTAT Version 10.0 (Systat Software, Inc., San Jose, CA). Due to the small sample size ($n = 8$ sites), we accepted $P \leq 0.10$ as statistically significant.

RESULTS

TRAPPING

Over 4134 trap-nights, a total of 264 captures of 117 individuals were recorded, with recaptures accounting for 55.7% of captures. Twenty eastern chipmunks were captured at three of the eight sites (although they were present at a fourth based on observation), and six red squirrels were trapped at four sites (although they were present at six, based on observation). Small mammal densities varied from 2.2–66.7 individuals/ha and biomasses varied from 8–1422.7 g (Table 1). White-footed and deer mice (listed jointly as *Peromyscus* spp.) accounted for 56.1% of captures followed by eastern chipmunks (16.3%) and southern red-backed voles (9.5%; see Hsia, 2007 for detailed capture data).

POSTDISPERSAL SEED FATE EXPERIMENT

Question 1.—Overall, we successfully recovered $92.2 \pm 0.01\%$ (mean ± 1 SE) of the seeds. The fates of the remaining seeds were unknown. Of the recovered seeds, $37 \pm 12\%$ were eaten, $5 \pm 1\%$ were cached, and the remaining seeds were neither eaten nor cached. Because of the low average proportion of seeds cached overall, this measure was not further analyzed.

TABLE 1.—Individual and total seed predator biomasses (B; grams) and estimated densities (D; # individuals/ha) for each of eight mixed forest sites in Michigan's Upper Peninsula in summer 2006

		Beaver Bog	Cranberry	Ed's Bog	Kickapoo	Long Lake	NE Gate	Palmer	Tenderfoot
<i>Myodes gapperi</i>	B	—	80	80.5	63	168.3	—	—	—
	D	—	11.1	8.9	8.9	15.6	—	—	—
<i>Napaeozapus insignis</i>	B	47	—	8.0	23	—	37	—	18
	D	4.4	—	2.2	2.2	—	4.4	—	2.2
<i>Peromyscus</i> spp.	B	216.9	199.8	347.8	514.3	73.5	79.6	229.6	163.6
	D	24.4	26.7	33.3	66.7	6.7	11.1	28.9	20
<i>Sciurus carolinensis</i>	B	—	—	—	—	—	—	525	—
	D	—	—	—	—	—	—	2.2	—
<i>Tamiasciurus hudsonicus</i>	B	308	119	272	182	—	—	—	—
	D	4.4	2.2	4.4	2.2	—	—	—	—
<i>Tamias striatus</i>	B	—	160	—	1422.7	—	—	1219.7	—
	D	—	4.4	—	26.7	—	—	28.9	—
<i>Zapus hudsonius</i>	B	—	—	15	—	—	15	—	—
	D	—	—	2.2	—	—	2.2	—	—
Total	B	571.9	558.8	723.3	2205	241.8	131.6	1974.3	181.6
	D	33.3	44.4	51.1	106.7	22.2	17.8	60	22.2

Question 2.—The proportion of seeds eaten (the proportion eaten) did not differ significantly between Jun. and Aug. ($F_{1,7} = 2.71$; $P = 0.14$), between sites ($F_{6,7} = 1.76$; $P = 0.24$) or with seed predator density ($F_{1,7} = 2.28$; $P = 0.17$). However, the proportion eaten varied with seed predator biomass ($F_{1,7} = 9.35$; $P = 0.02$) with no significant interactions ($P = 0.19$).

More specifically, the proportion eaten increased with greater seed predator biomass ($r^2 = 0.49$, $P = 0.05$) and with greater sciurid biomass ($r^2 = 0.45$, $P = 0.07$). The proportion of seeds eaten also increased with greater chipmunk biomass ($r^2 = 0.45$, $P = 0.07$). However, red squirrel biomass was not related to the proportion of eaten seeds ($r^2 < 0.01$, $P = 0.92$).

Question 3.—We found that seed predator biomass increased with proportion of deciduous trees, soil moisture and snag density but decreased with increasing Levins index across sites ($r^2 = 0.96$, $P = 0.02$, Table 2). 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 ($r^2 = 0.98$, $P < 0.01$, Table 3). Sciurid biomass also increased with increasing soil moisture ($r^2 = 0.77$, $P < 0.01$).

Our 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). Sites with chipmunks were positively correlated with immature sugar maple density, density of snags and soil moisture but negatively correlated with the density of downed logs. Downed log density was negatively related to immature sugar maple density and soil moisture ($r^2 = 0.90$, $P < 0.01$).

DISCUSSION

QUESTION 1

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

TABLE 2.—Forward stepwise regression results for vegetation characteristics and seed predator biomass for eight mixed coniferous and deciduous sites around UNDERC property, 2006. ASN indicates the variable was arcsine-transformed. Coefficients for the significant characteristics (a) and the overall regression ANOVA table (b) are provided ($r^2 = 0.96$)

(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		

behavior (Burt, 1957). However, according to our findings, this is unlikely during the summer months as caching was a relatively rare event, with seedless wings accounting for 5%, on average, of seed fates. Our finding that small mammals during the summer months serve as predators rather than dispersers of postdispersal sugar maple seeds was consistent with our expectations, and in line with Beckage and Clark's (2005) experiment on red maple seed predation conducted in late spring. One possible explanation is that eating provides immediate energy; therefore, 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 our seed fate experiment), small mammals do not rely on caches because deciduous areas have high food availability during the summer (Kemp and Keith, 1970), and eating the seeds should then also be more frequent.

TABLE 3.—Forward stepwise regression results for vegetation characteristics and non-sciurid biomass for eight mixed coniferous and deciduous sites around UNDERC property, 2006. ASN indicates the variable was arcsine-transformed. Coefficients for the significant characteristics (a) and the overall regression ANOVA table (b) are provided ($r^2 = 0.98$)

(a) Regression coefficients				
Effect	Coefficient	P(2 Tail)		
Constant	12.7	0.871		
Distance to nearest neighbor	324.1	< 0.001		
ASN soil moisture	212.6	0.099		
Levins index	-0.2	< 0.001		
(b) Analysis of variance				
Source	Sum-of-Squares	df	F-ratio	P
Regression	162,148	3	65.6	0.001
Residual	3294	4		

QUESTION 2

Our finding that the proportion of seeds eaten increased with seed predator biomass may be explained by the idea that a higher biomass of seed predators requires a larger supply of seeds. 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 because small mammals may achieve high abundance but contribute relatively little to consumptive biomass. Our finding that seed predator density had no effect on the proportion of seeds eaten further supports this idea. Also, smaller-bodied small mammals have a faster metabolic rate (Vaughan *et al.*, 2000) and thus must eat a larger proportion of their body weight, but the absolute amount they eat relative to larger-bodied small mammals may still be less. Thus, biomass appears to better indicate the relative contribution of potential small mammal seed predators to seed predation and should continue to be used in future seed predation studies.

The proportion of seeds eaten also increased with larger sciurid biomass. More specifically, the proportion of seeds eaten was unaffected by red squirrel biomass but was positively related to 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). Our finding that eastern chipmunks are important seed predators of sugar maple seeds during the summer months was consistent with the finding that they are important seed predators of red maple, white pine and red oak seeds (Plucinski and Hunter, 2001). Chipmunks are also considered seed predators because they store seeds in places that prevent germination such as hollow logs and burrows (Sork, 1983).

QUESTION 3

The biomass of seed predators increased with a higher density of snags and more deciduous trees but less vertical diversity. Non-sciurid biomass also increased with increasing nearest neighbor distance (*i.e.*, lower ground cover density) and decreasing vertical diversity. The increasing nearest neighbor distance and decreasing vertical diversity coincide with the increasing proportion of deciduous trees. This preference for more deciduous trees is consistent with findings from Chambers and MacMahon (1994)—that rodents are important predators of large-seeded deciduous tree species. 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. Furthermore, seed predator, sciurid and non-sciurid biomasses 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).

In particular, eastern chipmunk presence correlated positively with soil moisture, immature sugar maple density and snag density but correlated negatively with the density of downed logs. 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. 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 stand age.

CONCLUSIONS

Overall, a higher proportion of seeds were eaten in areas with higher seed predator and, in particular, eastern chipmunk biomasses. Thus, eastern chipmunks in this region are predators of sugar maple seeds. Consistent with trends for increased seed predator and sciurid biomasses, the habitat measures that best predicted chipmunk presence further emphasize the importance of eastern chipmunks as seed predators of postdispersal sugar maple seeds. In our study, about 50% of the sugar maple seeds were lost to predation during the summer in areas with eastern chipmunks. Thus, further study into the effects of these trends on sugar maple seed germination and seedling establishment is necessary because these factors may ultimately affect the distribution and abundance of sugar maples in the northern Great Lakes region. In fact, several studies have identified rodents as the main postdispersal seed predators with important effects on plant recruitment (Hulme, 1993; Edwards and Crawley, 1999; Peters *et al.*, 2004).

Our findings suggest that small mammals and, in particular, eastern chipmunks act primarily as seed predators of sugar maple during the summer months. If further studying of these trends reveals small mammals to have important negative impacts on the germination and establishment of sugar maple seeds and seedlings, then additional considerations for restoration strategies should be taken into account. For example, managers looking to regenerate sugar maples in the northern Great Lakes region should measure eastern chipmunk biomasses to best estimate seed loss due to predation. Furthermore, the varying seed supply of sugar maples influences the postdispersal 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 take over vacant territories shortly after the territory owner is removed (Boutin *et al.*, 1993).

To determine whether small mammals are predominantly predators or dispersers of sugar maple seeds and whether the effects change over time, future studies in this region should track seed fates during the other seasons, particularly in the fall when the most caching should occur (Snyder, 1982; Benhamou, 1996). 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 total biomass of eastern chipmunks in an area changes throughout the year affects the proportion of sugar maple seeds eaten also would provide more accurate predictions of seed loss due to predation by eastern chipmunks. Red squirrels also may be important predators

of sugar maple seeds, but more comparisons need to be made between the proportions of seeds eaten at sites with and without red squirrels, in particular at sites without eastern chipmunks.

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